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ECOLOGY OF THE NORTHERN GOSHAWK IN FENNOSCANDIA

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Abstract. We reviewed studies on the Northern Goshawk (*Accipiter gentilis*) carried out in northern Europe (Fennoscandia) since the 1950s concerning the following: diet composition, breeding performance, movements, home range, survival, and population trends. Goshawks feed mainly on forest grouse throughout the year in boreal forests but rely more on Ring-necked Pheasants (*Phasianus colchicus*) and hares (*Lepus* spp.) in mixed deciduous-coniferous forests in southern Fennoscandia. Breeding density of the goshawks varies from one–five pairs/100 km^2, on average three pairs/100 km^2. Mean clutch size (3.5), brood size (2.8), and productivity of fledglings (2) per occupied territory have remained stable over the decades irrespective of the decline of the forest grouse. Proportion of grouse in the diet as well as breeding output closely followed the density of grouse during the1950s–1970s with relatively dense grouse populations but this close connection has recently disappeared, probably due to a decline of grouse and disappearance of their multi-annual cycles. Goshawks are the most important cause of mortality among forest grouse, and grouse density, in turn, affects the dispersal distances of juvenile goshawks. Because of the narrower diet width of males compared to that of females, males tend to move over longer distances than females. Among adults, females move more than males, like in other raptors. Median distances moved by juveniles range from 50–100 km but some individuals can travel up to >1,000 km. After the dispersal phase, juveniles tend to establish more or less stable ranges before moving to the final breeding range. Not much is known about the site tenacity of breeders but in good conditions males, at least, likely remain on their territories throughout their life. Winter range size varies from 2,000–10,000 ha depending on sex, age, and the quality of the habitat or of the prey size. Juvenile males suffer from higher mortality than juvenile females but this difference disappears by the third year of life. Based on field studies and museum data, roughly one-third of juvenile hawks succumb because of starvation, one-third of trauma or trauma and starvation-disease, and one-fifth to one-third are killed by hunters. Productivity of goshawk populations has not changed during the years of declining trends found in many local studies, which may indicate an increased adult mortality. Annual mortality among the adults may likely not exceed 30% without a decline of the breeding population. The ultimate reason behind declining goshawk populations is likely the change in the forest bird community due to intensified forestry which has negatively affected the populations of main prey, forest grouse. Problems in nourishment of goshawks occur during the winter after migratory birds have moved to south.

Key Words: breeding, cause of death, diet, Fennoscandia, habitat choice, movements, Northern Goshawk, predation, survival.

ECOLOGÍA DEL GAVILÁN AZOR EN FENNOSCANDIA

Resumen. Revisamos estudios sobre el Gavilán Azor *(Accipiter gentilis)* llevados a cabo en el norte de Europa (Fennoscandia) desde 1950, relacionados a lo siguiente: dieta, composición, desempeño de reproducción, movimientos, rango del hogar, sobrevivencia, y tendencias de población. Los gavilanes se alimentaron principalmente de gallo del bosque (*Tetraonidae*) en bosques boreales, durante todo el año, pero dependían más en el Faisán de collar (*Phasianus colchicus*) y liebres (*Lepus spp*.) en bosques deciduos mixtos de coníferas, en el sur de Fennoscandia. La densidad de reproducción del azor varía de uno a cinco pares/100 km^2, en promedio tres pares /100 km^2. La media del tamaño de la puesta (3.5), el tamaño de la pollada (2.8) y la productividad de los volantones (2) por territorio ocupado, ha permanecido estable sobre los años, independientemente al decaimiento del gallo del bosque. La proporción del gallo del bosque en la dieta, así como la producción-rendimiento reproductivo, siguieron muy de cerca la densidad del gallo del bosque durante 1950s–1970s, con relativamente poblaciones densas de gallo del bosque, pero esta cercana conexión ha desaparecido recientemente, probablemente debido al decaimiento del gallo del bosque y a la desaparición de sus ciclos multi-anuales. Los Gavilanes son la causa más importante de la mortandad entre los gallos del bosque y de la densidad de los mismos, por lo tanto, influye en las distancias de dispersión de los gavilanes juveniles. Debido a la estrechez en la dieta de los machos, comparada con la de las hembras, los machos tienden a moverse sobre distancias más largas que las hembras. Entre los adultos, las hembras se mueven más que los machos, como en otros raptores. Las distancias medias en las que se mueven los juveniles van desde 50–100 km, pero algunos individuos pueden viajar por arriba de >1,000 km. Después de la fase de dispersión, los juveniles tienden a establecer rangos más o menos estables, antes de pasar al rango final reproductivo. No se conoce mucho acerca de la tenacidad de sitio de los reproductores, pero en buenas condiciones los machos al menos pueden permanecer en sus territorios por toda su vida. El tamaño del área de ocupación durante el invierno varía de

2,000–10,000 ha dependiendo del sexo, la edad y la calidad del hábitat, o del tamaño de la presa Los machos juveniles sufren de una mayor mortandad que las hembras juveniles, pero esta diferencia desaparece al tercer año de vida. Basado en estudios de campo y datos de museos, aproximadamente un tercio de halcones juveniles sucumben debido a inanición, un tercio por trauma o enfermedad de trauma e inanición, y de un quinto a un tercio son matados por cazadores. La productividad de las poblaciones de gavilán no ha cambiado durante los años de tendencias de declinación, encontradas en varios estudios locales, lo cual probablemente indique una incrementada mortandad adulta. La mortandad anual entre los adultos probablemente no exceda de 30%, sin un decaimiento en la población reproductiva. La última razón detrás del decaimiento de las poblaciones de gavilán, es probablemente el cambio en la comunidad de aves de bosque, debido a la intensa actividad forestal, la cual ha afectado negativamente a las poblaciones de la presa principal, gallo del bosque. Problemas en la alimentación del gavilán, ocurren durante el invierno, después de que las aves migratorias se han movido hacia el sur.

The Northern Goshawk (*Accipiter gentilis*) is one of the most numerous raptor species in northern Europe (hereafter Fennoscandia; Fig. 1). Due to its relatively high density and dietary preferences for small game species, especially forest grouse which are favored objects for sport hunting, the Northern Goshawk is probably the most hated species of bird of prey in much of Europe. It has been estimated that 5,000–6,000 goshawks were killed annually in Finland in the 1970s (Moilanen 1976) and 2,000 in the 1960s in Norway (Nygård et al. 1998). In spite that it has been now protected in all countries of North Europe—not until 1989 in Finland—it is still persecuted by humans. Research on Fennoscandian goshawks was initiated from diet investigations carried out in the 1950s in Finland and Sweden (Höglund 1964b, Sulkava 1964) and also in Norway (Hagen 1952). Since then, several studies on food habits during the breeding season have been carried out in Finland (Huhtala 1976, Wikman and Tarsa 1980, Lindén and Wikman 1983, Tornberg and Sulkava 1991, Tornberg 1997), Sweden (Widén 1987), and Norway (Selås 1989). Winter diet has been studied by stomach contents (Höglund 1964b)

FIGURE 1. Map of Fennoscandia showing main study sites of Northern Goshawks. 1. Sulkava (1964), 2. Höglund (1964a), 3. Huhtala (1976), 4. Lindén and Wikman (1983), 5. Kenward et al. (1981b), 6 Widén (1987), 7. Selås (1997a), 8. Kenward et al. (1999), 9. Tornberg (1997), 10. Nygård et al. (1998), 11. Byholm et al. 2003), and 12. R. Tornberg, E. Korpimäki, V. Reif, S. Jungell and S. Mykrä (unpubl. data).

and by radio tracking since the late 1970s in Sweden (Kenward et al. 1981, Widén 1987) and in Finland (Tornberg and Colpaert 2001). Breeding performance of goshawks is also well documented in all North European countries; most long-term studies have been carried out in Finland (Sulkava 1964, Lindén and Wikman 1980, Huhtala and Sulkava 1981, Lindén and Wikman 1983, Tornberg and Sulkava 1991, Sulkava et al. 1994, Byholm et al. 2002a) but also in Sweden (Widén 1985b, Kenward et al. 1999) and Norway (Selås 1997b). A countrywide survey of grouse was started in Finland in 1964, which enables a more accurate estimation of goshawk impact on grouse (Lindén and Wikman 1983, Tornberg 2001). In Sweden, an evaluation was done by Widén (1987). In farmland areas of Sweden, goshawks hunt pheasants more than grouse; Kenward et al. (1981b) estimated the impact of goshawk predation on released and wild pheasant stocks in central Sweden in the late 1970s.

Because goshawks use the same nesting territories year after year, they have become a popular species with bird banders. Around 2,000 goshawk nestlings are currently banded annually in Finland, mostly by volunteers. As a result, recovery rates of goshawks have been one of the highest among the banded birds (nearly 50,000 being banded since 1913 when bird banding was started in Finland; Valkama and Haapala 2002, Byholm et al. 2003). When shooting of goshawks was allowed, around 20% of banded goshawks were later recovered. These days recovery rates are around 10%. Total number of recoveries in Finland now exceeds 8,000 birds (Valkama and Haapala 2002) and similar situations prevail in Sweden and Norway. These large databases have enabled several analyses of movements, mortality, and causes of death of goshawks in all Fennoscandian countries (Haukioja and Haukioja 1971, Saurola 1976, Marcström and Kenward 1981a, Widén 1985b, Halley 1996, Byholm et al. 2003), as well as more specific studies on, e.g., sex allocation of goshawks in relation to varying environmental conditions (Byholm et al. 2002a, 2002b). As an easily trappable species, banded goshawks are often captured alive which has given more insight to their movements (Marcström and Kenward 1981b, Neideman and Schönebeck 1990). Large radio-tracking projects in central Sweden in 1970–1980 were also based on extensive live trapping that gave light to patterns of age- and condition-related movements (Kenward et al. 1981a). Pooling data from breeding performance, survival, and movements of an animal population facilitates building a population model. On the large Baltic Sea island of Gotland, Sweden, this was done using productivity data of breeding goshawks combined with extensive radio-tagging of juvenile and adult goshawks (Kenward et al. 1991, 1999).

Goshawks have also been an ideal species for museum work due to large collections of specimens in zoological museums. Earliest studies were on taxonomic aspects (Voipio 1946) and later killed and naturally dying birds were studied in relation to changes in morphology (Tornberg et al. 1999), causes of death (Tornberg and Virtanen 1997), or body condition (Marcström and Kenward 1981a, Sunde 2002).

In this paper we summarize all noteworthy published papers on the ecology of Northern Goshawks in Finland, Sweden, and Norway. We attempt to document the goshawk's position in those areas based on past and current studies and to conclude and predict the future development of goshawk populations, as well as to outline future needs in research. We add also some previously unpublished data on diet, breeding, and home range size collected near Oulu in northern Finland during 1987–2003. For a description of this study area and the methods, see Tornberg (1997) and Tornberg and Colpaert (2001).

STUDY AREA

Fennoscandia is composed of three north European countries, Norway, Sweden, Finland, and parts of western Russia (Kola peninsula and Russian Karelia). Although situated between latitudes 55–70º N this area is mainly characterized by boreal forests (between latitudes 60–70º N) and mixed coniferous-deciduous forests in southern Sweden and Norway (between latitudes 55–60º N). The northernmost parts of Finland and the Scandinavian mountain range, Köli, belong to the arctic zone. All important goshawk studies carried out in the area are shown in Fig. 1.

CHARACTERS OF THE FENNOSCANDIAN GOSHAWK

Scandinavian goshawks belong to the nominate race *Accipiter gentilis gentilis*. Finland is a transition zone between the nominate race and the eastern paler and larger *A. g. buteoides* (Voipio 1946). Finnish goshawks are larger than Swedish ones based on both body mass and wing length indicating that Finnish goshawks belong to the larger *buteoides* race (Table 1). Winter weights in Sweden are derived from extensive trapping of goshawks in central and southern Sweden (Marcström and Kenward 1981b). Weights of Finnish hawks were obtained

Table 1. Average measurements taken from Swedish and Finnish goshawks. Data from Sweden by Marcström and Kenward (1981a) and from Finland by Tornberg et al. (1999) and Tornberg (unpubl. data).

	Central Sweden				Northern Finland			
	Male	N	Female	N	Male	N	Female	N
Winter weight adult	866	52	1,328	60	933	12	1,485	18
Winter weight juvenile	839	289	1,229	215	828	11	1,384	21
Wing length adult	323	37	366	69	330	26	372	29
Wing length juvenile	323	308	363	197	327	79	367	86

from trapped birds in Oulu during 1990–1999. Wing lengths were measured from the flexed wrist to the end of longest primary with feathers flattened and straightened.

DIET

Breeding Season

A major proportion of the diet of the goshawk was woodland grouse (*Tetraonidae*) in all food habit investigations in Fennoscandia (Höglund 1964b, Sulkava 1964, Huhtala 1976, Lindén and Wikman 1983, Widén 1987, Selås 1989, Tornberg 1997). Four grouse species are preyed upon by goshawks—Capercaillie (*Tetrao urogallus*), Black Grouse (*Tetrao terix*), Hazel Grouse (*Bonasa bonasia*), and Willow Grouse (*Lagopus lagopus*). Grouse proportions in the goshawk diet are highest in western Finland declining to the west and south (Table 2). It must be remembered that proportions of grouse in diet studies based on the collection of prey remains may depend whether remains were collected only in the nest or also in the vicinity of the nest and whether the two groups are pooled (Sulkava 1964). Proportions of grouse in the diet at the beginning of the nesting season may be up to 80% but tend to decline later in the breeding season (Table 2). However, depending on the collection method, the proportion of soft and digestible grouse chicks might easily be underestimated in the diet (Höglund 1964b, Sulkava 1964, Grønnesby and Nygård 2000). Recently, with grouse numbers lower than in the 1950s, grouse proportions actually declined during the breeding season when more vulnerable prey, like juvenile corvids and smaller passerine birds,

Table 2. Diet composition of goshawks during the breeding season in different localities in Fennoscandia. Upper row for each prey species or group = diet composition during the nest-building and incubation periods and lower row = diet during the nestling period. Grouse chicks are found only during the nestling period.

	Locality[a]						
	1	2	3	4	5	6	7
Grouse adult	63.7		20.4	72.6	56.3	29.7	
	11.1	4.8	5.0	14.9	24.7	(14.5)[d]	14.0
Grouse juvenile	43.3	14.1		23.4	9.6		
Corvids	5.3		8.4		10.0	26.2	
	10.5	23.9	17.6	7.0	11.4	28.3	15.0
Other birds	9.0		49.5	(13.5)[b]	22.1	29.9	
	19.6	47.0	68.5	51.6	38.8	42.8	68.0
European red squirrel	15.2		12.5		4.7		
(*Sciurus vulgaris*)	10.2	7.9	5.1	0.8	6.3		
Other mammals	6.8		9.2	(14.0)[c]	6.9	(14.3)[c]	
	2.0	1.8	3.7	2.3	9.2	(14.5)	(3.0)[b]
Unidentified	3.2						
N	664		535	2101	557	462	
	342	772	641	128	649	442	367

[a] Location and source of data: 1. western Finland 1949–1959 (Sulkava 1964), 2. central Sweden. 1954–1959 (Höglund 1964b), 3. southern Finland 1977–1981 (Wikman and Tarsa 1980), 4. north-western Finland 1963–1976 (Huhtala 1976), 5. northern Finland 1965–1988 (Tornberg and Sulkava 1991), 6. central Sweden 1977–1981 (Widén 1985a), and 7. southern Norway 1983–1988 (Selås 1989).

[b] Includes corvids.

[c] Includes squirrels.

[d] Includes grouse chicks.

become available (Lindén and Wikman 1983, Selås 1989, Tornberg 1997). As grouse chicks grow, they become more and more profitable as prey and their proportion of the diet can increase up to 50% toward the autumn (Tornberg 1997).

The Black Grouse is generally the most important grouse species by number and biomass in the diet of goshawks (Huhtala 1976, Widén 1987, Selås 1989, Tornberg 1997). In Oulu (Fig. 1), its proportion during the breeding season was 25–30%. In more southern parts of the boreal forests, however, Hazel Grouse may be more important (Sulkava 1964, Lindén and Wikman 1983). When analyzing dietary proportions against availability in the field, the small grouse species, Willow Grouse and Hazel Grouse weighing 0.3–0.7 kg, may be preferred over the larger Black Grouse weighing 0.9–1.3 kg (Tornberg 1997). Large Capercaillies are relatively rare in goshawks' diet, limited to females weighing 2 kg during the breeding season. The proportion of mammals in the diet of goshawks varies between 10–20% in most studies. The most common mammal species is the European red squirrel (*Sciurus vulgaris*) whose proportion can sometimes reach 30%, particularly in poor grouse years (Sulkava 1964). Young mountain hares (*Lepus timidus*) are numerically the second most important mammalian prey but by biomass they can exceed red squirrels (Tornberg 1997). Interestingly, young mountain hares were very rare prey specimens in the 1950s (Sulkava 1964).

The well-documented decline of forest grouse in Finland (Lindén and Rajala 1981, Väisänen et al. 1998) has affected prey choice of goshawks. Changes of grouse density in the province of Oulu in northern Finland and the corresponding proportion of grouse in the diet of goshawks are presented in Fig. 2. A second order polynomial gave the best fit for both the grouse density ($r^2 = 0.587$, $F = 24.870$, $P < 0.001$) and proportions of grouse in the diet in spring ($r^2 = 0.476$, $F = 11.353$, $P = 0.003$). It seems that grouse are slowly recovering from the long-term decline. Correspondingly, goshawks have quickly responded to this recovery. During grouse lows, goshawks attempt to switch to preying more on corvids, thrushes, and pigeons (Tornberg and Sulkava 1991, Sulkava 1999). Interestingly, these species form the main diet of the goshawk in central Europe (Opdam et al. 1977, Toyne 1997); grouse are usually not found in the diet there but *Phasianidae* can sometimes form a considerable proportion in the diet (Manosa 1994).

Winter Diet

Systematically collected data on goshawk's winter diet are still scarce. Höglund (1964b) analyzed stomach contents in the 1950s–1960s in Sweden

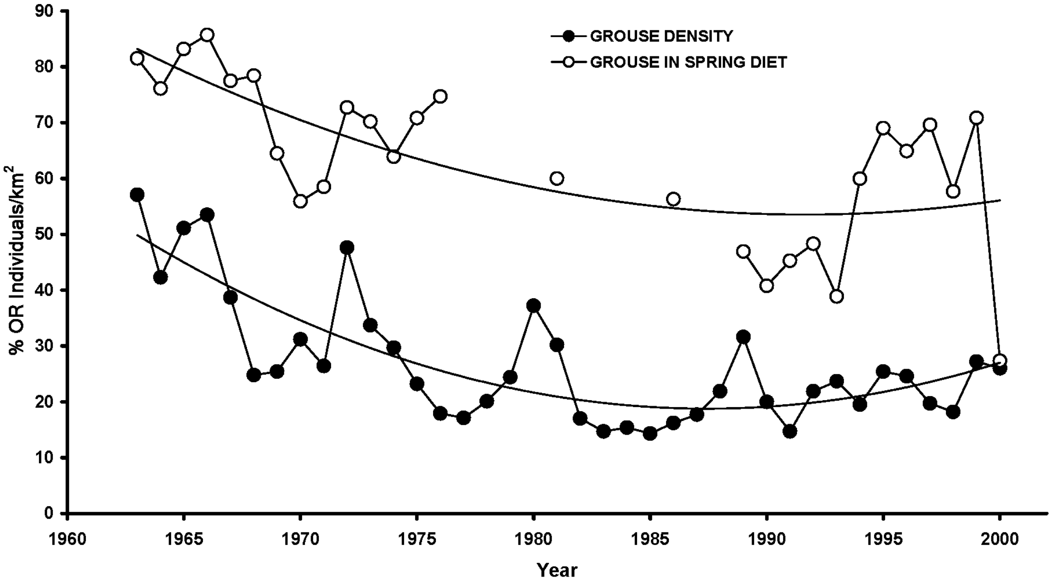

FIGURE 2. Density changes of forest grouse in the province of Oulu in northern Finland and corresponding proportions of grouse in the diet of the Northern Goshawk in spring. Density data for grouse were obtained from grouse censuses by the Finnish Game Research Institute and data for goshawk diets from the1960s and 1970s are from Huhtala (1976) and for the 1980s and 1990s are from Tornberg and Sulkava (1991) and Tornberg (unpubl. data).

(N = 130), and found that the proportion of grouse was only 8%, i.e., less than half of that in the summer diet whereas the proportion of mammals increased from 10–35%. Later studies carried out by radio tracking in Sweden partly confirmed Höglund's findings. In the winters 1977–1981, red squirrels alone comprised 84% (N = 61) of goshawks' winter diet in central Sweden (Widén 1987). In agricultural areas of central Sweden, goshawks killed mainly red squirrels (33%), Ring-necked Pheasants (23%) and European hares (*Lepus europaeus*) (14%) that were killed only by females (Kenward et al. 1981b). Due to the large size of hares (3–3.5 kg), they accounted for 37% of the food intake by females, whereas males got 43% of their food from pheasants but females only 3%. Based on a radio-tracking study in northern Germany, goshawks killed mostly pheasants (41%) and rabbits (*Oryctolagus cuniculus*) (27%, N = 145) during winter (Ziesemer 1983). In northern Finland, a radio-tracking study during 1991–1995 revealed that dietary proportion by number of mountain hares and red squirrels was 55% (N = 55) and the biomass of hares alone was 70% (Tornberg and Colpaert 2001). Mountain hares were killed only by females. Correspondingly, as in farmlands, males hunted red squirrels and grouse more than females did. We present here the combined data of Tornberg and Colpaert (2001) and new winter diet data from the vicinity of Oulu during 1999–2002. Excluding predation events near human settlements and a dump site where brown rats (*Rattus norvegicus*) were prey, the proportion of grouse was almost the same as in summer diet (37.6 % vs. 34.2%; Tornberg and Sulkava 1991; Table 3). Diet differed between the sexes in spite of few data being available for analysis. In farmland areas of central Sweden, an intersexual difference was found only for hares (Kenward et al. 1981b) but no difference was found in woodland areas (Widén 1987). During the breeding season, diets of the sexes were not found to differ substantially (Grønnesby and Nygård 2000).

FUNCTIONAL RESPONSE

When diet proportion or kill rate of a predator is plotted against the number of prey individuals, a functional response curve is obtained. Holling (1959) described three curve types: increase in the prey consumption of the predator may be linear (type I), convex (type II), or concave (type III) as a function of prey number. A type II curve is found when consumption in low prey density increases more rapidly than the number of prey and a type III curve occurs when consumption in low densities

TABLE 3. WINTER DIET OF GOSHAWKS IN THE OULU AREA, NORTHERN FINLAND. DATA ARE BASED ON PUBLISHED RESULTS BY TORNBERG AND COLPAERT (2001) DURING 1991–1995 AND TORNBERG (UNPUBL. DATA) DURING 1999–2002.

	Weight classes [a]	Male		Female		Total	
		N	%	N	%	N	%
Mountain hare adult	E			17	38.6	17	27.9
Capercaillie male (*Tetrao urogallus*)	E			2	4.5	2	3.3
Capercaillie female	D			1	2.3	1	1.6
Mountain hare juvenile	D	1	5.9			1	1.6
Black Grouse male (*Tetrao tertix*)	D			6	13.6	6	9.8
Black Grouse female	C	3	17.6	2	4.5	5	8.2
Willow Grouse (*Lagopus lagopus*)	C			1	2.3	1	1.6
Hazel Grouse (*Bonasa bonasia*)	B	4	23.5	4	9.1	8	13.1
European red squirrel (*Sciurus vulgaris*)	B	6	35.3	9	20.5	15	24.6
Great Spotted Woodpecker (*Dendrocopos major*)	A	1	5.9			1	1.6
Crossbill (*Loxia curvirostra*)	A	1	5.9			1	1.6
Small passerine	A	1	5.9			1	1.6
Small mammals	A			2	4.5	2	3.3
Totals		17		44		61	

[a] Weight classes of prey: A = 0–100 g, B = 100–500 g, C = 500–1,000 g, D = 1,000–2,000 g, E = >2,000 g.

increases slower than number of prey. All curve types level off at high prey densities because the predator becomes satiated. Curve types predict different outcomes for the stability in the predator-prey interaction. Type II tends to destabilize and type III to stabilize prey population (Holling 1959, Begon et al. 1996).

Based on the existing studies in Finland and Sweden, goshawks' functional response may be concave (Lindén and Wikman 1983), convex (Wikman and Tarsa 1980, Tornberg and Sulkava 1991), or only a weak response (Widén 1985a, Tornberg 2001). It is likely that goshawks show a type III response for grouse in southern areas of Fennoscandia where they are less dependent on grouse as a stable food and where alternative prey is richly available. Whereas in the north, where grouse form the major part in the diet and alternative prey are scarce, a concave or no response is found.

BREEDING OUTPUT OF GOSHAWKS

Breeding Density and Quality of the Breeders

Because goshawks use the same breeding sites fairly regularly year after year, breeding densities in intensively studied areas can be reliably estimated. Reliability is also increased by the fact that breeding territories are very regularly spaced in a continuous woodland area (Widén 1985b, Selås 1997b). In southern Norway, mean distances during 1980–1990 varied from 4.5–5.4 km (Selås 1997b). In the vicinity of Oulu, distance between regularly occupied territories was around 4 km (Tornberg 2001). Studies carried out in western and southern Finland during the 1950–1970s show that goshawk density was around five pairs/100 km^2 when all nests studied were active (Huhtala and Sulkava 1981). In more restricted coastland areas of south Finland a breeding density of five–eight goshawk pairs/100 km^2 was reported during 1977–1983 (Forsman and Solonen 1984). Breeding density may have declined since the 1970s and is probably around three pairs/100 km^2 at present in large parts of Fennoscandia (Widén 1997). In the vicinity of Oulu, breeding density is, however, still around five territories/100 km^2 (Tornberg 2001), but due to a yearly average occupancy rate of about 80%, real breeding density falls to four pairs/100 km^2 and recently even lower (R. Tornberg, unpubl. data). For comparison, densities in central and southern Europe tend to be higher but varying considerably depending on the area, e.g., in northwest Germany from 3.6–7.4 pairs/100 km^2 (Krüger and Stefener 1996) and in central Poland from 9–13.9 pairs/km^2 (Olech 1998).

Physiologically, goshawks are able to breed as yearlings. In reality this takes place in females but not in males that likely can not provide enough food for the females during the courtship phase. On the island of Gotland, males and females entered the breeding population in the second year (Kenward et al. 1991). Their proportion among breeders was <10%. Females did not breed as yearlings due to a saturated breeding population but had to wait for vacancies in their second year of life. In western Finland and in the Oulu area, percentage of females breeding as yearlings was about 5–10% annually (P. Byholm and R. Tornberg, unpubl. data).

Clutch and Brood Sizes

Goshawks start breeding very early in spring; nest building can be initiated in mild winters and in good food conditions by late February (Huhtala and Sulkava 1981). Initiation of nesting is likely connected with the start of breeding by grouse, which is stimulated by high temperatures (Nielsen and Cade 1990). Start of egg laying takes place in western Finland around 20 April (Sulkava 1964, Huhtala and Sulkava 1981, Tornberg 1997, Byholm et al. 2002a). Yearly average clutch size can vary from 2–4 depending on food conditions, usually the availability of grouse (Byholm 2005). Based on extensive data from western Finland during good grouse years in 1960s–1970s mean clutch size was 3.51 (± 0.06, N = 164; Huhtala and Sulkava 1981). In the vicinity of Oulu, yearly clutch size during poor grouse years in 1988–2002 varied from 2.9–4.2, ($\bar{x} = 3.59 \pm 0.07$, N = 148). Consequently, grouse density seems not to strongly determine the mean clutch size, although high peaks or deep lows of grouse usually are reflected in the clutch size (Sulkava 1964, Huhtala and Sulkava 1981, Sulkava et al. 1994). Clutch size declines significantly with the postponing of the start of egg laying (Huhtala and Sulkava 1981, Sulkava et al. 1994, Byholm et al. 2002a). In lowland Britain, clutch size seem to higher than in Finland 3.96 (± 0.11, N = 47; Anonymous 1990), but is, on average, the same in central Poland (3.54, N = 143; Olech 1998).

Brood size in large data sets is always about 0.5–0.6 lower than clutch size due to partial brood loss (Byholm 2005) Hence, average brood size in western Finland has varied in the 1950–1970s in data collected in different localities, from 2.78–3.13 (Huhtala and Sulkava 1981). In the vicinity of Oulu, during 1988–2002, average brood size was 2.89 (± 0.12, N = 163). Mean brood size for whole Finland during 1989–1998 was 2.79 (± 0.05, N =

2,822; Byholm et al. 2002a). Hence, it seems that mean brood size has not declined since the 1950s in Finland although numbers of main prey, grouse, have decreased remarkably since then (Lindén and Rajala 1981). This is not necessarily surprising because alternative prey (migratory birds) is richly available during summer. Greatest mortality in goshawks' broods takes place soon after hatching when the youngest nestling in the brood usually dies or one egg does not hatch (Sulkava 1964, Huhtala and Sulkava 1981, Anonymous 1990, Byholm 2005). Mortality is higher in nests originally having four eggs than those having three eggs (Byholm 2005). Mortality is relatively low during the post-fledging dependence period. Interestingly, goshawk brood size is spatially well synchronized over large area up to over 300–400 km (Ranta et al. 2003). In England, brood size based on a small data set collected over several years was somewhat lower than in Finland 2.76 (± 0.16, N = 45; Anonymous 1990), but higher in central Poland 2.91 (N = 400; Olech 1998).

Goshawk nestlings leave the nest at the age of 44–46 d (Kenward et al. 1993a) and reach independence at the age of 75–82 d (Kenward et al. 1993b). In the vicinity of Oulu, where mean hatching date is 1 June, young goshawks leave their nesting territory around mid-August. Reaching independence means a jump in the mortality of young goshawks, which continues high during the first winter as illustrated by the accumulation of dead goshawks to the Zoological Museum of the University of Oulu (Fig. 3). This has been verified by a large radio-tracking project on Gotland (Kenward et al. 1999). Adult mortality peaked in late winter-early spring (Haukioja and Haukioja 1971).

Occupancy Rate and Productivity

In birds of prey using serviceable breeding sites—old stick-nests, cliffs, or nest-boxes—occupancy rate counted as breeding sites used per sites available gives a reasonable estimate of size of the breeding population (Forsman and Solonen 1984). Populations of birds living in stable and predictable conditions can also be stable from year to year (Hunt 1998). Goshawks living in northern areas and having high winter mortality very seldom fill serviceable breeding sites for long periods. In southern Finland, mean occupancy rate was 68% in an 8-yr study of around 30 territories checked annually (Lindén and Wikman 1983). In a long-term study carried out in western Finland during 1979–1996, mean occupancy rate was 45% (Hakkarainen et al. 2004, Tornberg et al. 2005). In this study, the number of territories checked annually increased from 16 to 173 during the study. In the vicinity of Oulu, the corresponding figure was 83% during 1987–2003; number of territories annually checked increased from

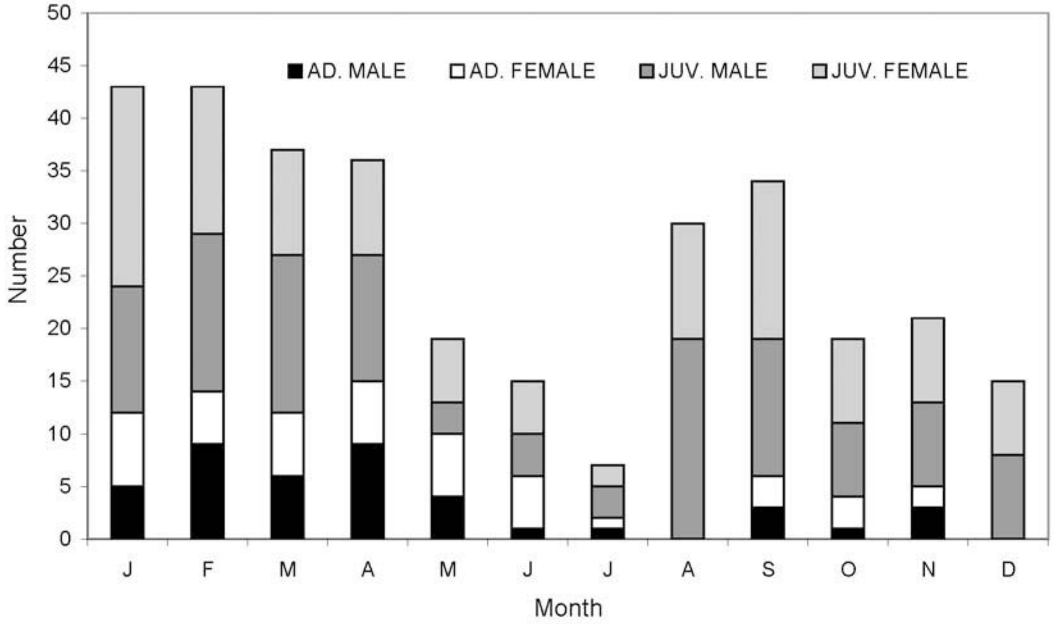

FIGURE 3. Number of Northern Goshawks accumulated monthly by the Zoological Museum of University of Oulu, 1964–2003.

10–32. In the study area at Oulu, occupancy rate declined strongly but remained stable in study area of western Finland (Hakkarainen et al. 2004) during the study years. Declining occupancy rates during a long study may depend on the improving familiarity of the research area in the course of investigation when less used territories are discovered. It is not surprising that in the western Finland study area the number of occasionally used territories increased during the study years (Hakkarainen et al. 2004).

Productivity is measured as young produced per breeding pair, i.e., per occupied territory (Steenhof 1987). Productivity in the previous studies varied from 1.8–2.1. Annual variation was substantial, being highest in southern Finland (C.V = 32.3%) and lowest in western Finland (C.V = 17.1%). In the vicinity of Oulu, C.V. was 22.6%. Productivity on Gotland during 1977–1981 was much lower at 1.36 young/occupied territory (Kenward et al. 1999). Even farther south in northwest Germany, Kruger and Stefener (1996) reported productivity to vary between 0.5–1.8. In central Poland, in a long-term study, it was fairly high at 2.25 (Olech 1998). Obviously, goshawks tend to compensate for higher mortality by man/natural causes or both in the north and east by higher productivity (see Kenward et al. 1991)

Numerical Response

It is not surprising that breeding output as estimated by average clutch and brood sizes follows the population density of grouse. Breeding attempts of goshawks failed almost totally after a very cold winter and poor grouse population in western Finland in 1956 (Linkola 1957, Sulkava 1964). No obvious differences were found in the mean clutch and brood sizes between good grouse years in 1950–1970s and relatively poor grouse years in the 1980–1990s. Yet, yearly clutch and brood sizes tend to follow grouse population fluctuations (Lindén and Wikman 1980), usually with a 1-yr time lag (Sulkava et al. 1994). Connection between grouse population density and goshawks' breeding output seems to be strongest in central and zone of the boreal forest (Lindén and Wikman 1980, Sulkava et al. 1994, Tornberg et al. 2005) while it seems to disappear in southern zone of boreal forest (Lindén and Wikman 1983). In Norway, breeding success of goshawks seems not to follow grouse fluctuations but may be indirectly linked with multi-annual vole cycles (Selås and Steel 1998).

Clutch and brood sizes may often poorly represent the dynamics of the whole goshawk population. We did not find any obvious correlation between brood size of goshawks and grouse density in Oulu area during the 1990s. Better estimates in this sense may be population productivity and occupancy rate that also take into account the failed pairs (Steenhof 1987). In the Oulu area, population productivity closely followed the density variation of grouse until 1996 ($r = 0.863$, $N = 10$, $P < 0.001$), but thereafter the connection disappeared (Fig. 4). Yet, the overall correlation during the whole study period was significant ($r = 0.558$, $N = 17$, $P < 0.05$). In addition, a positive correlation ($r = 0.549$, $N = 19$, $P < 0.05$) between grouse density and territory occupancy rate of goshawks with a 2-yr lag was found in western Finland in a long-term study during 1979–1996 (Tornberg et al. 2005). Similar relationship seems to prevail between winter censuses of goshawks and multi-annual fluctuations of forest grouse (Tornberg and Väisänen, unpubl. data). However, we found no correlation between occupancy rate of goshawks and density indices of grouse in the Oulu area with any time lags. A reason for these discrepancies in brood size and occupancy rates may be the decline of grouse populations and disappearance of the multi-annual cycles in grouse population fluctuation (see Fig. 2).

GOSHAWK PREDATION ON GROUSE—TOTAL RESPONSE

Pooling functional and numerical responses yields a total response or kill rate of the predator to varying densities of prey. Predation impact is defined as a function of kill rate to density of prey. Further, predation rate is obtained when predation impact is plotted against density of prey. (Keith et al. 1977, Lindén and Wikman 1983; Korpimäki and Norrdahl 1989, 1991). Three studies of the goshawk's predation impact on woodland grouse (Lindén and Wikman 1983, Widén 1987, Tornberg 2001) and one study on pheasants (Kenward 1977, Kenward et al. 1981a) have been carried out in Fennoscandia. Lindén and Wikman (1983) reported that goshawks took 12% of the adult Hazel Grouse in southern Finland during the 4-mo breeding season; on an annual basis predation impact would be 36%. In central Sweden, territorial goshawks killed 14% of Black Grouse males and 25% of females during the breeding season, but during winter, predation on grouse was negligible (Widén 1987). A grouse study carried out in the same area by radio-tagged birds gave almost the same mortality estimate (20%) for Black Grouse females during the breeding season (Angelstam 1984). In northern Finland, goshawks prey on all four available grouse species (Tornberg 2001). Based on a recent predation estimate for the breeding season, goshawks killed 22% of Willow

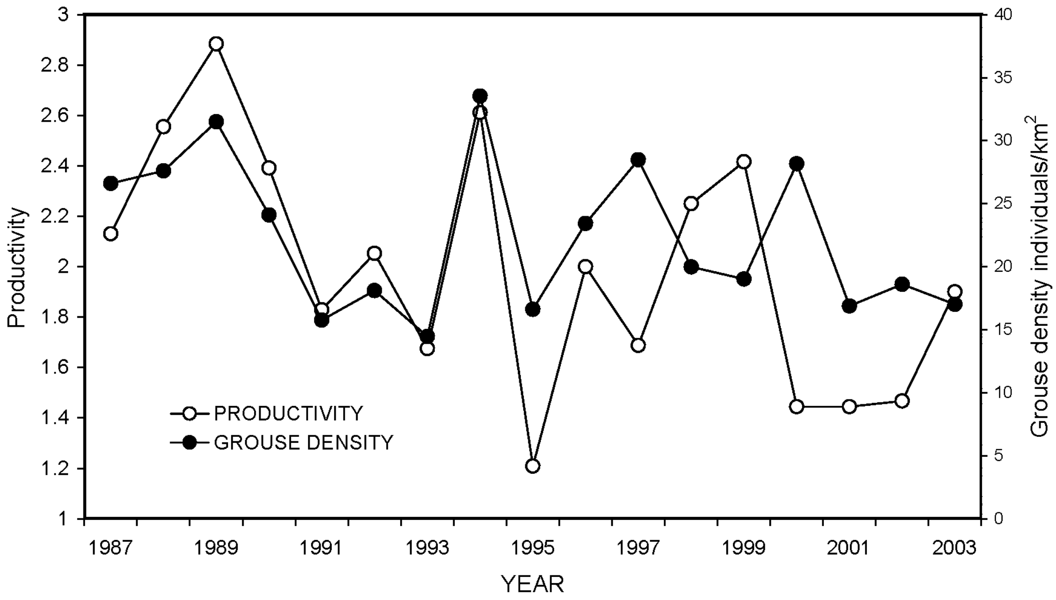

FIGURE 4. Productivity of the Northern Goshawk population and grouse density of the previous autumn in the Oulu area from 1987–2003.

Grouse, 16% of Hazel Grouse, 9% male Black Grouse, 14% of female Black Grouse, 4% female Capercaillies, and 7% of grouse chicks. On an annual basis, numbers for adult grouse were almost the same (Tornberg 2001). It seems that the goshawk is the most important predator of adult grouse during the breeding season accounting for 30–50% of adult grouse mortality excluding large Capercaillies (Widén 1987, Tornberg 2001). Impact of winter predation by the goshawks on woodland grouse is still unresolved due to incomplete and small data sets on winter diet, but in most years it might be as large as mortality during the breeding season.

Goshawks kill substantial numbers of pheasants in southern Fennoscandia, their predation impact being strongly density dependent. Where wild pheasant stocks prevail, loss by goshawk predation was 55% for females and 18% for males, but where captive-born pheasants were released, losses were substantially higher, goshawks were responsible for 90% of kills during the winter (Kenward 1977, Kenward et al. 1981b). Predation studies usually neglect the impact by non-breeders, which can be considerable in years of increasing and high predator populations (Rohner 1996). Healthy raptor populations should minimally contain around 30–40% non-breeders (Hunt 1998).

Elsewhere, we (Tornberg 2001, Tornberg et al. 2005) have suggested that goshawk predation may have a destabilizing effect on grouse population due to obvious time lags in numerical response of goshawks to varying grouse densities and a high proportion of grouse in the diet also during poor grouse years (Fig. 5). In this sense, the predation impact of goshawks on forest grouse appears to be similar to the predation impact of Gyrfalcons (*Falco rusticolus*) on ptarmigans (*Lagopus* spp.) in Iceland (Nielsen 1999). The lagging numerical response of goshawks to varying densities of grouse is obviously different from numerical responses of various vole-eating owls and raptors to multi-annual vole cycles in Fennoscandia, because their numerical responses track varying vole densities without obvious time lags (Korpimäki 1985, 1994). In conditions more natural than the present in northern European boreal forests, goshawks may have had a remarkable role in driving grouse cycles.

MOVEMENTS OF GOSHAWKS

The goshawk is regarded as a resident raptor but individuals in their first year of life are mobile and some of them show directional movement southward in autumn and northward in spring (Marcström and Kenward 1981b). These movements can take young birds >1,000 km from their natal areas (Sulkava 1964, Saurola 1976, Halley 1996). However, most of the birds do not orient systematically southward but disperse randomly around their natal area (Sulkava 1964, Saurola 1976, Marcström and Kenward

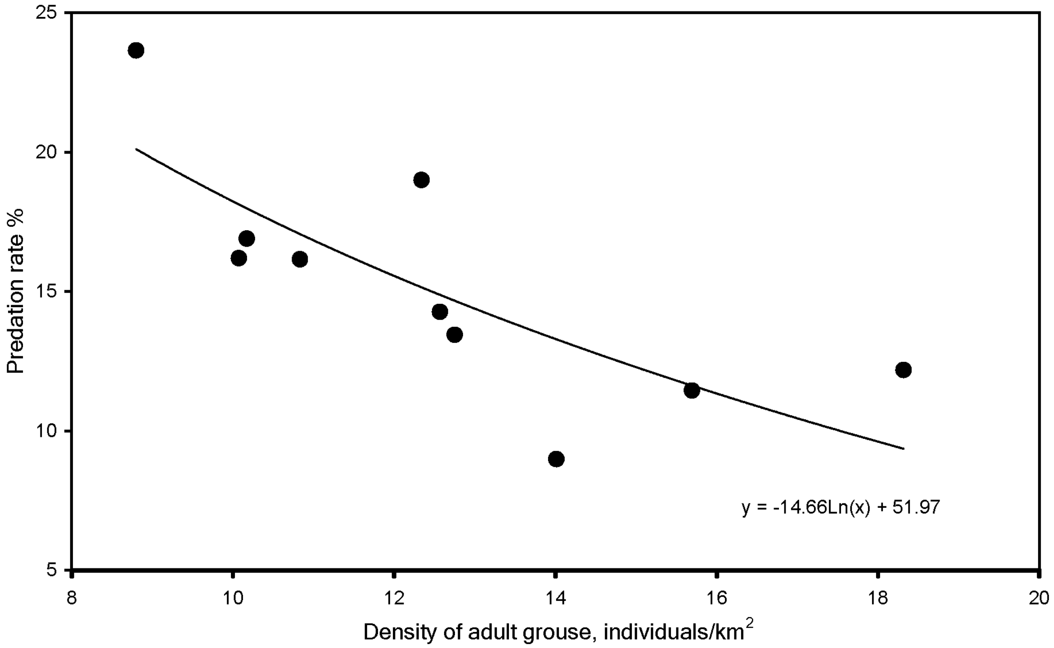

FIGURE 5. Predation rate by the Northern Goshawk on adult grouse in the Oulu area, 1989–1998 (redrawn from Tornberg 2001).

1981b, Halley 1996, Byholm et al. 2003). Sulkava (1964) showed that dispersal distances of the young goshawks were negatively related to abundance of grouse in the natal area. Byholm et al. (2003) confirmed this finding recently and also showed that birds in late broods dispersed farthest, especially males. Dispersal distances also seem to be related to sex and age. Juvenile males tend to be most mobile (Kenward et al. 1981b, Marcström and Kenward 1981, Neideman and Schönbeck 1990, Byholm et al. 2003, but see Halley 1996). Median distance for male hawks banded as nestlings and found dead during the first winter after reaching the independence was 80 km but only 34.5 km for females (N = 213; Byholm et al. 2003). In Norway, however, females moved more (median 109 km) than males (median 68.5 km, N = 77; Halley 1996). Hawks found dead in adult plumage had moved less far than those found as juveniles (Halley 1996, Byholm et al. 2003). Because birds could not be tracked, this may hint at return movements to the natal area after maturity (Halley 1996). Distance traveled by adults of both sexes tends to be the reverse of that found in juveniles. A similar tendency has been found also in radio-tracking studies (Kenward et al. 1981b) and when trapping and banding hawks after the breeding season (Marcström and Kenward 1981). Figure 6 illustrates the spread of juvenile goshawks banded as nestlings in the Oulu area. Most birds are found on the coastline of Bothnia Bay, Baltic Sea. Long-distance travelers seem to have moved in various directions.

Higher mobility of juvenile males than females is also apparent in trapping results from southern Sweden (Neidemen and Schönebeck 1990). A reason may be that food supply for males is lower than that for females. Tornberg (2000) estimated that food base of females is three times larger than that of males, mainly due to mountain hares (weighing 3–4 kg) and Capercaillie males (weighing 4 kg), prey that is nearly out of the males' hunting capacity. Kenward et al. (1993b) found that juvenile males moved further than females on Gotland when young rabbits reached full size. The food scarcity hypothesis is also supported by the trapping results in southern Sweden that showed an increase in proportion of males in years 1984–1987 when grouse population numbers were exceptionally low (Fig. 2). Juvenile males also starve more often than females (Tornberg et al. 1999, Sunde 2002). Southward migrations of goshawks in North America are related to food scarcity, especially during low phases of the 10-yr population cycles of snowshoe hares (*Lepus americana*; Keith and Rusch 1989). There, however, differences between the

FIGURE 6. Finding sites of the juvenile Northern Goshawks banded as nestlings in the the Oulu area, 1962–2002. Data obtained from the Ringing Centre of the Natural History Museum of the University of Helsinki.

sexes in the length of migration, has not been documented.

In adult goshawks, males seem to be the more philopatric sex (Kenward et al. 1981b, Widén 1985b, Byholm et al. 2003), a fact common in many raptors (Newton 1979a, Korpimäki et al. 1987, Korpimäki 1993). Higher philopatry in males might be connected to their more active role in territory defense and brood rearing (Newton 1979a, Byholm et al. 2003). Also, males trapped as adults are less reluctant to leave their home ranges than females (Kenward et al. 1981a, Widén 1985b). In the Oulu area, one breeding radio-tagged female deserted her family during the fledging period of her young and shifted to nest in a different territory in the next year. The fledglings were then successfully reared by the male. Another female trying to nest near the city dump of Oulu in 1994 was found 2 yr later 100 km south eaten by an Eagle Owl (*Bubo bubo*). Fairly little is still known about site and mate tenacity in breeding goshawks in Europe and further study is badly needed.

One may argue that dispersers moving farther are in a poorer condition than those moving less. Investigating movements of trapped and either banded or radio-tagged hawks in Sweden did not explain the length of the movement or site tenacity of the trapped birds (Kenward et al. 1981a, Marcström and Kenward 1981b, Widén 1985b). In fact, males that were generally in poorer condition in late winter were more reluctant to leave the study area than females (Widén 1985b).

HOME RANGE

Juvenile goshawks are very mobile during their first year of life; post-fledging dispersal can take them >1,000 km from their natal areas but most of the young hawks settle within 100 km. Young hawks tend to maintain home ranges before settling in the final breeding territory (Halley et al. 2000). Those juvenile hawks that were radio-tracked during November–December usually stayed near the trapping site in central Sweden and northern Finland (Kenward et al. 1981b, Tornberg and Colpaert 2001). Winter ranges of different goshawk individuals can overlap extensively. This happens especially in areas with high food supply like near release pens of pheasants (Kenward 1977). So, wintering goshawks seem not to defend their home ranges. This was the

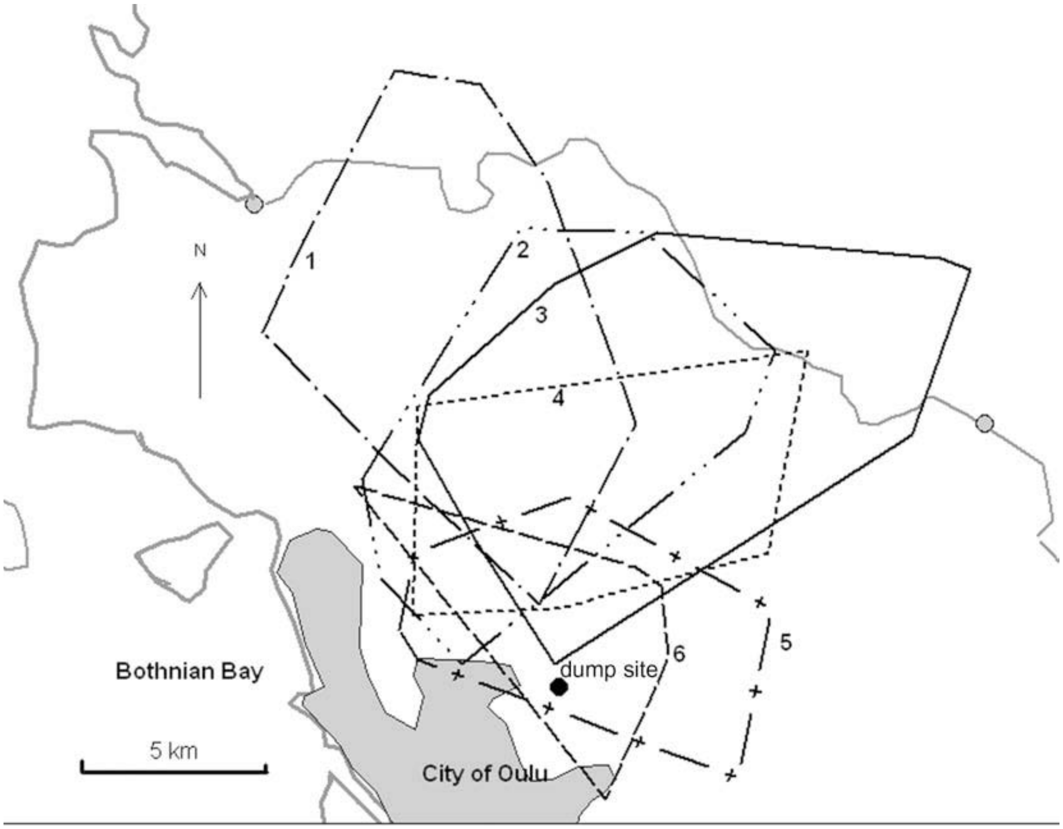

FIGURE 7. Winter ranges of the Northern Goshawks near Oulu in the winter 1992–1993. Ranges marked as follows: 1. adult female (breeding in the area), 2. adult male, 3. adult male (breeding in the area), 4. adult female (breeding 15 km southwest from the area), 5. adult female (breeding near dump site), and 6. juvenile female.

case also in Oulu (Fig. 7) where breeding birds did not try to displace visitors. Some observations of resident breeders hint that they know the core areas of their neighbors and avoid visits there.

Winter range sizes have been found to be related to landscape structure. In farmland areas of Sweden, range size correlated negatively with the amount of forest edge in the range (Kenward 1982). Because most of the kills took place near woodland edges, range size seems to relate negatively to the amount of good habitat, i.e., forest edge. Correspondingly, range size correlated negatively with the amount of mature forest, a preferred hunting habitat, in boreal forests of northern Finland (Tornberg and Colpaert 2001). Range size seems to respond flexibly either to the quantity or the quality of the food resource. Hawks that kill mostly large prey or live in areas with high food supply have the smallest ranges (Kenward 1982, Nygård et al. 1998). It is no wonder that juveniles being less experienced hunters than adults have larger ranges (Kenward et al. 1981b). One might also expect larger winter home ranges for males that have a narrower food base than females. However, in boreal forests of central Sweden males' range size (5,110 ha, maximum polygon) was even slightly smaller than that of females' (6,179 ha). In this study, however, goshawks fed mainly on squirrels that might be more suitable prey for smaller males than larger, less agile females (Widén 1987). In the Oulu area, average winter range size (maximum polygon) was 7,091 ha (± 3,935 ha, N = 9) for males and 5,710 ha (± 664 ha, N = 15) for females, but the difference was not statistically significant.

HABITAT CHOICE

Goshawks are known to be old-forest specialists. This is, however, largely based on studies of the characteristics of the breeding habitats (Widén 1997, Penteriani 2002). Radio-tracking studies have shed light over the habitat use of goshawks outside and during the breeding season. As stated above, goshawks favored forest edges in farmland areas of central Sweden. Yet, in a more forest-dominated area radio-tagged birds thrived best in large patches, avoiding edges (Widén 1989). They preferred mature forests over younger stands. Correspondingly, goshawks also preferred mature forests in Oulu, but rather average sized patches that hint at favoring edges as hunting habitats. Goshawks used young forests proportionately to their availability but avoided open areas (Tornberg and Colpaert 2001). Because locating a goshawk is possible only when the bird is perched, it is impossible to know how much they fly over open terrain. Goshawks hunt with a short-stay, perched technique, perching 3–5 min and then flying 200–300m to a new perch (Widén 1984).

SURVIVAL AND CAUSES OF DEATH

A large number of banded hawks and good success at recapturing them have enabled reliable estimates of goshawk survival. Haukioja and Haukioja (1971) estimated the mortality of goshawks to be 63% in the first year assuming that 60% of the bands found were returned, 33% in the second year, 20% in the third, and stabilizing at around 10% in older age classes. Using a larger data set, Saurola (1976) estimated corresponding numbers as 64%, 35%, 18%, and 15%. It must be remembered that goshawks in Fennoscandia were under heavy persecution in 1960s–1970s with 5,000–6,000 goshawks, a remarkable proportion of the annual production, being killed annually by humans in Finland alone (Moilanen 1976). Analyses based on band recoveries may be biased, however, because young age classes are likely to be found easier than older specimens. Moreover, during the time when shooting was allowed, hawks killed by humans were likely to be overrepresented in total recoveries and young hawks prevailed among those being shot. Kenward et al. (1991, 1999) found in a large radio-tracking study on Gotland that 47% of the band recoveries were from killed hawks, whereas only 36% from radio-tagged birds. In addition, radio-tagged hawks showed an unbalanced mortality in young age classes in relation to sex—by 1 April, 46% of the males had died in their first year but only 31% of the females. In the second year, still more males (41%) than females (29%) died, but in older age classes mortality was balanced being 21% for both sexes.

Telemetry data collected in the Oulu area during 1991–1995 (N = 26; Tornberg and Colpaert 2001) were analyzed along with new data on eight tagged birds from the winters 1999–2003 (four adult males, one yearling male, two adult females, and one juvenile female) to get a survival estimate for winter months from 10 November to the end of February. We pooled the data over the years using a staggered entry method (Pollock et al. 1989). Mortality in adults (N = 26, males and females together) was 37% and for juveniles, 81% (N = 8). Because this method is very sensitive to small sample sizes, our estimate for juveniles is probably unreliable. The estimate for adults is very high compared to those obtained from band recoveries or telemetry data collected in more southern areas but is not necessarily unrealistic. Annual mortality may be a bit higher than estimated for winter months because natural mortality of adult hawks can still be high in March and April (Fig. 3).

Autopsies of naturally dying hawks on Gotland revealed that starvation was the most important cause of death (37%; Kenward et al. 1991), 33% of hawks died of trauma, and 22% of the combination of disease and starvation. Based on autopsies of goshawks brought to the Zoological Museum of the University of Oulu, 35% of hawks had died of starvation, 25% from collisions, 15% from a combination of trauma and starvation, and only 13% from shooting (N = 165; Tornberg and Virtanen 1997). Among banded hawks, the most important cause of death in the 1960s–1970s was killing by humans (83%; Saurola 1976). Similarly, shooting was the most common cause of death in Norway; before protection about 50% of birds found had been shot. After protection this cause of death fell to 5% (Halley 1996). After full protection of goshawks in 1989 in Finland, killing by humans declined but starvation may have increased due to intensified competition for food. Earlier, hawks prone to starve were often shot when they approached human settlements (Haukioja and Haukioja 1971). Hence, the cessation of shooting did not necessarily increase the number of young hawks because starvation among juveniles may have increased.

POPULATION STATUS AND TRENDS OF THE GOSHAWK IN FENNOSCANDIA

It is reasonable to argue that decline of a prey population induces a decline in the population of its predators. This typically concerns specialized predators (Begon et al. 1996) because generalists can switch to another prey if one prey type declines. The Northern Goshawk could be considered a generalist predator based on the wide spectrum of prey species in its diet. Because most diet studies have been performed during the breeding season when the greatest variety of suitable prey species, especially vulnerable juveniles, is available, food niche can be very wide. More focus should be directed to winter when availability of prey is more restricted.

Recent estimates show that goshawk still is one of the most common raptors in Fennoscandia. Several studies carried out in different localities in Fennoscandia, however, hint at a decline in breeding densities of goshawks. Widén (1997) reviewed nine studies and found a decline in eight of them. Selås (1998a) reported a decline in the breeding density in southern Norway from nine pairs/100 km^2 in the 1950s to three pairs to the 1980s but a slight increase to four pairs/100 km^2 in the mid-1990s. Recently, density has fallen back to the previous three pairs/100 km^2 (Selås 1998b, Selås, pers. comm.). In central Norway, breeding density in the 1990s was very low, only one pair/100 km^2 (Nygård et al. 1998). It is still difficult to evaluate whether declines reported in some studies indicate only local declines or whether they indicate a more general trend. A Finnish country-wide monitoring program of breeding populations of birds of prey which was initiated in1982 does not indicate declining density until the mid-1990s (Väisänen et al. 1998), even though during the 1990s a slight declining trend was detected (Björklund et al. 2002). The Swedish monitoring project from 1975 onward for winter and summer censuses show a 20% declining trend for winter but a slight increase for summer densities (Svensson 2002). In Sweden and Norway, increasing numbers since the 1980s are, however, expected and obvious as Selås (1998a) has pointed out. This is due to a sarcoptic mange epidemic in red foxes (*Vulpes vulpes*) that caused fox numbers to crash and caused a corresponding increase in grouse numbers (Lindström et al. 1994). Hence, monitoring initiated in the 1970s–1980s does not necessarily reveal the long-term development of the goshawk population. Goshawk populations in central and south Europe seem to be more or less stable or even increasing (Kruger and Stefener 1996, Olech 1998)

In the Oulu area, occupancy rate of the goshawk population showed a strong negative trend during the 1990s (Fig. 8). We analyzed the population development by Moffat's equilibrium model (Hunt 1998) which assumes a fixed number of serviceable breeding sites. The model further assumes that juveniles start breeding in their second year. Simply by altering productivity of breeders and survival of juveniles, sub-adults, and adults, the model predicts future structure and development of the population. We used a series of survival values of 63% for adults (obtained from telemetry data), adjusting survival values for sub-adults (51%) and for juveniles

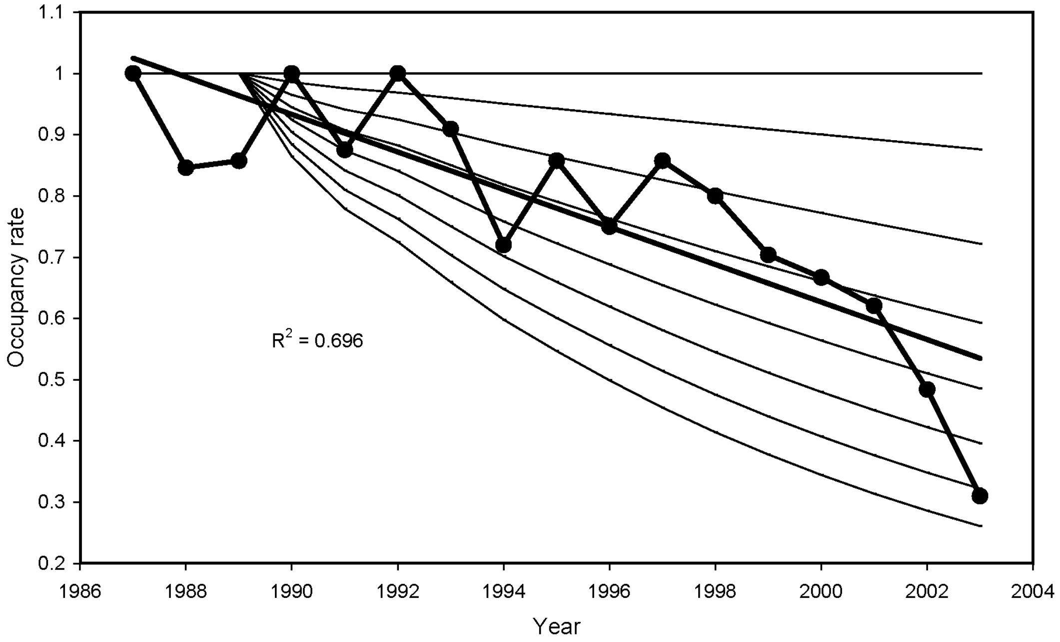

FIGURE 8. Occupancy of Northern Goshawk territories in the Oulu area (thick line) and simulations of the number of breeders with different survival rates by Moffat equilibrium model (Hunt 1998). Uppermost line denotes a survival value of 0.7 declining by 0.1 in each step.

(46%) according to estimates obtained from data by Kenward et al. (1999). We then modeled survival estimates by increasing each age category by1%. We set population productivity at two fledglings/breeding pair. By the lowest series of values, the decline was steeper than observed which hints that the survival values used obtained from the telemetry study are too low. Using values 4% higher yielded a model that matches the observed line (Fig. 8). With these values, the population does not contain non-breeders which could explain the poor correlation between the occupancy rate of goshawk territories and grouse density because non-breeders are capable of responding quickly to changes in prey population. It seems that productivity is not a problem in a goshawk population but rather the poor survival of adults (Hunt 1998). Using values obtained from band recoveries in Finland (82%, 65%, and 36%) and productivity of two fledglings/pair gives a balanced breeding population containing 20% non-breeders. The goshawk population on Gotland remained stable, adjusted by lower proportion of the females breeding annually (40%) than the males (70%), which means that proportion of non-breeders of the breeders was around 40–50%.

CONCLUSIONS

Recently, a lot of debate has centered on reasons for changes in avian fauna of boreal forests in Fennoscandia (Haila and Järvinen 1990, Mönkkönen et al. 1999). The general conclusion derived from ornithological reports has been that old-forest species have declined and species living in young successional stages have increased or remained stable (Väisänen et al. 1986). This is considered to be due not only to the decline of the mature-forest stands but also to the fragmentation yielding patches too small to maintain meta-populations of certain old-forest specialists (Andrén 1994). The goshawk has been considered as an old-forest bird based on the nest-site selection (Penteriani 2002). Widén (1997) concluded that the goshawk has suffered from forestry because of the decrease of its main hunting habitat—old forests. Young successional stages of boreal forests, although basically maintaining higher grouse densities, are often too dense for successful hunting of the goshawk (Beier and Drennan 1997). Hence, Widén (1997) considers that habitat degradation is a more important reason for decline of goshawks than decline in the prey supply as such. It is, however, quite evident that the supply of the main prey, forest grouse, has declined.

In Finland, where grouse counts have been made since the mid-1960s, decline in all forest grouse species has been >50% (see Fig. 2). Modern forestry with extensive clear cuts, draining of the peat land bogs, and construction of a dense network of forest roads have had negative impacts on forest grouse (Kurki et al. 1997). Clear-cuts may have increased grasslands that maintain voles and their predators. During crashes of vole populations, small mammal predators switch to hunting grouse chicks and thus lower the productivity of grouse (Angelstam et al. 1984, Henttonen 1989). Removal experiments of mammalian predators have resulted in higher grouse populations or at least higher reproductive rate compared to control areas (Marcström et al. 1988, Kauhala et al. 2000). We conclude that shrinkage in the area of mature forests does not explain the observed negative trends in the goshawk population per se, but rather the availability of suitable sized prey during the non-breeding season. Goshawks are able to live in areas where forest cover is <20% of the area but where enough prey is accessible (Kenward 1982). In the Oulu area, goshawks preferred fairly small patches of forests. Surprisingly, the composition of the winter diet is close to that found in farmland areas of central Sweden with the difference that grouse replaced the pheasants (Kenward et al. 1981a; Table 2). Habitat of kill sites did not differ much from that of the habitat composition available (Tornberg and Colpaert 2001).

Forest fragmentation has caused a decline in forest grouse and perhaps also in red squirrels, whereas it may have increased mountain hare numbers. Comparisons of mountain hare densities between Finland and Russian Karelia show a three-fold higher hare population in Finland compared to Russian Karelia where forest stands are mostly at mature stage (Lindén et al. 2000). As found in winter diet studies, females can but male goshawks unlike cannot kill full-grown mountain hares. This has led to a curious situation where females may have benefited from forest fragmentation but males suffered. This appears to result in a higher starvation risk and poorer winter condition in male goshawks (Widén 1985b, Tornberg et al. 1999, Sunde 2002). It may also explain why breeding output expressed as clutch and brood sizes do not match well with the density fluctuations of grouse. Females in good condition in spring can lay eggs with a minimal aid from the males. Therefore, recent changes in forest structure may have even affected their morphology. Tornberg et al. (1999) found, based on museum material from the last 40 yr, that adult males have become smaller and females larger. This change was more on the outer morphology (body, wing, tail, and tarsus length) than bone length. This might be explained by dietary changes caused by a general decline of grouse populations—females have found larger alternative prey than males. Another interesting adaptation that probably originates from a tighter dependence of males on grouse, appears as a changing sex ratio in goshawk broods as a function of grouse density (Byholm 2003). Goshawk pairs produce significantly more males in good grouse years compared to poor years. This might be a compensative response for higher juvenile mortality of males induced by natural selection.

When evaluating the conservation needs for a declining raptor species, focus should not be on only one apparently important fact, but on a wider scale, e.g., how the change in habitat has affected the food supply. One must also realize when the food supply is a limiting factor, it is not likely to be limiting during the breeding season at northern latitudes. Kenward (1996) presumes that problems faced by the goshawks in the sub-boreal region of North America might be due to poor food supply in winter. Protection of the goshawks has not increased goshawk numbers. It can be possible that nowadays, when more young probably are entering the winter than during the years when many juveniles were killed by humans, intra-specific competition for food in goshawk populations has intensified. This may lead to more starving young birds but also a weaker winter supply for adults and poorer breeding performance in the next spring (Haukioja and Haukioja 1971). In a specialist predator-prey interaction, a decline of the predator may lead to an increase in prey population. In goshawk-grouse systems, this does not necessarily happen these days because increased impact by mammalian predators harvests grouse populations independently of their density (Angelstam et al. 1984, Marcström et al. 1988, Korpimäki and Norrdahl 1997). In fact, mammalian predators and goshawks are competing for a common resource, grouse, which is of vital importance for the goshawks but not necessarily for mammalian predators (Selås 1998a). Modern forestry improves the conditions of mammalian predators and at the same time harms forest grouse and the predators dependent on them. All in all, habitat restoration is the ultimate solution for the sustainable populations of forest grouse and goshawks.

Future research effort should be directed to winter ecology of goshawks. Topics like: (1) winter food supply, (2) predation rates on the most important prey species, (3) hunting habitats with precise data on kill sites, (4) movements, survival, and causes of death of different age classes, and (5) relationships to competitors, should be investigated with modern field techniques. In addition, we badly need individual-level studies on goshawks during both the breeding and non-breeding seasons in boreal forests. For example, it could be important to know how the reproductive effort of individual pairs and members of pairs varies in relation to temporal and spatial density fluctuations of main prey, and how sexual differences in the main food supply induced by modern forestry practices (beneficial for females, costly for males) affects reproductive effort, division of duties during the breeding season, and reproductive success of individual goshawks.

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