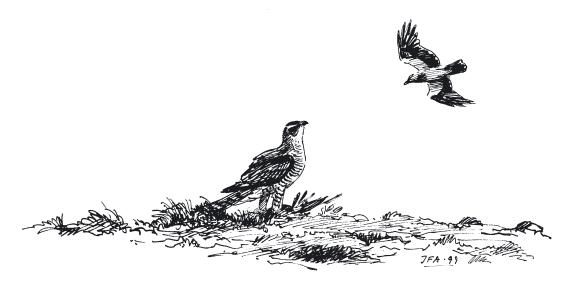
Prey selection of Goshawks *Accipiter gentilis* during the breeding season in Vendsyssel, Denmark

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(Med et dansk resumé: Duehøgens fødevalg i yngletiden, Vendsyssel 1977-1997)

Introduction

Population densities of raptors are often limited by food availability (see review by Newton 1979), which also influences the breeding success (e.g. Newton & Marqiuss 1981, Wiehn & Korpimäki 1997). Thus, like in many other avian groups (Martin 1987), food supply is one of the main factors influencing the ecology of raptors. Knowledge of prey selection of a species is therefore important in understanding its ecology.

Since the early 1970s members of the Danish Raptor Research Group, a study group under the Danish Ornithological Society, have conducted long term field studies on several raptor species (see Jørgensen 1989). As part of this work, JTN has collected data on the prey selection of Goshawks *Accipiter gentilis* in Vendsyssel since 1977. The aim of this paper is to describe the diet of the Goshawk in that area and analyse the annual and spatial variation in prey selection. Data from the first nine years of the study have been published previously (Nielsen 1986). In this paper the number of prey species is considered, but not their biomass, since the focus will be on the prey selection of Goshawks and not their nourishment.

Methods

The study area covered 2417 km² of Vendsyssel, Denmark, which was monitored by JTN for breeding Goshawks each year during 1977-1997. Based on marked heterogeneity in habitat and landscape type the study area was divided into eight subregions: (1) The dune plantations of the northern part of Jutland. (2) The forests around Frederikshavn and north of Sæby. (3) The east coast of Vendsysel from Sæby to Aså. (4) The east coast from Aså to Hals. (5) Hammer Bakker. (6) Jyske Ås with hilly moraine country. (7) The area approximately between Tolne and Hjørring and north of Øster Vrå. (8) The western part of Vendsyssel. A detailed description of the different subregions and their demarcation is given in Nielsen & Drachmann (in press).

During the breeding season (March-July) JTN visited all known Goshawk territories within the study area and identified and counted prey remains at the nest and at plucking sites within 100-150 m from the nest. Prey items were recorded in all territories from the onset of breeding until the fledglings had left the nest site, or the nest had been abandoned. Depending on the occurrence of

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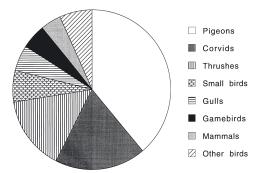


Fig. 1. Percentages of the eight main prey groups killed by Goshawks in Vendsyssel during the breeding season (means for 1977-1997).

Den procentvise fordeling af otte grupper af byttedyr taget af Duehøg i Vendsyssel i yngletiden (gennemsnit for 1977-1997). Pigeons: duer; Corvids: kragefugle; Thrushes: drosler; Small birds: småfugle; Gulls: måger; Gamebirds: hønsefugle; Mammals: pattedyr; Other birds: andre fugle.

young, two to six visits were made per nest site. Prey remains in the nests were recorded when the young were banded, and again 2-3 weeks after the fledglings had left the nest. Prey remains used to identify the prey species included feathers, hairs, breast bones, skulls and feet. For each item found, date of collection, species, quantity and approximate date of killing were recorded. Whenever possible, birds were aged as full-growns, fledglings or nestlings, according to the stage of development of the flight and tail feathers. Hawk pellets found in the study area were often of limited use, because they mainly consisted of greyish feather fragments which were difficult to identify, and bones more or less digested. However, bone fragments (mainly from mammals) and identification rings from domestic pigeons were found in fairly large numbers in the hawk pellets. In total, 20937 items representing at least 19670 prey animals were identified from 953 Goshawk breeding attempts.

Data analysis

When remains of a particular prey species were found both in the nest and on plucking sites on the ground it could be difficult to decide whether the remains were from one or more individuals. Therefore, all potential doubles were excluded. Data from 1987 could not be included in the analyses, since no standardised recording of prey remains were conducted that year.

The prey species were subdivided into eight taxonomic groups (Fig. 1), and the proportion of

each prey group taken by Goshawks per year calculated. Simple linear regressions of arcsine transformed prey proportion on year were performed for each prey group to investigate whether there were any trends in the prey proportions taken during the study period. To test if there was any association between the different prey proportions taken each year, a Pearson correlation matrix of the annual prey proportions of each prey group was constructed. To control for annual trends in the proportions of prey taken, the residuals from the regressions of prey proportion on year were used to construct the correlation matrix.

To test if the mean proportion of each prey group varied significantly between the subregions Friedman's nonparametric analysis of variance was performed on each prey group. Subregion 5 had to be excluded from this analysis, since only 1-3 Goshawk pairs bred there each year and few prey items were recorded. Likewise, the years 1977-1979 were excluded from this analysis, since too few prey items were found in these years.

All statistical tests were performed according to standard procedures (Zar 1996) with a 5% significance level.

Results

A total of 89 bird and 16 mammal species were identified as Goshawk prey during the breeding season. Divided into eight taxonomic groups (Fig.

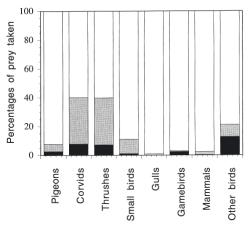


Fig. 2. The percentage of nestlings (black), fledglings (grey) and full-grown birds (incl. juveniles; white) within each of the eight prey groups.

Den procentvise andel redeunger (sort), flyvefærdige unger (gråt) og udvoksne fugle (incl. juvenile; hvidt) i byttedyrgrupperne. Vedr. grupperne, se Fig. 1.

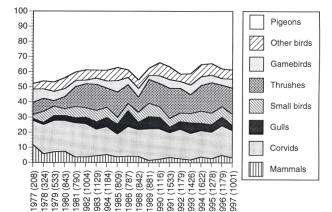


Fig. 3. Annual variation in the proportion (%) of the different prey groups. The number of prey items recorded each year is indicated in brackets.

Den årlige variation i andelen af de forskellige byttedyrgrupper (%) (jf. Fig. 1). Antal byttedyr registreret hvert år er angivet i parentes.

- 1) the prey species were, in descending order of frequency:
- 1) Pigeons (Columbidae), constituting 40% of all prey items identified, were mostly domestic pigeons *Columba livia* (53% of pigeons) and Wood Pigeons *Columba palumbus* (42%). Most pigeons were full-grown (92%, Fig. 2).
- 2) Corvids (Corvidae) constituted 19% of all prey items, the three most important species being Jay *Garrulus glandarius* (52%), Magpie *Pica pica* (34%) and Crow *Corvus corone* (12%). A large proportion of the corvids were taken as fledglings (32%, Fig. 2).
- 3) Thrushes (Turdidae), constituting 14%, were mainly Blackbirds *Turdus merula* (56%), Song Thrushes *Turdus philomelos* (22%) and Mistle Thrushes *Turdus viscivorus* (14%). As in corvids, a large proportion were fledglings (33%, Fig. 2).
- 4) Small birds (passerines other than corvids and thrushes) made up 7% of the diet, with Starling *Sturnus vulgaris* (47%) and Skylark *Alauda arven*-

Tab. 1. Regression coefficients (b) and significance levels (p) for arcsine transformed prey proportions regressed against year.

Regressionskoefficienter (b) og signifikansniveauer (p) ved regression af arcsin-transformeret byttedyrsandel mod årstal.

Prey category	b	p
Pigeons Duer	-0.65	0.002
Corvids Kragefugle	-0.24	0.30
Thrushes Drosler	0.66	0.002
Small birds Småfugle	0.44	0.06
Gulls Måger	0.44	0.05
Gamebirds Hønsefugle	-0.13	0.58
Mammals Pattedyr	-0.67	0.001
Other birds Andre fugle	0.35	0.13

- sis (25%) being the predominant species. Most small birds were taken as full-growns, with only 10% being fledglings (Fig. 2).
- 5) Gulls (Laridae), constituting 5% of the prey, were predominantly Black-headed Gulls *Larus ridibundus* (86%). No gulls were taken as nestlings and less than 1% as fledglings (Fig. 2).
- 6) Gamebirds (Phasianidae) constituted 5% of the Goshawk diet, of which Partridge *Perdix perdix* (58%) and Pheasant *Phasianus colchicus* (33%) were the most important species. The majority of the gamebirds were taken as full-growns (97%, Fig. 2).
- 7) Mammals made up only 4% of the prey; 34% of the mammals were squirrels *Sciurus vulgaris*, 20% brown hares *Lepus capensis*, and 42% rodents other than squirrels (mice, rats). The largest mammals killed were hares and a single domestic cat *Felis catus*, but judged from the size most hares were young animals, as was the cat.
- 8) Other bird species, constituting 6%, were grebes (Podicipedidae, 1), herons (Ardeidae, 1), ducks (Anatidae, 157), raptors (Accipitridae and Falconidae, 254), rails (Rallidae, 98), waders (Charadriidae and Scolopacidae, 299), cuckoos (Cuculidae, 10), owls (Strigidae, 170) and woodpeckers (Picidae, 183).

The proportion of each of these prey groups fluctuated between years (Fig. 3). However, only three of the prey groups showed a significant trend over the 21 years of study, with the proportion of pigeons and mammals declining and the proportion of thrushes increasing (Tab. 1).

One might expect that the prey groups would tend to correlate negatively, since a disproportionately high frequency of one prey group in any year necessarily means fewer of the other groups combined. From Tab. 2 it appears that there was

Tab. 2. Pearson correlation matrix showing the relationship between the eight different prey groups. The values used in the correlations were the residuals from prey group on year regressions.

Korrelationsmatrix visende de indbyrdes korrelationskoefficienter mellem de otte byttedyrgrupper. Som den enkelte byttedyrgruppes andel er anvendt residualerne fra den lineære regression af andel mod årstal (jf. Tab. 1).

	Gamebirds	Gulls	Pigeons	Corvids	Thrushes	Small birds	Mammals
Gulls <i>Måger</i> Pigeons <i>Duer</i>	-0.395 0.428	-0.442					
Corvids Kragefugle	-0.725***	0.205	-0.085				
Thrushes Drosler	-0.377	0.098	-0.739***	-0.168			
Small birds Småfugle	-0.550*	0.029	-0.272	0.466*	0.136		
Mammals Pattedyr	0.569**	-0.511*	0.430	-0.394	-0.384	-0.519*	
Other birds Andre fugle	0.108	0.221	-0.502*	-0.200	0.173	-0.001	-0.151

^{*} p < 0.05; ** p < 0.01; *** p < 0.001

indeed a significantly negative correlation between several prey groups, especially between corvids and gamebirds and between thrushes and pigeons. However, positive correlations were found between small birds and corvids and between gamebirds and mammals.

The proportion constituted by each prey group within seven of the eight subregions for the years 1980-1997 appears from Fig. 4. There was a significant difference in the mean proportion taken per subregion for all eight prey groups (Friedman test with df = 6: Pigeons: χ^2 = 38.1, p < 0.0001; Corvids: χ^2 = 25.2, p < 0.0003; Thrushes: χ^2 = 23.0, p < 0.0008; Gulls: χ^2 = 57.0, p < 0.0001; Small birds: χ^2 = 28.0, p < 0.0001; Gamebirds: χ^2 = 55.5, p < 0.0001; Mammals: χ^2 = 16.0, p < 0.05 and Other birds: χ^2 = 25.2 p < 0.0003).

Discussion

Three types of bias were likely in the collected material of prey remains. First, large or pale prey items (such as gulls and pigeons) may be more easily discovered or last longer than pluckings from small birds and mammals. Second, small prey species may be swallowed whole, leaving only few or no remains. The frequency of small prey species would hence be underestimated in studies based on prey remains, an effect that was confirmed in a recent Norwegian study (Nygård et al. 1998). Third, prey found near active Goshawk nests may not be representative for the diet in general of full-grown Goshawks in the area. More than 50% of all first-year females and 30% of the second-year females in the study area did not breed (own unpubl. data), and during the breeding season non-breeders could be expected to kill a larger proportion of large prey than breeding birds because females take larger prey than males (Opdam 1975, Ziesemer 1983), and during the incubation and early chick stages breeding females do not hunt (Holstein 1942). So the data presented here only represent the prey selection of breeders and are likely to underestimate small prey.

Despite the wide range of prey species taken, relatively few species emerged as really important. The five most frequent prey species (domestic pigeon, Wood Pigeon, Jay, Blackbird and Magpie) provided 63% of all items, and among prey groups pigeons, corvids and thrushes constituted 73%. Inexperienced fledgling birds would be expected to be highly vulnerable to predators, but 80% of all birds were taken as full-growns and only 15% as fledglings and 5% as nestlings (Fig. 2), although the proportion of nestlings probably is underestimated due to the effects mentioned above. Only fledglings of corvids and thrushes were common, constituting 32% of all corvids and 33% of thrushes. For Jay and Mistle Thrush more than 40% of the individuals killed by Goshawks were fledglings. However, a large proportion of the prey classed as full-grown (based on wing and tail feathers) may actually have been juveniles, so the predation on young individuals was probably much more marked than apparent from Fig. 2. In the Starling – where full-grown juveniles can be distinguished from adults by the colour of the flight feathers - 81% of all individuals taken were

Since gamekeepers often kill Goshawks near gamebird rearing pens, it was interesting to examine the proportion of gamebirds in the hawk diet. Over the 21 years of study only 309 Pheasants and 544 Partridges (less than 5% of the prey items) were recorded killed by Goshawks during the

breeding season. Without knowing the number of Pheasants and Partridges in the study area, it was not possible to estimate the proportion that was predated, but it was probably no more than a few percent. However, in other parts of Denmark where the release of Pheasants and other gamebirds is more widespread than in Vendsyssel, gamebirds may constitute a larger proportion of the Goshawk diet, since the hawks tend to prey on the most abundant prey species (see below). Outside the breeding season the Goshawk may also be a more important predator on gamebirds in Vendsyssel. Inexperienced yearling Goshawks with poor hunting skills are likely to be attracted by concentrations of gamebirds at rearing pens, and during winter, when food is often scarce, adult Goshawks may also be expected to take more gamebirds. That people keeping pigeons in Vendsyssel consider the Goshawk a pest also during the breeding season may be justified by the high proportion of domestic pigeons (21%) in the diet according to our results. For a thorough discussion of Goshawk predation on domestic pigeons in the study area, see Nielsen (1998).

The proportion of the different prey groups fluctuated between years (Fig. 3). In years with few pigeons killed, the Goshawks preyed more heavily on thrushes and "other birds", and in years with few corvids and "small birds" a larger proportion of gamebirds was found (Tab. 2). The strong negative relationships found between pigeons/thrushes ($r^2 = 0.55$) and corvids/gamebirds ($r^2 = 0.53$) indicate that these prey groups were truly complementary, possibly reflecting overlapping habitat use within these pairs of prey groups. Corvids and gamebirds often live in the same kind of habitat, and at least Wood Pigeons live in similar habitat as the thrushes, while domestic pigeons to some extent share its habitat with the Blackbird. Overlapping habitats may also explain why positive correlations were found between corvids/small birds and gamebirds/mammals, since small birds and mammals constituted only small proportions of the diet and may have been killed opportunistically of Goshawks hunting for corvids and gamebirds, respectively.

Several other studies have been conducted on the diet of the Goshawk in Europe (Uttendörfer 1952, Opdam et al. 1977, Lindén & Wikman 1983, Ziesemer 1983, Bezzel et al. 1997, Nygård et al. 1998). These studies show geographical variation in the main prey types selected, e.g. tetraonids and thrushes in Finland (Lindén & Wikman 1.c.) and thrushes and pigeons in Germany (Bezzel et al.

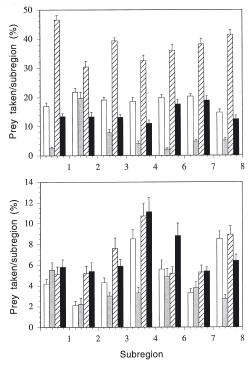


Fig. 4. Percentages of prey groups in seven of the eight subregions of the study area (means for the years 1980-1997). Top: Corvids (white), gulls (grey), pigeons (hatched), thrushes (black). Bottom: Gamebirds (white), mammals (grey) small birds (hatched), other birds (black).

Byttedyrgruppernes andel (%) i de forskellige delområder (gennemsnit for 1980-1997). Øverst: Kragefugle (hvidt), måger (gråt), duer (skraveret), drosler (sort). Nederst: Hønsefugle (hvidt), pattedyr (gråt), småfugle (skraveret), andre fugle (sort).

l.c.). Even on the small geographical scale of this study, the diet differed significantly in composition between subregions (Fig. 4), paralleling differences in local prey abundance. The frequency of gulls in the diet of Goshawks exemplifies this, since gulls constituted 20% of the prey in subregion 2 (Fig. 4) on the east coast of Vendsyssel, where 20 000 pairs of Black-headed Gulls breed on the adjacent Hirsholmene (Olsen 1992). In no other subregion did gulls constitute more than 8% of the diet. Likewise, gamebirds were most frequent as prey in subregions 4 and 8 (Fig. 4) which exhibited the best gamebird habitats, i.e. large agricultural areas and small forests with extensive forestry. Thus, even though the Goshawks predominantly preyed upon pigeons, corvids and thrushes, they apparently hunted more or less opportunistically for the most abundant species within the size range from Blackbirds to Wood Pigeons.

Acknowledgments

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Resumé

Duehøgens fødevalg i yngletiden, Vendsyssel 1977-1997

Rester af Duehøgens Accipiter gentilis bytte i yngletiden blev indsamlet af JTN i Vendsyssel 1977-1997, i alt 19670 forskellige byttedyr fra 953 yngleforsøg, fordelt på 89 fuglearter og 16 pattedyrarter. De fem mest hyppige var Tamdue, Ringdue, Skovskade, Solsort og Husskade, som tilsammen udgjorde 63%. Duer udgjorde 40%, kragefugle 19% og drosler 14% af Duehøgens bytte, eller tilsammen 73% (Fig. 1). Kun blandt kragefuglene og droslerne så nyudfløjne unger ud til at være vigtige (Fig. 2), men generelt udgjorde juvenile sandsynligvis en stor andel. Hos Stæren, hvor juvenile kan skelnes fra adulte på svingfjerenes farve, var hele 81% af de "fuldvoksne" individer blandt bytteresterne således juvenile. Fordelingen mellem de forskellige byttedyrgrupper svingede en del fra år til år (Fig. 3). En korrelationsanalyse (Tab. 2) viste blandt andet, at i år, hvor Duehøgene tog færre duer, tog de forholdsvis flere kragefugle og "andre fugle", mens i år hvor færre kragefugle og småfugle blev taget, tog høgene forholdsvis flere hønsefugle. Ligeledes var der forskelle i den relative andel, de forskellige byttedyrgrupper udgjorde i de enkelte delområder i undersøgelsesområdet (Fig. 4). Således blev der taget langt flest måger i delområdet på Vendsyssels østkyst ud for Hirsholmene, hvor 20000 par Hættemåger yngler. Duehøgene i Vendsyssel var således mere eller mindre opportunistiske og jagede de lokalt mest almindelige fuglearter i størrelsesspektret fra Solsort til Ringdue.

References

- Bezzel, E., R. Rust & W. Kechele 1997: Nahrungswahl südbayerischer Habichte *Accipiter gentilis* während der Brutzeit. Orn. Anz. 36: 19-30.
- Holstein, V. 1942: Duehøgen. H. Hirschsprungs Forlag. Jørgensen, H. E. 1989: Danmarks Rovfugle. – Frederikshus, Danmark.
- Lindén, H. & M. Wikman 1983: Goshawk predation on Tetraonids: availability of prey and diet of the predator in the breeding season. – J. Anim. Ecol. 52: 953-968
- Martin, T. E. 1987: Food as a limit on breeding birds: A life-history perspective. Ann. Rev. Ecol. Syst. 18: 453-487
- Newton, I. 1979: Population Ecology of Raptors. T&AD Poyser: Calton.
- Newton, I. & M. Marqiuss 1981: Effect of additional food on laying dates and clutch sizes of Sparrowhawks. – Ornis Scand. 12: 224-229.
- Nielsen, J. T. 1986: Duehøgen i Vendsyssel 1977-85. -Accipiter: 133-174.
- Nielsen, J. T. 1998: Duehøgens prædation på Brevduer i Vendsyssel. – Dansk Orn. Foren. Tidsskr. 92: 327-332.
- Nielsen, J. T. & J. Drachmann in press: Development and productivity in a Danish Goshawk *Accipiter gentilis* population. Dansk Orn. Foren. Tidsskr.
- Nygård, T., D. J. Halley, B. Wiseth, S. Grønnesby & P. M.Grønlien 1998: Hva skjer med hønsehauken? Foreløpige resultater fra et forskningsprosjekt om hønsehaukens arealkrav, næring, dødsårsaker og vandringer. Vår Fuglefauna 21: 5-10.
- Olsen, K. M. 1992: Danmarks Fugle en oversigt. Dansk Ornitologisk Forening.
- Opdam, P. 1975: Inter- and intraspecific differentiation with respect to feeding ecology in two sympatric species of the genus *Accipiter*. – Ardea 63: 30-54.
- Opdam, P., J. Thissen, P. Verschuren & G. Müskens 1977: Feeding ecology of a population of Goshawk Accipiter gentilis. – J. Orn. 118: 35-51.
- Uttendörfer, O. 1952: Neue Ergebnisse die Ernährung der Greifvögel und Eulen. Ulmer, Stuttgart.
- Wiehn, J. & E. Korpimäki 1997: Food limitation on brood size: experimental evidence in the Eurasian kestrel. – Ecology 78: 2043-2050.
- Zar, J. H. 1996: Biostatistical analysis. Prentice Hall, New Jersey.
- Ziesemer, F. 1983: Untersuchungen zum Einfluss des Habichts (*Accipiter gentilis*) auf Populationen seiner Beutetiere. – G. Hartmann, Kronshagen.

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