Development and productivity in a Danish Goshawk *Accipiter gentilis* population

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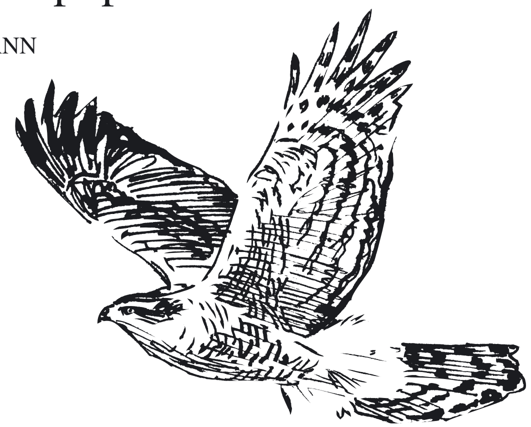


(Med et dansk resumé: Populationsudvikling og ungeproduktion hos Duehøgen i Vendsyssel)

Introduction

The Goshawk *Accipiter gentilis* population in Denmark was, like in other European countries (Kalchreuter 1981), seriously decimated during the first half of the century due to heavy human persecution (Paludan 1967) and, possibly, also due to environmental pollutants (Dyck 1972). However, after the legal protection of Danish Goshawks in 1967 and a reduction in the use of environmental pollutants during the 1970s, the population of breeding Goshawks in Denmark started to increase (Jørgensen 1989). Since the beginning of the 1970s the Danish Raptor Research Group, a study group under the Danish Ornithological Society, has been monitoring raptor populations in various parts of Denmark (Jørgensen 1989). One of the most intensively studied species has been the Goshawk (Storgaard & Birkholm-Clausen 1983, Nielsen 1986, Laursen 1987).

Here we present data from a long term study in Vendsyssel, where JTN during 1977-1997 collec-ted data on Goshawk population development and breeding performance. Data from the first nine years of the study has been published previously (Nielsen 1986). The aim of this paper is to present and analyse the population development, productivity, and female age at first breeding of the Goshawks during the last 21 years, with a discussion in relation to regional differences within the study area.

Methods

Study area

The study was conducted in Vendsyssel, Denmark, where each year during 1977-1997 JTN monitored all potential forests for breeding Goshawks in an area covering 2417 km^2 (Fig. 1). The study area was divided into eight subregions according to the general landscape, soil quality, forest type and forestry as follows: (1) The northern dune plantations with coniferous forests on poor sandy soils. State forests with slow-growing trees and intensive forestry. (2) Mainly deciduous forests with extensive forestry on hilly moraine country. (3) The forests in the northern part of this subregion were mainly coniferous forests on poor soil, while those in the southern part predominantly were deciduous forests on rich soils. There was intensive forestry in the entire subregion. (4) Primarily small deciduous forests on elevated sea bed, with extensive forestry. (5) Hammer Bakker; one large coherent coniferous forest on poor sandy soil, with intensive forestry. (6) Very hilly moraine country, primarily coniferous forests on rich soils with intensive forestry. (7) Hilly moraine with soils of varying quality, mainly coniferous forests with intensive forestry. (8) Mostly small scattered coniferous plantations rarely exceeding 25 ha, extensive forestry.

The forests in subregion 2 to 8 were all private forests. The size of each subregion and the proportion covered in forest were calculated in the programme Arcview by Ib Krag Pedersen (National Environmental Research Institute), and are given in Tab. 1. Taken as a whole 8.4% of the study area was covered in forest.

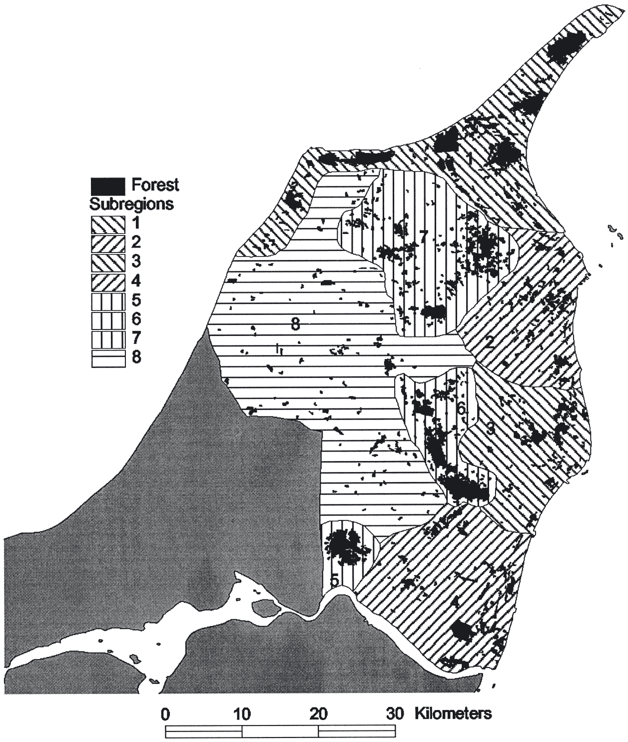
Breeding censuses

Time spent assessing individual forest stands each year varied from as little as 15 min to as much as several days per site, depending on the activity of breeding birds. If adult birds were not present at the previous year's nest or known alternate sites,

Tab. 1. Characteristics of the eight subregions. Breeding density, nest success and proportion of 2y females among the breeders are shown as mean (range) for 1977-1997, while brood size is presented as mean ± s.e. of all nests (uppermost) and of successful nests only (lowermost). The estimated number of available breeding territories in the 1990s is also shown. The annual variation in population size in each subregion is shown in Fig. 3.
Delområdernes størrelse og skovdække, samt yngletæthed, ynglesucces, kuldstørrelse og andelen af ét-årige (2K) blandt de ynglende hunner. Yngletæthed, ynglesucces og andel ét-årige hunner er angivet som gennemsnit (variationsbredde) for 1977-1997, mens ungeproduktion er gennemsnit ± s.e. dels for det totale antal reder (øverst), dels for de vellykkede yngleforsøg (nederst). Desuden er antallet af potentielle yngleterritorier i 1990-97 angivet.

Subregion *Delområde*	No. of potential territories *Potentielle territorier*	Area *Areal* km^2	Forest *Skov* pct	Pairs per km^2 forest *Par pr km^2 skov*	Successful nests *Vellykkede yngleforsøg* pct	Mean no. of young/brood *Kuldstørrelse*	Proportion 2K females among breeders (%) *Andel 2K hunner (%)*
1	17-19	347	17.8	0.12 (0.03-0.21)	62.9 (25-88)	1.82 ± 0.12 2.75 ± 0.10	12.1 (0-40)
2	11-13	230	6.4	0.24 (0.07-0.40)	80.7 (25-100)	1.93 ± 0.21 2.63 ± 0.14	7.9 (0.50)
3	11-16	231	6.6	0.38 (0.20-0.47)	71.7 (29-100)	1.85 ± 0.14 2.59 ± 0.10	11.7 (0-43)
4	13-16	325	7.2	0.30 (0.13-0.39)	62.0 (33-100)	1.50 ± 0.13 2.51 ± 0.10	12.3 (0-43)
5	3	55	23.6	0.15 (0.08-0.23)	61.7 (0-100)	1.89 ± 0.27 2.92 ± 0.20	10.0 (0-100)
6	15-16	134	23.0	0.30 (0.19-0.35)	65.1 (44-100)	1.62 ± 0.11 2.50 ± 0.08	12.7 (0-43)
7	22-25	312	10.3	0.37 (0.28-0.53)	62.2 (38-87)	1.60 ± 0.09 2.49 ± 0.07	17.8 (0-58)
8	19-21	782	1.6	0.55 (0.15-1.00)	55.8 (33-80)	1.36 ± 0.13 2.55 ± 0.10	37.5 (0-75)

Fig. 1. The study area in Vendsyssel, Denmark, with forest stands and the demarcation of the eight subregions indicated.
Undersøgelsesområdet i Vendsyssel med de enkelte skove og delområdernes afgrænsning indtegnet.



an extensive search for a new nest was conducted. Early in the breeding season Goshawks were relatively easy to discover due to their vocal activity near the nest site, and their intense response to playback of conspecific calls (Kennedy & Stahlecker 1993). Therefore, based on the intensive nest survey combined with the use of playback in the early part of the breeding season, it was assumed that 95-100% of all breeding attempts within the study area were recorded each year. All potential breeding habitats were visited 2-6 times per year, depending on the occurrence and outcome of the given breeding attempts. To reduce disturbance at the nest sites, and owing to the large number of Goshawk territories to be monitored every year, clutch sizes were not recorded. Nest trees with successful nests were climbed when the nestlings were ringed at an age of 14-30 days, and these nests were revisited later to record the number of fledged young. A breeding attempt was defined as a pair of Goshawks displaying territorial behaviour and nest building, and the productivity of each breeding attempt was measured as the number of fledged young.

Based on the characteristics of shed flight feathers found near the nesting sites breeders could be aged according to calendar year as 2y, 3y, and 4y+ (Opdam & Müskens 1976, Kühnapfel & Brune 1995, Rust & Kechele 1996). It was not possible to distinguish 4y birds from older individuals. Female Goshawks are known to display high site fidelity after they have started to breed (Ziesemer 1983), i.e., the majority stay in the same forest throughout their reproductive life. Therefore, females were assumed to have started breeding in the first year they were found at a nest within the study area, if they had not previously been found breeding elsewhere. Breeding males were difficult to age since they shed their flight feathers over a wide area, whereas females shed them at the nest site during incubation. Therefore, the age at first breeding could only be determined for females.

Statistical analyses

The number of young produced per nest was known for 89-100% of all nests recorded in a given year during the study period, except for 1977 (the first year of study) and 1987, when JTN did not monitor the number of fledged young himself. In 1977 and 1987 the number of fledglings produced per nest were known with certainty only in 42% and 62% of the nests recorded, respectively. These two years were therefore excluded from the statistical analyses of the variation between subregions and years in nest success, productivity and proportion of 2y females among breeders. Subregion 5 was also excluded from these analyses, since only one to three breeding attempts occurred per year within this subregion (Fig. 3). The variation in nest success and the proportion of 2y females were analysed by logistic regression models, while two-way analysis of variance was used to test the variation in productivity. All statistical tests were performed according to standard procedures (Zar 1996), using a 5% significance level.

Results

The population of Goshawks within the study area increased from 31 breeding pairs in 1977 to 63 in 1997 (Pearson correlation: r = 0.93, n = 21, P < 0.0001), with a maximum of 72 breeding pairs in 1994 (Fig. 2); the breeding density within the study area hence increased from 1.28 breeding pairs per 100 km^2 in 1977 to 2.98 pairs per 100 km^2 in 1994. With forest covering 8.4% of the study area this corresponds to 0.15 breeding pairs/km2 forest in 1977 and 0.35 pairs/km^2 forest in 1994. From the structural characteristics of forest stands selected by the Goshawks for nesting we estimated that the number of potential breeding territories within the study area increased from 86 in 1977-1982 to 111-128 in 1993-1997, due to the maturation of forests during the study period. The cumulative number of different territories occupied in 1977-1997 is indicated in Fig. 2.

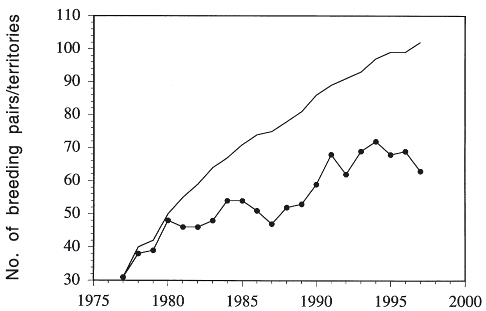


Fig. 2. Population development during the 21 years of study, shown as the number of breeding pairs per year. The solid line indicates the cumulative number of territories occupied 1977-1997.
Populationsudviklingen (antal par) hos Duehøgen i Vendsyssel gennem 21 år. Den øverste linie viser det kumulative antal territorier besat 1977-1997.

In Fig. 3 the population development within the eight subregions is shown, together with the cumulative number of territories occupied in each subregion. The present number of potential breeding territories within each subregion is shown in Tab. 1. The mean density of breeding Goshawks per 100 km^2 varied significantly between the eight subregions (Kruskal Wallis one-way anova: H = 126.3, df = 7, P < 0.0001), with the lowest breeding density in subregion 8, due to the small area covered by forest in this subregion.

The number of fledglings produced per nest was recorded for a total of 1080 nests. 80 nests produced only one young, 219 nests produced two, 305 nests produced three, and 86 nests raised four young in a single brood. A large proportion (390 nests) failed to raise any young. The annual variation in nesting success (Fig. 4) fluctuated between 54-56% (1984, 1996 and 1997) and 70-72% (1979, 1980, 1983, 1993 and 1994). The variation in nesting success among years and subregions was analysed by a logistic regression model. The likelihood-ratio revealed that both year and subregion had a significant effect on nest success ($\chi_1^2 = 9.34$, P < 0.05 and $\chi_6^2 = 23.68$, P < 0.001, respectively), and there was also a significant subregion-year interaction ($\chi_6^2 = 23.68$, P < 0.001). On average Goshawks breeding within subregion 8 had the lowest proportion of successful nests, while the highest proportion was found in subregion 2 (Tab. 1). Overall the average breeding success declined during the study period, but within subregions this trend was only apparent in subregion 2, 4 and 8. The logit model as a whole was likewise significant ($\chi_{13}^2 = 38.02$, P < 0.001), so subregion and year seemed to be adequate predictors of breeding success.

When including both successful and unsuccessful breeding attempts, the mean number of fledglings produced per nest was 1.66 ± 0.04 (SE). Considering only the nests producing one or more fledglings gave 2.58 ± 0.03 fledglings per successful nest. The annual variation in the number of young raised is shown in Fig. 4. The combined effects of year and subregion on the number of young raised per nest were analysed by two-way anova. A significant effect of subregion on the number of young produced per nest was apparent when all breeding attempts were included in the model (F = 2.39, df = 6, P < 0.05), with the lowest number of young being produced within subregion 8 (Tab. 1). However, there was no effect of year (F = 1.29, df = 18, P > 0.15) or any subregion-year interaction (F = 0.88, df = 108, P > 0.80).

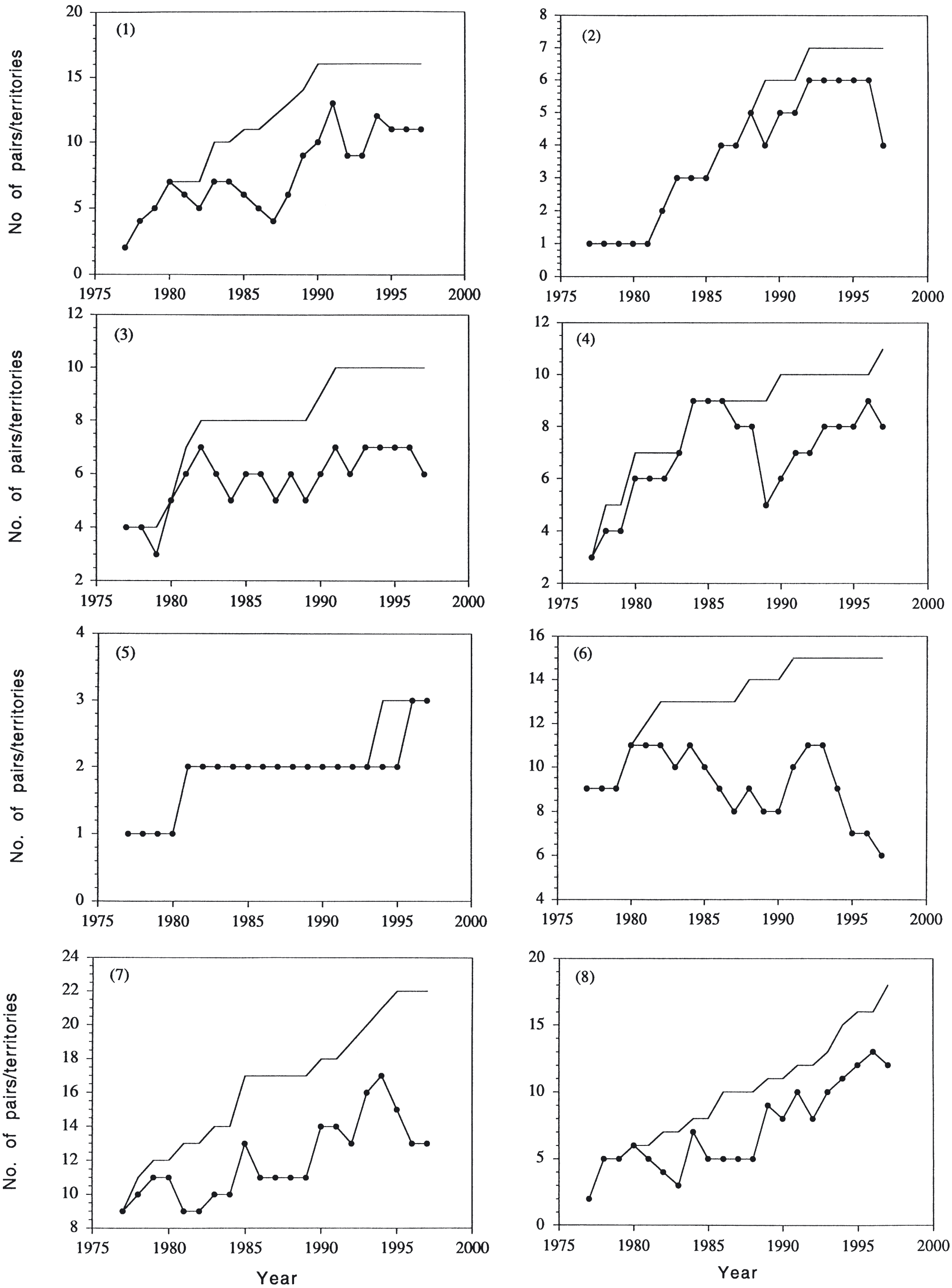


Fig. 3. The population development within the eight subregions (1-8) in 1977-1997. In each graph the solid line indicates the cumulative number of territories occupied during the study period.
Populationsudviklingen (par) i hvert af de otte delområder (1-8) fra 1977 til 1997. Den øverst linie i hver graf angiver det kumulative antal territorier besat 1977-1997.

The mean annual productivity for both the total number of nests and for the successful nests fluctuated considerably, apparently following a 4-5 year cycle (Fig. 4). When unsuccessful nests were excluded from analysis, the significant effect of subregion on the number of fledglings produced per nest disappeared ($F = 0.45$, df = 6, $P > 0.80$), and the effect of year and the subregion-year interaction remained non-significant ($F = 1.47$, df = 18, $P > 0.05$ and $F = 1.04$, df = 108, $P > 0.25$, respectively). Thus, the lower productivity within subregion 8 was due to a higher proportion of unsuccessful breeding attempts within this subregion.

The total number of young raised per year, calculated as the mean number of young raised per successful pair multiplied by the number of successful pairs, is shown in Fig. 5. There was a significant correlation between population size and the total number of young raised in the previous year (Pearson correlation: $r = 0.85$, $n = 20$, $P < 0.0001$, Fig. 6). However, according to Fig. 6 this relationship seemed to level off when the total annual production exceeded 100 young, indicating that the production of more than 100 young per year did not lead to a further increase of the population.

The age at first breeding was recorded for 312 females, of which 147 (47%) started to breed in their first year of life (2y), 104 (33%) in their second year (3y), and 61 (20%) in their third year or later (4y+). Thus, the majority of the breeding females in this population started to reproduce at an early age. A logistic regression model showed a significant variation in the proportion of 2y females among the breeders in the different years ($\chi_1^2 = 7.96$, $P < 0.005$), declining from 20-25% early in the study period (1978-1980) to only 5-10% in recent years (1995-1997). The analysis did not reveal any effect of subregion on the proportion of breeding 2y females ($\chi_6^2 = 9.39$, $P > 0.15$), although the proportion of 2y females was much higher in subregion 8 than in any of the other subregions. This absence of a significant effect of subregion was probably a consequence of a greatly varying proportion of breeding 2y females between years (Tab. 1). The subregion-year interaction was also non-significant ($\chi_6^2 = 9.31$, $P > 0.15$). However, the logit model as a whole was significant ($\chi_{13}^2 = 58.76$, $P < 0.0001$), indicating that year was a good predictor of the proportion of females breeding in their first year of life.

Discussion

When the Goshawk population in Vendsyssel levelled off in the mid 1980s, Jørgensen (1989) hypothesised that it had stabilised, but actually it continued to increase until the early 1990s, after which it has been fluctuating around 67 pairs (Fig. 2). The population size in a given year was positively associated with the total number of young produced in the previous year (Fig. 5), but apparently only until annual productivity exceeded 100 fledged young, as it did during the 1990s. This could indicate that the population size has reached an upper limit. However, the cumulative number of territories used (Fig. 2) and the estimated number of potential territories (111-128) showed that the population was not limited by lack of breeding habitat.

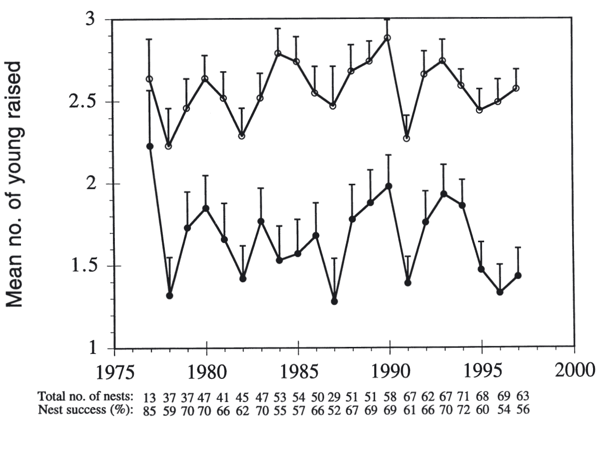


Fig. 4. Annual breeding performance of Goshawks in Vendsyssel 1977-1997 shown as the mean number (+ s.e.) of young raised per nest (filled dots) and per successful nest (open dots). Sample size and the percentage of successful nests per year are indicated below the graph.
Det gennemsnitlige antal unger (+ s.e.) produceret pr yngleforsøg (sorte prikker) og pr vellykket yngleforsøg (hvide prikker) i Vendsyssel 1977-1997. Tallene under årstallene er stikprøvestørrelse og andel af vellykkede yngleforsøg (%) de enkelte år.

A possible explanation of the population stagnation observed during the 1990s is that the high number of fledgling Goshawks triggered an increased persecution by humans. With more than 100 fledglings present in the study area, there would have been a relatively high predation pressure on both pigeons and gamebirds (see Nielsen & Drachmann (1999) for a description of the Goshawk diet in Vendsyssel), which might have elicited an increased human persecution. However, a similar population development was seen in the mid 1980s, possibly indicating that the dynamics of the Goshawk population in Vendsyssel is governed by intrinsic or extrinsic factors resulting in population cycles of approximately 10 years. Similarly, cycles of 4-5 years duration was seen for the number of young produced per nest (Fig. 4). Thus, cyclic population dynamics independent of human persecution could lay behind the observed population trends in our study population, in which case a further population increase may be expected until the carrying capacity of the study area is reached.

The mean of 2.58 fledged young per successful nest was similar to the number observed in several other European studies (Fischer 1980, Bühler et al. 1987, Bezzel et al. 1997). The proportion of nest failures (36%) was also fairly normal (cf. Fischer 1980, Selås 1997). Most nests failed due to natural causes (e.g. unfertilised eggs, predation, or young and inexperienced breeders), but 37% of them were caused by human disturbance, logging, egg or chick collection, or shooting (J. T. Nielsen unpublished data). Weather conditions may also influence the annual nest failure rate, since Goshawk nesting success has been shown to be correlated with the mean temperature in May (Kostrzewa & Kostrzewa 1990). The highest proportions of failed nests recorded in this study (44-46%) were caused by logging and clean-up after a storm in 1984, and by a combination of cold weather during May-June and human persecution in 1996 and 1997. The difference in nesting success found between subregions seemed mainly to be caused by regional differences in the proportion of breeding 2y females. The highest and lowest success rates were found in subregion 2 (81%) and 8 (56%), respectively, which simultaneously had the lowest (8%) and highest (38%) proportion of 2y females among the breeders (Tab. 1). Females breeding in their second calendar year have a much higher proportion of unsuccessful breeding attempts than older females (Nielsen 1986). However, even though the proportion of 2y females in the breeding population declined during the study period, there was no simultaneous increase in nesting success. On the contrary, overall there has been a decline in nesting success in recent years, possibly reflecting an increased human persecution.

Overall, 147 of 312 females (47%) started breeding in their second calendar year. This is an unusual high proportion compared to other European populations (Höglund 1964, Ziesemer 1983, Würfels 1994). The low number of 2y females among breeding Goshawks in Fennoscandia

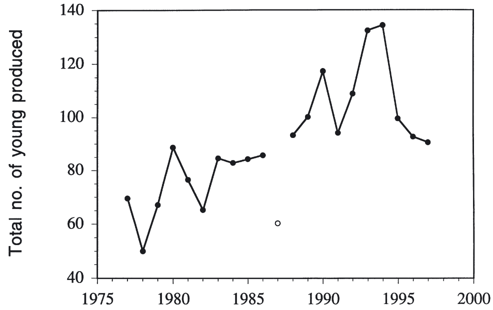


Fig. 5. Total number of young fledged per year in the study area. The young production in 1987 was probably underestimated.
Det totale antal flyvefærdige unger produceret pr år (tallet for 1987 er sandsynligvis et underestimat).

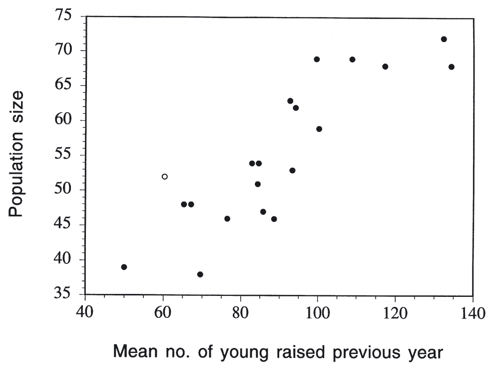


Fig. 6. The relationship between the population size in a given year and the total number of young raised in the previous year. The open dot indicates the year 1987 where the young production was probably underestimated.
Sammenhængen mellem bestandsstørrelsen i et givet år og ungeproduktionen i det foregående år. Den åbne cirkel angiver 1987, hvor ungeproduktionen formentlig blev underestimeret.

(Höglund 1964, Haukioja & Haukioja 1970, Marcström et al. 1990) has been associated with saturated breeding populations, and in Vendsyssel the proportion of breeding 2y females declined as the population size increased during the study period. In saturated breeding populations all good territories will be occupied by old and experienced females, leaving only the poorer breeding habitats for 2y females. The age at first breeding could not be estimated for males, but the age of breeding males was determined in 468 breeding attempts, of which 2y males constituted only 5%. Males are the principal food providers during the nesting season (Holstein 1942), so foraging experience is a prerequisite for successful nesting. The less experienced 2y males may be subject to a greater risk of accident while foraging, and may spend more energy on territorial establishment and defence than older males (Reynolds 1972), which may explain the absence of first-year breeding males in our study population.

When summarising the regional effects on Goshawk breeding performance, subregion 8 clearly was the area with the poorest breeding conditions (Tab. 1). This area was mainly agricultural land, and had the lowest forest coverage. The Goshawks breeding in the subregion were probably food limited to a higher extent than Goshawks in other subregions, since brood sizes of four were rarely encountered. Poor breeding conditions may also explain the high proportion of breeding 2y females in the subregion.

Acknowledgments

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Resumé

Populationsudvikling og ungeproduktion hos Duehøgen i Vendsyssel

Bestanden af Duehøg *Accipiter gentilis* i Vendsyssel blev fulgt nøje gennem 21 år fra 1977 til 1997 i et område dækkende 2417 km^2. Undersøgelsesområdet blev inddelt i otte delområder efter jordbonitet, landskabsform og skovtype (Fig. 1). Duehøgepopulationen voksede fra 31 par i 1977 til 72 par i 1994, hvor bestanden nåede et maksimum. Siden er bestanden gået tilbage, og i 1997 ynglede der kun 63 par (Fig. 2). Yngletætheden har således varieret mellem 1,28 par pr 100 km^2 i 1977 og 2,98 par pr 100 km^2 i 1994, svarende til mellem 0,15 og 0,35 par pr km^2 skov. Ungeproduktionen blev registreret i 1080 yngleforsøg, hvoraf 80, 219, 305 og 86 resulterede i henholdsvis én, to, tre og fire unger. De resterende 390 forsøg (36%) mislykkedes. De fleste af disse 0-kuld skyldtes naturlige årsager såsom ubefrugtede æg, prædation og uerfarne forældrefugle, men hele 37% skyldtes dog menneskelig aktivitet (forstyrrelse, skovning, beskydning, fjernelse af æg og unger). Andelen af mislykkede kuld varierede mellem de forskellige delområder (Tab. 1) og steg signifikant i løbet af undersøgelsesperioden. Den gennemsnitlige produktivitet var 1,66 unger pr yngleforsøg og 2,58 unger pr vellykket yngleforsøg (Fig. 4).

En stor andel af hunnerne i undersøgelsesområdet begyndte at yngle allerede i deres andet kalenderår (147 (47%) af 312 førstegangsynglende hunner, hvis alder var kendt). Andelen af 2K hunner i ynglebestanden faldt dog fra 20-25% til 5-10% i perioden 1977-1997, hvilket sikkert skyldtes den øgede bestandstæthed, som gav mindre plads til de uerfarne 2K fugle. Regionale forskelle i populationsudvikling, ungeproduktion og andelen af 2K fugle blandt de ynglende hunner præsenteres i Fig. 3 og Tab. 1.

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