

Population dynamics and lifetime reproductive success in Sparrowhawks *Accipiter nisus* in a Dutch-German study area

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ABSTRACT

This paper deals with a 23-years study of a Dutch-German Sparrowhawk population in a 100 km² forest area. In 1969 the population was nearly extinct due to the adverse effects of organochlorine pesticides. After the ban on organochlorines in 1968/1969 direct mortality decreased immediately, so that a population increase from 2 to 18 breeding pairs could be assessed between 1969 and 1973. Breeding success, however, did not recover before 1976. In 1977 a further population increase occurred, later followed by a stabilisation at approximately 50 breeding pairs. Annual fluctuations in breeding numbers were regulated by weather conditions in the winter. After severe winters yearlings bred in relatively small numbers, after extremely mild winters in relatively large numbers. The number of adult breeders was not affected by weather conditions in the winter.

Lifetime reproductive success (LRS) of 228 females revealed that (a) individual production ranged from 0 to 31 fledglings, (b) birds living from 1976 onwards raised on average twice as many fledglings during their life as those which lived prior to 1976 (6.7 and 3.5 fledglings respectively), (c) most of the variation in LRS is explained by variation in lifespan, and (d) overall, only 6% of all fledglings produced more than 50% of the total offspring. In comparison with Sparrowhawk populations in southern Scotland, females produced on average 20% more fledglings during their lifetime. This is unexpected, since annual survival of the Scottish adult females is about 10% higher. The difference in LRS may be explained by a higher proportion of successful nests and a larger mean brood size in the Dutch-German population.

INTRODUCTION

During the 1960s Sparrowhawk *Accipiter nisus* and other raptor populations in western Europe suffered from the adverse side-effects of organo-chlorine pesticides (Newton 1979, 1986). In the Netherlands during the late 1960s the use of dieldrin and related compounds for seed dressings resulted in mass mortality among birds of prey (Koeman *et al.* 1969). In the early 1970s the Dutch Sparrowhawk population recovered rapidly, after the banning of these compounds in 1968-69 (Opdam 1985; Opdam *et al.* 1987). The use of DDT, however, was not prohibited by the Dutch government until 1973. DDE causes embryo mortality and eggshell thinning resulting in frequent egg breakage (Ratcliffe 1970; Newton & Bogan 1974). Dutch Sparrowhawk populations were

contaminated by DDE, which caused a reduction in reproductive output (Koeman *et al.* 1972). The recovery in reproductive output of the Dutch Sparrowhawk population became apparent in the mid-1970s, although DDE residues remained at largely the same level from 1975 up to 1983 (Burgers *et al.* 1986, see also Fuchs & Thissen 1981). Opdam *et al.* (1987) discussed the presumed role of DDE as a main factor suppressing Sparrowhawk populations. They concluded that the onset of recovery must have been caused by decreased adult mortality (after disappearance of dieldrin), whereas DDE retarded only the recovery.

Lifetime Reproductive Success (LRS) is given by the total number of young raised by an individual during lifespan. It combines two key characteristics of individual performance, namely survival and annual breeding success, into a single overall measure of performance (Newton 1985, 1989). Furthermore, it provides a basis for estimating biological fitness (Clutton-Brock 1988; Newton 1989). This paper indicates the trend of a Dutch-German Sparrowhawk population during 1969-1991. The aim is to study the impact of pesticides and weather conditions during the winter. We have further examined the lifetime reproductive success of female Sparrowhawks, based on a sample of 228 individuals, which were identified from year to year by comparing shed feathers. The aims were: (1) to relate lifetime fledgling production by female Sparrowhawks to the birds' features, (2) to assess the impact of pesticides, resulting in suppressed reproductive output until 1977, on the LRS, and (3) to estimate the proportion of individuals that raised young, enabling us to assess the relative contribution from one generation to the next. Finally, differences in life history strategy between the Dutch-German Sparrowhawk population and Sparrowhawk populations in Britain, studied by Newton, will be discussed.

METHODS

Study area

The study was carried out in an extensive partly forested moraine complex area, between the towns of Nijmegen (The Netherlands), and Kleve and Goch (Germany), south of the river Rhine (51° 45' N and 6° E). There is a difference in altitude between the forested moraine (20 - 95 m above sea level) and its cultivated surroundings (10 - 20 m a.s.l.). Two isolated forests are found in the area, one of 40 km² on the Dutch side (Rijk van Nijmegen) of the frontier and another one of 60 km² on the German side (Reichswald). Conifer woods are prevalent (about 60% of surface) in the area over broad-leaved and mixed woods. Pine (*Pinus sylvestris*) is the most common tree species. Both forests and agricultural land are intensively managed. There are a number of medium-sized villages, mainly on the Dutch side, which are very attractive hunting grounds for the Sparrowhawk, because of the high density of song birds.

Population dynamics and breeding success

In order to find all breeding pairs, the woods were searched systematically every year during springtime for prey remains, droppings, shed feathers and nests. Only breeding pairs in which the female laid at least one egg were counted as breeders. Reliable data concerning non-breeders could not be obtained. Each nest was visited at least thrice during the breeding season in order to collect data on clutch size, brood size at hatching and fledging, and the cause of failure in those cases in which a pair was not successful. From 1978 onwards, the young were ringed when they were between one and three weeks old. Breeding success was measured as the mean number of fledglings in successful nests.

Recognition of individuals and lifetime reproductive success

Sparrowhawks moult each year in summer, overlapping extensively with breeding (Newton 1986). The shed feathers are a useful tool to identify individuals in the field without the need to catch the birds. Opdam and Müskens (1976) proposed the use of shed feathers to identify individual Sparrowhawks. Newton (1986) in Britain and Van Diermen (*pers. comm.*) in the Netherlands were able to check the method's reliability with known ringed birds. Using shed feathers turned out to be a reliable method.

Shed feathers of each female were collected annually during the breeding season. Since males hunt during the entire breeding season, they moult more slowly than females. So less male than

female shed feathers were found.

Age and sex of the bird which shed the feathers are easily distinguished by length (females are larger than males) and by the differences in pattern and colour (Figure 1). The basic pattern - irrespective of age - is one of dark bars alternating with light bars on the inner vane. In yearling plumage the feathers are light reddish brown (greyish on the photograph), unlike the deep brown feathers of adults. Further characteristic details are the marked white patches on the shaft of the central tail feather and the pale edge on the top of the secondary coverts in yearlings' plumage.

After the first year of life, each bird shows a consistent feather pattern each year. This is illustrated by the first and fifth primary of an individual, collected in different years (Figure 2). The equivalent primaries of an individual are very similar in both pattern and length each year.

The equivalent primaries of different individuals differ (a) in number and shape of the dark bars, (b) in the pattern of the light bars, and (c) in length (Figure 3).

A few remarks must be made concerning the method of calculating Lifetime Reproductive Success (LRS). First, LRS could only be calculated for females, because insufficient material (shed feathers) was available to identify males in subsequent years. Secondly, the following selection criteria were used: (1) breeding performance of females had to be known precisely for their entire lifetime, (2) individuals that started breeding after 1989 were excluded (identification took place until 1992), (3) individuals not identified as a breeding bird for two years or more were taken to be dead.

Thirdly, identification of individuals between their yearling and adult plumage is disputable (there are more comparisons possible). For this reason LRS is based only on breeding performance during adulthood. This means that LRS was underestimated for certain individuals (see also discussion).

Figure 1. Shed feathers of yearling and adult female Sparrowhawks. From left to right (yearlings and adults, respectively): fifth primaries, central tailfeathers, secondaries, and two pairs of secondary coverts.

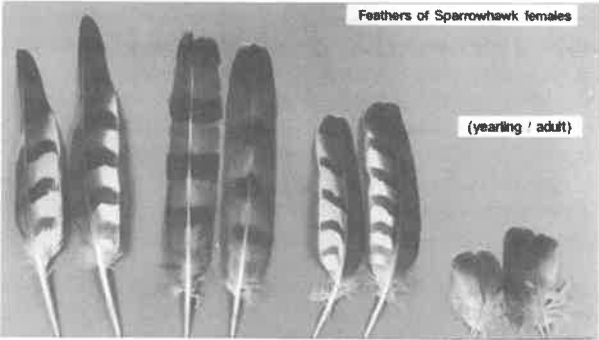


Figure 2. First and fifth primary of the same female showing that equivalent primaries are identical in different years.

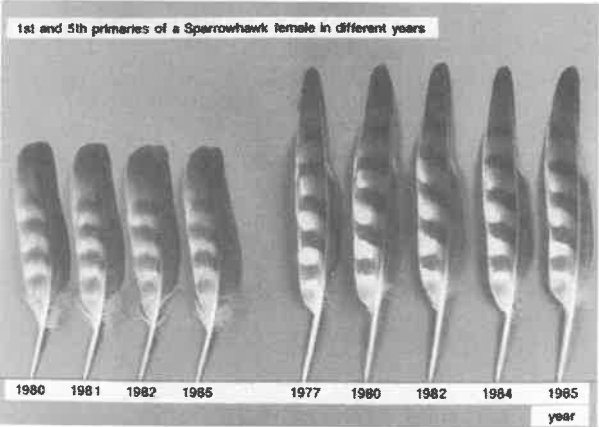
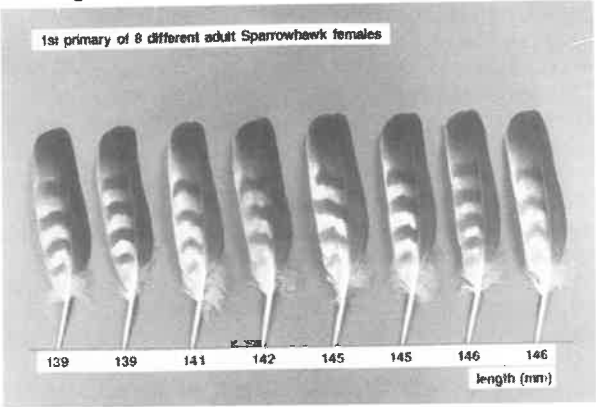


Figure 3. First primaries of eight different females, showing variation in length, shape and pattern in flight feathers between individual birds.



RESULTS

Population trend

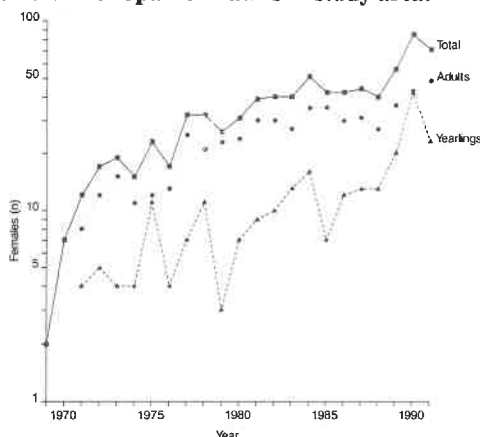
The Sparrowhawk became almost extinct in the study area during the 1960s. Only two pairs were known to breed successfully in 1969 (Figure 4). Their territories were in the middle of extensive woodland and were probably not or only marginally affected by pesticides. Figure 4 shows that the population recovered rapidly in the early 1970s to about 20 pairs in the middle of the 1970s. This was followed by a remarkable increase from 1976 to 1977 when the number of breeding pairs almost doubled. Thereafter, the number increased slowly to around 50 breeding pairs per year until 1988. The increase to nearly 100 pairs during the last few years is mainly due to an increase in yearling breeders in the population following extremely mild winters, such as the winters of 1988/1989 and 1989/1990 (Table 1). In Table 1 is shown that the predicted value of yearling breeders is 44% following extremely mild winters. After severe winters, for instance 1978/1979 and 1984/1985, the proportion of yearling breeders was at a very minimum (15%), while the number of adult breeders remained on the same level (see Figure 4). Statistical analyses pointed out that there was no significant relationship between mortality among adult breeders in the population and weather conditions during the preceding winter. Thus, fluctuations in the total number of breeding pairs is related to the proportion of yearling breeders in the population, which is regulated by the weather conditions during the preceding winter.

Table 1. Relationship between the proportion of yearling breeders in the population and weather conditions during the winters 1969-1991. The year 69 is the winter from November 1968 until April 1969, etc. (winters categorized according to Ljnsen 1991). Proportion of yearlings are predictions acquired from a regression model.

Category (1-7)	Years	Yearlings (%)	s.e.
Extremely mild	89,90	43,97	3,84
Very mild	75,88	38,10	5,63
Mild	77-78,83	29,81	4,12
Fairly mild	72-74,76,80-81,84	25,93	2,93
Normal	91	32,39	5,11
Cold	69-71,82,86-87	26,53	3,55
Severe	79,85	14,71	3,95

Significance between categories: 1-3*, 1-4, 1-6, 1-7, 7-2, 7-3, 7-5, whereby* $p < 0.05$; $p < 0.01$, $p < 0.005$ (Likelihood-ratio test).

Figure 4. Population trend of Sparrowhawks in study area.



Annual breeding success

Breeding performance of the Sparrowhawks in the study area remained low until 1976. Between 1971 and 1976 the brood size varied between on average 2.4 and 3.3 young (Figure 5A). In the same period the proportion of successful nests varied between 50% and 70% (Figure 5B). Breeding performance reached its lowest level in 1972. The reduced reproductive output during this period was mainly due to eggshell breakage and embryo mortality, resulting in partial or complete losses of clutches. In 1976 breeding performance recovered very suddenly: mean brood size reached over 4 young (Figure 5A), while less than 15% of all nests failed (Figure 5B). From 1976 onwards the proportion of successful nests fluctuated around 80% (Figure 5B), which is similar to a Sparrowhawk population studied in Germany during a 30-year period before organochlorine pesticides came into use (Kramer 1973)

Lifetime reproductive success

Figure 6 shows that adult plumaged females raised 0 to 31 young throughout their life. From the selected 228 individuals 16% failed to raise any young at all. The majority produced 2 to 6 fledglings during their lifespan. On average, lifetime reproductive success amounted to 6.2 fledglings per individual. If these results are compared with a Sparrowhawk population in south Scotland (Newton 1989), it is obvious that both LRS diagrams are highly similar (Figure 6), notwithstanding that female Sparrowhawks in Scotland produced on average 1.13 fewer young during their life. The difference is statistically significant (Student's *t*-test, $P < 0.0005$).

Much of the variation in lifetime reproductive success can be explained in terms of variation in lifespan (Figure 7). Of the sample of 228 females, lifespan reached up to 11 years old. In the age group with a lifespan of 2 years a relatively large number failed (26 out of 102 (= 25%) during 1976-1989, and 9 out of 16 (= 56%) during 1969-1976), but those that succeeded in that year class raised up to 7 fledglings. Although lifespan explains 69.2% (total data set) of the variation in lifetime reproductive success, there is still considerable variation within age groups. For instance, in the 5 year age group, one female raised only one young, whereas another female raised 24 fledglings (Figure 7). Part of the variation can be explained by the restrained reproductive success until 1976. Females that lived during 1976-1989 raised on average twice as many fledglings as those that lived during 1969-1976 (6.7 ($n=194$) and 3.5 ($n=34$) fledglings, respectively). Annual survival of adult females in the breeding population did not differ between both periods.

The relative contribution of individuals to future generations was not equally distributed. We estimate, on account of ringing recoveries (unpublished data), that at least 75% of the female fledglings died before they could breed in adult plumage. The contribution of the remaining 25% breeders is clearly skewed (Figure 8). Females with a lifespan of 2 years (slightly more than 50% of all females), produced only 22% of all fledglings. A minority (only 25%) of the females reached a lifespan of 4 years or older, but they produced 55% of the total offspring. Overall, only 6% of all fledglings (25% of all breeders) raised more than 50% of the total offspring, which corresponds with Sparrowhawk population studies in Britain (Newton 1985, 1988, 1989).

Figure 5. Breeding success of successful pairs (A) and proportion of successful Sparrowhawk nests (B).

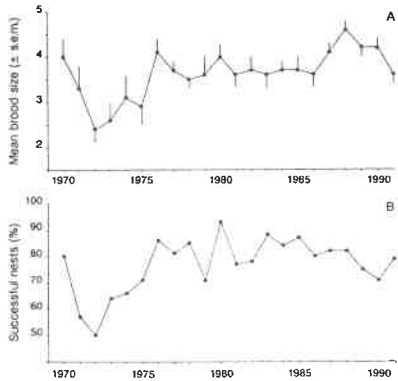


Figure 6. Lifetime fledgling production of female Sparrowhawks in the study area (mean per female = 6.16 young, n = 228), compared with females in southern Scotland (mean per female = 5.03 young, n = 194; after Newton, 1989).

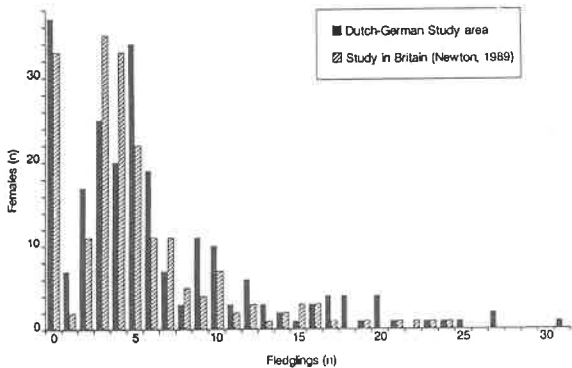


Figure 7. Lifetime fledgling production of adult females in relation to lifespan. Data represent the number of individuals with an equal number of offspring. Relationship between lifetime production (y) and lifespan (x) for period 1969-1976: $y = -2.55 + 1.967x$, $r = 0.716$, $P < 0.025$. For period 1976-1989: $y = -2.853 + 3.042x$, $r = 0.858$, $P < 0.005$. For both periods together: $y = -2.981 + 2.939x$, $r = 0.832$, $P < 0.005$.

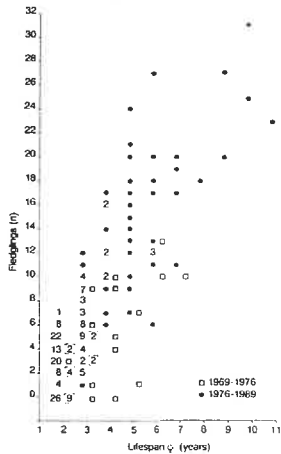
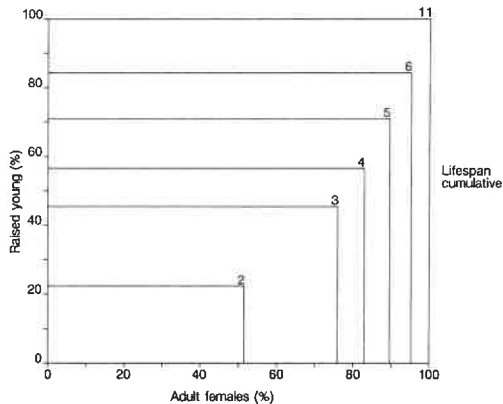


Figure 8. Cumulative presentation of lifetime reproductive success of females in relation to lifespan.



DISCUSSION

The number of Sparrowhawks breeding in the study area increased dramatically during the study period. The population recovery during the early 1970s was probably caused by a decrease in mortality due to disappearance of dieldrin and related compounds from the environment (Opdam *et al.* 1987).

A further increase in nest numbers followed after the breeding performance recovered suddenly in 1976. Burgers *et al.* (1986) showed that the eggshell thickness in Dutch Sparrowhawks (including birds from this study area) increased significantly from 1975 (Ratcliffe index 1.13) to 1977 (1.26), and so passing the presumed critical value of 1.16 for breeding success in 1976. This could explain why the recovery in breeding success from 1976 onwards was so abrupt (see also Opdam *et al.* 1987).

The role of winter weather conditions on population fluctuations is apparent. We found the highest proportion of yearling breeders in the population after extremely mild winters and the lowest proportion after hard winters. In contrast, the number of new adult recruits and the losses among established adult breeders did not show such a relationship. Kramer (1973) recorded that Sparrowhawk nest numbers in the southern Lausitz, Germany, dropped markedly after hard winters, as in 1939/1940, 1941/1942, 1946/1947 and 1962/1963. Unfortunately, he gave no information on the number of yearling and adult breeders in the population. Newton (1986) found in a fairly stable Sparrowhawk population in southern Scotland that both density-dependent factors and weather in early spring regulate the nest numbers. He suggested that: "The weather in early spring intervened to prevent a perfect density-dependent system: cold wet conditions in March-April led to greater decline, or less marked increase, than expected from nest numbers the previous year". We found no such density-dependent relationship for the Dutch-German Sparrowhawk population. The population increase until 1990 may be the reason why a density-dependent relationship could not be determined.

Between 1969 and 1977 females produced on average 3.5 fledglings during their life, or about 0.9 fledgling, when females which died before they could breed are included. Theoretically, each female must produce 2.0 young (by equal proportion of male and female offspring) to maintain population stability. For 1976-1989, replacement was calculated to be on average 1.7 young. One would, however, even expect a replacement greater than 2.0 young, because the population was increasing slightly. First, survival during the pre-breeding period may have been underestimated. Secondly, by using shed feathers to identify individual birds some bias in measuring LRS is introduced, because yearlings which died after their first breeding attempt are not selected. Furthermore, breeding success of the selected individuals in their first year of life could not be included. In some cases we doubted whether shed feathers were from the same individual or not. In these cases the feathers were classified as originating from different individuals. Displacement of individuals was checked, so that females that changed territory were found again. This occurred regularly (mean distance: 2.7 km). Displacements outside the study area might have occurred

occasionally, which will have resulted in some underestimation of LRS.

Measurement of the lifetime production of females revealed that (a) females produced between 0 and 31 fledglings during their life, (b) most of the variation in LRS can be explained by variation in lifespan (up to 11 years), and (c) overall, only 6% of all fledglings produced more than 50% of the total offspring.

These results can be compared with Newton's (1985, 1986, 1988, 1989) findings of British Sparrowhawk populations. It appears that LRS in the Dutch-German study area score about 20% higher than in southern Scotland. This difference might be somewhat smaller, because, in contrast with Scottish data, females with lifespan 1-year were not included in our analysis. The larger lifetime production cannot be explained by a higher survival of the Dutch-German Sparrowhawks. The annual survival of adult females in this study of 53% (unpublished 1970-1985 data) is even lower than the 64% survival rate found in southern Scotland (Newton *et al.* 1983). The higher proportion of successful nests (80% against 57%) and the larger mean brood size per successful nest (3.8 against 3.4) we found explain, however, the difference in LRS between both populations to a large extent. It may be that natural circumstances (e.g. food supply) are more favourable in the Dutch-German study area than in southern Scotland. Human settlements and activities may also have increased food supply and consequently breeding performance, but on the other hand, these may have decreased the birds' annual survival (e.g. more window and traffic casualties). The high density of the predator Goshawk *Accipiter gentilis* in the Dutch-German study area (absent in southern Scotland) contributes furthermore to a high mortality among our Sparrowhawks.

Some of the individual variation in LRS can be explained by the restrained reproductive success until 1976. Most of the variation (69%), however, is caused by the variation in lifespan. This corresponds with Sparrowhawk population studies in Britain (Newton 1985, 1988, 1989). The remaining variation might be explained by the age of first breeding, territory quality, quality of the partner or by chance, but these aspects need further examination.

The outcome that only a small proportion of individuals contributes to the next generation to a large extent is a common phenomenon in (long-living) birds, and has been discussed thoroughly elsewhere (Newton 1989).

ACKNOWLEDGMENTS

We wish to thank all friends who helped to collect data in the field, especially Johan Thissen, Paul Opdam, Peter Verschuren, Mark Verschuren and Jan Jacobs. We are also grateful to Johan Thissen, Paul Opdam, and Arie Spaans who gave useful comments on the manuscript. We thank Joop van Osch, Ruud Wegman and Roel van Beek for preparing the photographs and figures.

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