

Effects of Legislative Protection on Survival Rates and Status Improvements of Birds of Prey in Denmark

by

HENNING NOER & HANNE SECHER

Med et dansk resumé:
Jagtlovsændringers indflydelse
på overlevelse og statusforbedringer
af danske rovfuglearter

Резюме на русском языке:
Влияние изменений охотничьего устава на
переживание и улучшение благосостояния
датских видов хищных птиц.

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Abstract

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Ringling recoveries of Danish Buzzards *Buteo buteo*, Sparrowhawks *Accipiter nisus* and Goshawks *A. gentilis* were analysed in order to assess the influence on survival of two changes in shooting regulations: a change in the start of the open season to 1st November in 1954 and in 1967 the introduction of year-round protection. Survival rates were estimated by means of an extension of the Haldane-model and for each species substantial increases in survival rates – in particular first year survival – were found after 1967. Status of the analysed species improved considerably during the 1970's. Changes in brood-sizes were found for both Sparrowhawk and Goshawk, but these changes showed no temporal coincidence with changes in population trends and hence could not explain these trends. When combined, the observed reproductive and survival rates model the changes in population sizes closely, and this lends increased credibility to the survival rate estimates. It is therefore concluded that: 1) the population growth was caused by increases in survival, and 2) the major cause of the increased survival was the 1967 Protection. In spite of the relatively weak data sets and statistical models, the evidence supporting these conclusions is fairly strong. Secondary decreases in survival rates were found for both Buzzard and Sparrowhawk when population growth ceased in 1978. These results are discussed in relation to the present limitation/regulation of population sizes.

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Introduction

The growing awareness of the negative impacts of modern human communities on wildlife has resulted in increasingly restrictive legislation in many countries. This situation is new and still under development, and analyses of long term effects of legislative policies are still few and much needed.

The population dynamics of many birds of prey since 1945 offer opportunities to analyse such a situation. The drastic declines of most West European populations of birds of prey between 1945 and 1970 (Bijleveld 1974, Newton 1979) led to legislative measures in many countries, in many cases followed by status improvements. The negative trends included Danish populations (Dyck 1972, Dybbro 1976, Strandgaard & Asferg 1980) and, in consequence, various measures were started in 1967. In 1967, the three species remaining with an open season – the Buzzard *Buteo buteo*, the Sparrowhawk *Accipiter nisus* and the Goshawk *A. gentilis* – were protected. Certain commonly used pesticides were suspected to influence population sizes of birds of prey negatively. As a result, the use of DDT for agricultural purposes was reduced from 1969 onwards and the use of Thallium for rodent regulation was prohibited in 1976. Use of Aldrin ceased gradually during the 1960's and early 1970's, while Dieldrin is still in use although not for agricultural purposes.

From about 1970 onwards, the negative trends in population sizes reversed (Dybbro 1976) and, during the period 1970-80, populations of the most common species increased rapidly (Dyck et al. 1981, Bomholt 1983). Although stagnation of population sizes after 1980 has been reported by Jørgensen (1989), the breeding populations of these species are undoubtedly much larger today than they were in the 1960's.

These status improvements might be

taken to indicate that the legislative policies were successful, but a rigorous demonstration that the observed population increases were caused by the legislative measures taken since 1967 is still lacking. Moreover, results reported by Grandjean (1976), Clausen & Karlog (1977) and Dyck et al. (1981) did not suggest reductions in environmental loads during the period of population growth, and Noer & Secher (1983) showed that survival rates of Danish Kestrels *Falco tinnunculus* increased significantly following the 1967 Protection. Hence, even if it is assumed that the legislative measures caused the subsequent population increases, the relative contributions of protection and of reductions in the use of certain pesticides are even less understood.

This lack of insight is mostly due to the fact that few records exist for the period before 1970. However, Noer & Secher (1983) argued that ringing recoveries contain information that is highly relevant in this context. For the Kestrel, analysis of recoveries revealed increases in survival rates in 1931 – when the species was protected – and in 1967, when the three species still with an open season were protected. After 1967, monthly distributions of recoveries changed from a peak in autumn to peaks in July-August and January-February. Brood-sizes increased slowly throughout the period 1945-80, but these changes were not significant. Accordingly, it was possible to conclude that the effects of reducing shooting pressure were probably greater than the effects of environmental loads for this species.

In the present paper, the ringing recoveries of the three species protected in 1967 are analysed in a similar way, the primary purpose being to evaluate the effects of the 1967 Protection and the reductions in the

use of DDT and Aldrin. Other changes in protective legislation (p. 6) may have influenced survival rates and the analyses are extended to cover this point as well.

In Denmark, population sizes and reproduction of the Buzzard, the Sparrowhawk and the Goshawk have been thoroughly investigated (e.g. Dybbro 1976, Dyck et al. 1977, Dyck et al. 1981, Bomholt 1983, Dyck 1983, Storgård & Birkholm-Clausen 1983a and b, Jørgensen 1985, 1987 and 1989). In contrast, survival has only been analysed in depth for the Kestrel (Noer & Secher 1983). As population trends are the net outcome of reproduction and mortality, the analyses presented here supply information that has hitherto been missing. The second purpose of this paper is therefore to attempt a synthesis of the total results at a general level.

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from the Scandinavian Airlines System to research birds of prey in Scandinavia. We wish to express our thanks to all of these persons and Agencies.

Legislative measures taken in Denmark

Protective legislation

Paludan (1967) summarised legislative protection of birds of prey in Denmark. The legislative measures relevant to this paper are summarised in Table 1. In conjunction with the 1967 Game Act which abolished the open season for Buzzards, Sparrowhawks and Goshawks, another Act was passed concerning the control of certain wildlife species under specific circumstances. This Act allowed control of Buzzards, Sparrowhawks and Goshawks to be carried out within 50 m of houses with for example pigeon stocks or poultry, or by dispensation within 50 m of Pheasant pens, if the hawks had caused damage that could be proven. Thus, although the three species concerned no longer had an open season after 1967, limited shooting of individuals has continued.

In addition to the 1967 Protection, the change of the start of the open season to 1 November (Table 1) may have caused changes.

Thus, for the three species treated in this paper, there have been two critical years with changes in legislative protection since 1945: 1954 and 1967.

Use of and bans on pesticides

The pesticides considered in this paper are those generally assumed to have influenced populations of birds of prey. Of these, the use of DDT in agriculture presumably declined after 1969. In Danish forestry,

however, its use was not discontinued until about 1980. Aldrin was used in Denmark from the late 1950's. From about 1963 its use was restricted to seed dressing which, in turn, was discontinued from 1968-69. In all cases, however, these "bans" were effected through withdrawals from the manufacturers on recommendation of the Danish Authorities and not through formal prohibitions (E. Bendixen, pers. comm). Use of DDT, for instance, was not formally prohibited in Denmark until 5th September 1984 (by Government Order). This implies that the actual use ceased gradually as stocks were exhausted. Although no exact

information could be found about the extent of the use of Aldrin, it is known that the somewhat less toxic Thiodan was much more widely used. At its height, Thiodan was used on 35,000 ha/year. The other two organo-chlorines assumed to have caused the crash of the British Sparrowhawk population (Newton 1986), Dieldrin and Heptachlor, were never used in Danish agriculture. The ban on Thallium, a rodenticide seed-dressing, came as late as April 1976 (Clausen & Karlog 1977). As this date is much later than the start of the population growth, effects of the Thallium ban are not treated here.

Table 1. Survey of legislative protection of birds of prey in Denmark. Years when changes to open seasons were made by Government Order (not enacted) are given in parentheses. Dates delimit the open season; + means totally protected, and - no protection. After Paludan (1967).

	1861	1871	1894	1922	(1928)	1931	(1954)	1967
Osprey	-	-	-	1/8-31/1	+	+		+
<i>Pandion haliaëtus</i>								
Eagles	-	-	-	1/8-31/1	+	+		+
<i>Aquila spp.</i> + <i>Haliaëtus albicilla</i>								
Honey Buzzard	2/11-31/1	-	-	15/9-31/1	+	18/9-31/1	+	+
<i>Pernis apivorus</i>								
Buzzard	2/11-31/1	13/9-31/1	16/9-31/1	15/9-31/1		18/9-31/1	1/11-31/1	
<i>Buteo buteo</i>								
Roughlegged Buzzard	-	-	-	15/9-31/1		+		+
<i>Buteo lagopus</i>								
Red Kite	-	-	-	+		+		+
<i>Milvus milvus</i>								
Goshawk	-	-	-	1/8-31/1		1/8-31/3	1/11-31/3	
<i>Accipiter gentilis</i>								
Sparrowhawk	-	-	-	1/8-31/1		1/8-31/3	1/11-31/3	+
<i>Accipiter nisus</i>								
Harriers	-	-	-	1/8-31/1		1/8-31/3	+	+
<i>Circus spp.</i>								
Peregrine	-	-	-	1/8-31/1		1/8-31/3	+	+
<i>Falco peregrinus</i>								
Hobby	-	-	-	1/8-31/1	+	+		+
<i>Falco subbuteo</i>								
Merlin	-	-	-	1/8-31/1	+	+	+	
<i>Falco columbarius</i>								
Kestrel	2/11-31/1	-	-	15/9-31/1	+	+		+
<i>Falco tinnunculus</i>								

Methods

The hypotheses to be tested

The hypotheses to be investigated are: 1) that the population growth was caused by the 1967 Protection, and 2) that the population growth was caused by reductions in the use of DDT and/or Aldrin.

If the 1967 Protection caused the population growth, the expected results are those discussed by Noer & Secher (1983). Survival rates would be expected to show measurable increases starting in 1967 and, at the same time, changes in monthly distributions of recoveries might take place. As shooting is expected to affect first year individuals more heavily, the largest increase is expected for first year survival.

Newton (1986) summarised the known effects of DDT, Aldrin and Dieldrin (Fig.

1). Effects of DDT should include measurable changes in brood-sizes and, due to the slow turnover of DDE and the presumably gradual decrease in use, the effects of the 1969 DDT "ban" should typically exhibit a delay of some years after 1969. Aldrin should affect survival but, contrary to the effects of shooting pressure, the expected outcome for this pesticide is that adult survival should at least be as heavily affected as juvenile mortality (Newton & Hass 1984, Opdam et al. 1987). In particular, Newton (1986) has emphasised that the population crash of British Sparrowhawks, which is ascribed to the introduction of cyclodiene organo-chlorines, could not be explained unless considerable adult mortality was involved. Thus, to the extent that the cause of the

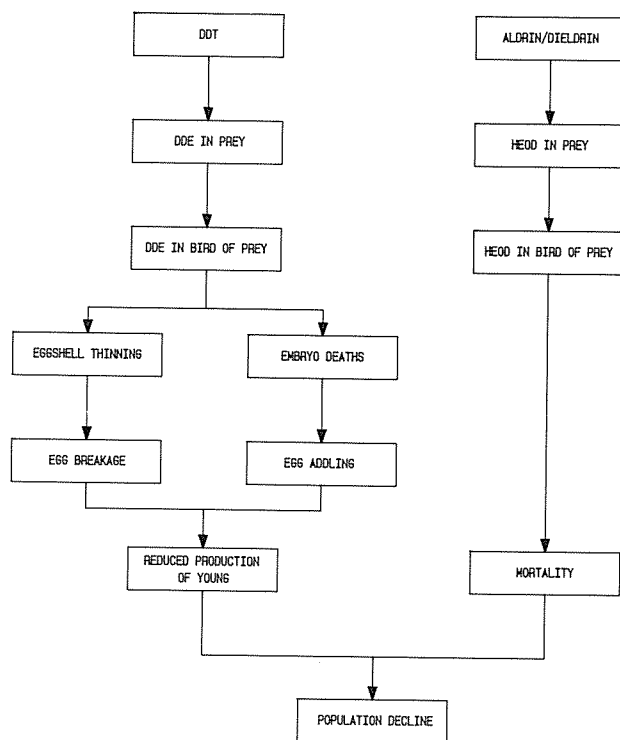


Fig. 1. Diagrammatic illustration of the causal links between DDT/DDE and HEOD, respectively and population decline. After Newton (1986).

population growth was a result of reductions in the use of DDT and/or the Aldrin ban, changes should be observable in brood sizes and/or mortality, particularly adult mortality. Typically, these changes should be gradual and not evident until some years after 1969, as was the case for the British and Dutch Sparrowhawk populations (Newton 1986, Opdam et al. 1987).

Changes in population dynamics after growth

In addition to the population growth and its causes, the changes in survival rates in later years are of interest too. As argued by Noer & Secher (1983), secondary changes in reproductive parameters and/or survival rates are expected to take place as the population eventually stabilises on a new and higher level. The time at which this happens cannot be predicted, but analysis of this phase may potentially contribute valuable information on the factors that limit or regulate the new (and larger) population sizes.

Specifically, Noer & Secher (1983) predicted that survival rates would decrease after the period of population growth. This prediction, which was confirmed for the Kestrel, rested on the implicit assumption that population sizes are regulated through mortality rather than through reproduction. The present paper elaborates on this point by the inclusion of information on reproductive success. Parameters such as percentage of successful pairs and average brood-size are readily observed and have been studied in Denmark since 1973 (e.g. Jørgensen 1989), whereas both age at first reproduction (reflecting generation time) and non-breeding are difficult to observe and very little information is available.

Regulation of population sizes through reproductive rates could be mediated through any of these parameters. As birds of prey are territorial, it is conceivable that

limitation could take place through an increased age at first reproduction and/or the build up of a fleeting (or surplus) population and, at least for the Sparrowhawk, there is some evidence that increased age at first reproduction can result from a lack of suitable territories (Newton 1986, Newton & Marquiss 1986). Evidence of the existence of fleeting populations is largely circumstantial (Newton 1979) and based on case stories where losses among breeding pairs have been observed to be followed by rapid substitutions.

However, it is in principle possible to predict the size of a given fleeting population under rather simple assumptions. Consider a population at, for example, the time of year when the young have just left the nest. The population will then consist of three distinct subsets of individuals: 1) the year's cohort, newly recruited into the population, 2) the territorial adults (which, potentially at least, can be counted during the breeding season), and 3) the total (unobservable) "fleeting" population, including both immatures and non-territorial adults. If the number of surplus individuals is denoted N_F and the number of territorial adults N_T , the latter can be subdivided into a group that bred successfully, N_{TS} , and a group that did not, N_{TU} . Then $N_T = N_{TS} + N_{TU}$. The number of yearlings is kN_{TS} , where k is the average brood-size. If it is assumed that the population is stable, the number of births must balance the number of deaths within any one year. If survival of first year individuals is denoted b and survival of older birds s , the following equation must be valid

$$kN_{TS} = (1-b)kN_{TS} + (1-s)(N_T + N_F).$$

All of these variables are known in principle, either from field observations or from estimates of survival rates from ringing recoveries, except N_F .

To find N_F , the formula can be rewritten

$$N_F = kb_{N_{TS}} / (1-s) - N_T, \text{ or}$$

$$N_F/N_T = kb_{N_{TS}}/N_T / (1-s) - 1 .$$

This equation simply postulates that, as a given pair of successful breeders have to replace the loss through mortality of firstly themselves, secondly their newly-born young (before these reach maturity), thirdly of the unsuccessful territorial pairs and, finally of the fleeing population, it follows that successful breeders can only support a fleeing population of a certain size.

The two crucial points that emerge from these considerations are:

- 1) In principle, the size of the fleeing population is determined completely by parameters which are either known or at least measurable. Thus, it is theoretically possible to calculate the size of the fleeing population from existing knowledge, and
- 2) Survival rates will decrease secondarily only to the extent corresponding to the size of the fleeing population. Thus, study of the extent to which survival rates decrease during a period of population stabilization is presently the only possible means of indicating how large a fleeing population is built up. In particular, an increase in the generation time should increase the number of "immature" individuals and, as these are counted in the surplus population in the formulation given above, the derived expressions can be taken to show that, insofar as an increase in generation time contributes to the stabilisation of the population, survival will not decrease to its former level.

Thus, even though no information has been published with respect to age at first reproduction for Danish birds of prey, an increase in the generation time as populations become denser should theoretically be revealed through a lesser than expected

decrease in survival rates. As it is generally known that birds of prey breed earlier in less dense populations (e.g. Newton 1979), the expectation is that some build up of fleeing populations – at least when immature individuals are included as in the formulation given above – should take place during and after a period of population growth.

Treatment of recoveries

Recoveries were obtained from a number of different sources (p. 13). Within each of the investigated periods, recoveries from different sources were pooled. Individuals found as "long dead", "remains", and "skeleton", fledglings found dead at the nesting site, and recoveries of shot birds have all been omitted from calculations of survival rates. The latter omission is discussed by Noer (in press) and below. A number of older records with no information on cause of death probably referred to shot individuals. All of these were excluded as well. In all cases, a year of living has been counted from 1 July to 30 June.

For some recoveries the exact date of finding is unknown. Based on the dates of the letter from the finder to the ringing centre, the age distributions of these recoveries were found to be identical to age distributions of recoveries with exact finding dates, and hence the two data sets were pooled. These recoveries were not included in the monthly distributions.

For all species there exists a number of recoveries of individuals ringed as fully fledged. Brownie et al. (1985) recommend that the problems in estimating survival rates for birds ringed as pulli are solved by combining results from ringing of both pulli and adults. The validity of this approach has been questioned by Lakhani (1987a). In the present case, a very large proportion of the individuals ringed as fully fledged are undoubtedly in their first

year (cp. the survival rate estimates given for each species below), and an unknown proportion are migrants belonging to other Fennoscandian populations. Hence, the use of the combinative models of Brownie et al. (1985) might be very misleading. For these reasons, the data sets for pulli and fully fledged have been treated separately throughout, and regarded as replications rather than as data resulting from extended ringing schemes.

Statistical analyses

Estimation of survival rates

Due to lack of information on numbers ringed for older records, calculations are based on the model developed by Lack (1943 and 1951), as extended by Haldane (1955) to cover periods of incomplete data. When a hypothesis of a sudden change in survival rates, e.g. caused by protection, is to be investigated, the main problem of estimation concerns individuals that live across the change and so live in both survival regimes. Noer & Secher (1983) extended Haldane's model (1955) to cover this situation, but the analyses presented here necessitate two further extensions of this model: 1) to cover estimation of a separate survival rate for first year individuals, and 2) to permit a generalised analysis of hypotheses of more than two periods of different survival rates. Even though the secondary decrease in survival rates predicted to follow the period of population growth is expected to be gradual, the actual observations show that, at least for the Buzzard and the Sparrowhawk, population growth was abruptly arrested after the severe winter 1978/79 (Jørgensen 1989). Accordingly, any secondary decrease in survival rates is assumed to be abrupt, and analysis of survival rates in relation to protection principally concerns estimation over three consecutive time periods, one be-

fore and two after protection. Moreover, analysis of the effects of the change in the start of the open season in 1954 introduces one more time boundary. Accordingly, the analyses presented here estimate survival rates in four different periods, with hypothetical changes taking place in 1954, 1967 and 1978. In some cases, however, the material is too small to permit analysis of the effects of the 1954 Regulation and, in these cases, only the two most recent time limits are used. As an example, introduction of this model means that the probability that a bird born in 1952 died in 1972 (before 1 July) is $b_1s_1(s_2)^{13}(s_3)^4(1-s_3)$, while the probability that a bird born and ringed in 1966 died in 1983 (before 1 July) is $b_2(s_3)^{10}(s_4)^4(1-s_4)$. Estimates are derived by Noer (in press) for the general case of P periods (complete data) and for three periods and incomplete data. Extension to four periods with incomplete data is straightforward though cumbersome and is done by extending the Likelihood function from 6 to 10 components.

The data presented below show that the age distribution of individuals recovered as shot differs from that of birds which died from other causes. As the probability that a shot individual is reported is far higher than that of (most) other death causes, pooling of these two data sets will lead to underestimation of survival. Accordingly, all calculations in the following are carried out for non-shot individuals only. As shown by Noer (in press), adult survival rates are unaffected by this omission, while estimates of first year mortalities become slightly biased. This bias is negligible for the data sets presented here.

Tests of significance for differences in survival rates

Comparisons between periods are done by means of Likelihood-ratio tests (e.g. White 1983). For each data set, a sequential test

procedure as recommended by Noer (in press) is carried out. This tests 1) the hypothesis H_4 of four periods of survival rates against the hypothesis H_0 that all periods have identical survival rates, and 2) if, and only if, H_0 is rejected, H_4 is tested against a series of hypotheses postulating that two periods are identical in survival rates: H_{3A} : that survival rates before 1954 were identical to those of 1954-66, H_{3B} postulating that survival rates of 1954-66 were identical to those of 1967-77, and H_{3C} that survival rates of 1967-77 were identical to those of 1978-87. If all of these hypotheses are rejected it is concluded that three changes in survival took place. If not, the two periods having the lowest corresponding χ^2 test statistic are pooled, and the analysis proceeds by investigating two of the following hypotheses: H_{2A} : that only one change in survival rates took place - in 1967, H_{2B} : that the only change in survival was in 1978, and H_{2C} : that the change

was in 1954. The combination of these hypotheses chosen depends on which of the H_3 hypotheses were accepted. A survey of the hypotheses is given in Fig. 2. Note that the tests only compare consecutive periods. Though it has been argued above that comparisons of survival rates during periods with stable breeding populations are potentially interesting (i.e. the first and last periods observed), such comparisons are presently outside the scope of the statistical testing under consideration.

Pairwise comparisons between periods can also be done by means of z-tests (Seber 1973). By this test procedure a hypothesis of equal survival rates in any two periods is tested by means of the statistic

$$z = \frac{(z_1 + z_2)}{\sqrt{2}}$$

where

$$z_i = \frac{(b_i - b_{i+1})}{\sqrt{b_i(1-b_i)/N_i + b_{i+1}(1-b_{i+1})/N_{i+1}}}$$

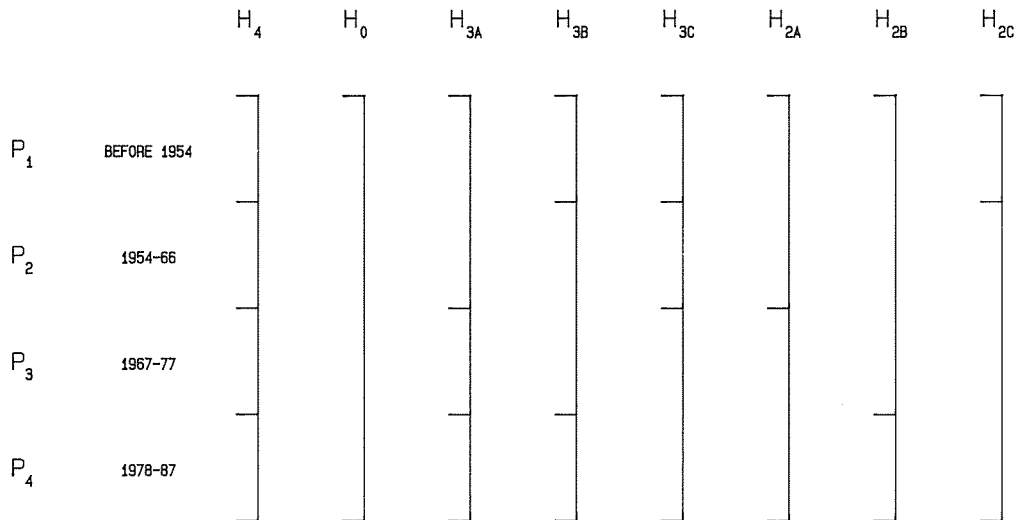


Fig. 2. Structure of the set of hypotheses associated with analysis of survival rates in four different periods (P_1 - P_4). For each hypothesis is shown - in addition to its labelling - the structure of periods of different survival rates that it postulates. Note that the sequence of tests is initiated by testing H_4 (all periods have different survival rates) against H_0 (all periods are identical). Ideally, the sequence of tests proceed if and only if H_0 is rejected.

and

$$z_2 = \frac{(s_i - s_{i+1})}{\sqrt{\text{var}(s_i) + \text{var}(s_{i+1})}}$$

Under H_0 , z is asymptotically normal distributed with parameters $(0;1)$. This test procedure is valid for moderately large data sets and was used for the Kestrel by Noer & Secher (1983). For the Kestrel and the species presented here, the two test procedures lead to virtually identical conclusions and significance levels.

Computation of population growth

In order to evaluate the findings, changes in population sizes were calculated according to the estimated survival rates. These computations were done by means of Leslie matrices (e.g. Pielou 1969). The age structured population at time t is written as a vector

$$\mathbf{N}_t = \begin{pmatrix} N_{t1} \\ N_{t2} \\ N_{t>2} \end{pmatrix}$$

where the choice of three age categories (i.e. pooling of all age classes more than two years old) is arbitrary. In the present case, where only first year survival has been estimated separately, the structure of the corresponding Leslie matrix is

$$\mathbf{L} = \begin{pmatrix} f_1 & f_2 & f_{>2} \\ s & 0 & 0 \\ 0 & s & s \end{pmatrix}$$

where f is the fecundity measured as the number of young surviving to the start of the following breeding season and s the adult mortality.

Given these two matrices, the age-structured population size in following generations can be found by matrix multiplication

$$\mathbf{N}_{t+1} = \mathbf{L}\mathbf{N}_t, \text{ or generally}$$

$$\mathbf{N}_{t+k} = \mathbf{L}^k\mathbf{N}_t.$$

At the same time, the stable age distribution corresponding to a given set of juvenile and adult survival rates and fecundities is given as the first right eigenvector of the matrix \mathbf{L} (Pielou 1969). In all the following calculations which use this technique, the age distribution at the start of a period after a change of survival rates has been taken to be the stable age distribution corresponding to the survival rates of the previous period. For the first period starting any of these calculations, the population has been assumed to be in its stable age distribution.

In the structure of the matrix given above, fecundity is calculated as the number of young surviving to the start of the following breeding season, i.e. the product of the first year survival b , the brood-size k , and the probability that a breeding pair is successful. In doing this, a slight error was introduced as survival rates have been calculated on the basis of a year counted from 1st July to 30th June. As very few first year individuals have been recovered in April-June this source of error can be assumed to be very small. Information on reproductive success derives from Jørgensen (1989).

Materials

To investigate the above-mentioned hypotheses information on recoveries and brood-sizes was compiled. The total number of recoveries available for the present study was 731, 901 and 586 for the Buzzard, Sparrowhawk and Goshawk respectively. These recoveries were obtained from a number of different sources. Sources are shown separately for each species (Tables 2, 13, and 25). Information from the Odense Ringing Station was taken from Larsen &

Simonsen (1968), and some other recoveries derive from Pedersen (1954) and Jensen (1955).

Information on numbers ringed could be obtained only from the files at the Zoological Museum, Copenhagen, i.e. for recoveries from that source. Information on brood-sizes is therefore based exclusively on these files. There is no information on chicks that were not ringed, either because they were judged too small at ringing or because they were fledged. This means that the brood-sizes presented are underestimates. This bias is considered small and constant throughout the investigation period.

Results

Buzzard

Material

Recoveries of Buzzards are fairly evenly distributed throughout the investigated periods (Table 2). Since 1945, the majority have been ringed by the Zoological Museum, Copenhagen. The material for this species is relatively homogeneous (cp. materials of Sparrowhawks and Goshawks given in Tables 13 and 25 below), with the exception of the intensification of ringing of fully fledged individuals since 1967.

Brood-sizes

Information on brood-sizes and reproductive success of Buzzards, including comparisons between recent and older records, is given by Jørgensen (1989) and will not be repeated here. No changes in reproductive success have been found for this species (Jørgensen 1989), though comparisons are complicated and weakened by local differences in brood-sizes (see below, p. 34). In spite of this, it is reasonable to assume that

Table 2. Sources of recoveries of Buzzards in three different periods.

	Recovered		Recap- tured
	Ringed as:		
	Pulli	Juv.-ad.	
<i>1916-1944:</i>			
Zoological Museum, Copenhagen	25	1	1
P. Skovgaard, Viborg	87	1	4
Total	112	2	5
<i>1945-1966:</i>			
Zoological Museum, Copenhagen	134	29	19
P. Skovgaard, Viborg	1		
Game Biology Sta- tion, Kalø		19	
Odense Ringmærk- ningscentral	9		
Total	144	48	19
<i>1967-1987:</i>			
Zoological Museum, Copenhagen	196	89	29
Game Biology Sta- tion, Kalø	1	61	25
Total	197	150	54

no changes have taken place. To our knowledge no such differences have been published. Furthermore, it is generally assumed that species at the trophic level occupied by the Buzzard have been much less affected than restrictively bird-eating species (e.g. Joiris & Delbeke 1981).

Survival rates

The Buzzard is a very long lived species; this is clearly reflected in the age distributions of the different groups of recoveries (Tables 3-5). The oldest recovered individual was 26 years old, which means that

Table 3. Age distributions of recoveries of Buzzards ringed as pulli and recovered in Denmark. Individuals recovered as shot are excluded (see Table 12). Age distribution of recoveries before 1945 is pooled. Underlined entries indicate: periods of unchanged hunting legislation (changes effected in 1954 and 1967); the year in which growth in the population stopped (1977), and the last year investigated (1987).

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19...25
Year born																			
Before																			
1945	24	3	3	5		1				1	1	1							
1945	1									—									
46				1						—									
47	2	1								—									
48	1									—									
49	1									—		1							
1950	2																		
51	2																		
52	2																		
53	<u>1</u>		2		1												1		
54	3	2																	
1955	5	1		2															
56	1		1																
57	1		2									1	1						
58	5																		
59	6	3																	
1960			1																
61	2																		
62	2	1																	1
63	1																		
64	1																		
1965	3	<u>1</u>		2					1										
66	<u>2</u>			1															
67	3	1				2			1	1									
68	5		3		1		1	1						1					
69	7		1	1							1			1					
1970	7		1								2	1		1				1	
71	3		2																
72	1	2																	
73	2	1	1																
74	3				2														
1975	1																		
76	3	<u>1</u>	1			1													
77	<u>2</u>	1	3							1	1								
78	1																		
79	3		2																
1980	2	1	1																
81	7				1														
82	1			1															
83	5	1		1															
84	7																		
1985	5																		
86	2																		
87	<u>3</u>																		

Table 4. As Table 3. Age distributions of Buzzards ringed as pulli and recovered outside Denmark. Individuals recovered as shot are excluded (see Table 12).

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Year born																					
Before																					
1945	5	1																			
1945																					
46	2																				
47	4																				
48																					
49	1																				
1950	2																				
51																					
52																					
53	1																				
54																					
1955	3	2	1	2		1															
56	1	3																			
57																					
58	1																				
59	2	1	1																		
1960	1																				
61																					
62	2																				
63																					
64	1		1		1								1								
1965	5		2																		
66																					
67	2		2																		
68	2	2		1																	
69	4	1			1		1														
1970	1	1																			
71				1																	
72	2																				
73	3																				
74		1																			
1975	4	1						1		1											
76			1			1															
77	1																				
78	1	1																			
79	1																				
1980	2																				
81	1																				
82	2																				
83	1																				
84	1																				
1985	2																				
86		1																			
87																					

Survival Rates and Status Improvements of Birds of Prey

Table 5. As Table 3. Age distributions of Buzzards ringed as fully fledged and recovered in Denmark. Individuals recovered as shot are excluded.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Year born																				
1945																				
46																				
47																				
48																				
49																				
1950																				
51																				
52																				
53																				
54	1				1															
1955	1																			
56	1	1																		
57																				
58																				
59				1																
1960	4				1						1									
61																				
62																			1	
63	3																			
64	5														1					
1965	1																			
66																				
67	4	2																		
68	3																			
69	7	1									1			1					1	
1970	1		1								1									
71	1																			
72															1					
73	5																			
74				1							1									
1975	2	1		1	1	1														
76	2		1	1				1												
77	2		3	1		1			1											
78	5		1						1											
79	5	1	1						1											
1980	1		3				1													
81	5	2	1																	
82	2																			
83	4																			
84	2	1																		
1985	3																			
86	1																			
87																				

data from before 1967 still have to be considered as incomplete. This is the reason why the model presented by Noer (in press) and the extension to four periods used in this paper treats all data as incomplete, in contrast to the model used for the Kestrel by Noer & Secher (1983). The individual recovered at 26 years old is erroneously not shown in the table given by Noer (in press), though it is included in the survival rate estimates in that paper.

The old ages obtained by Buzzards are reflected in the estimated survival rates. Adult survival is generally about 0.80, in reasonable agreement with other published estimates (Newton 1979) based on the Haldane method (Table 6). In the comparison of survival rates between different periods, results for the total material of non-shot individuals ringed as pulli reject H_0 , while both H_{3A} and H_{3B} are accepted (Table 7).

According to the criteria given above, H_{3A} is chosen, and after that all hypotheses at level 2 are rejected. Hence, survival 1967-77 was higher than survival before 1967 and after 1977. It should, however, be noted that this significance depends on the pooling of data before 1967. The estimated survival rates corresponding to the accepted hypothesis and the total material of birds ringed as pulli indicate

Table 7. Results of sequential Likelihood-ratio tests of differences between periods in survival rates for the total material for Buzzards ringed as pulli. Survival rate estimates are given in Table 6.

	χ^2	df	P
H_4 vs. H_0	23.6676	6	0.06%
$H_4 - H_{3A}$	4.2410	2	12.00%
$H_4 - H_{3B}$	5.3576	2	6.86%
$H_4 - H_{3C}$	14.0630	2	0.09%
$H_{3A} - H_{2A}$	14.1066	2	0.09%
$H_{3A} - H_{2B}$	9.4468	2	0.89%

that first year survival increased by some 14% following the 1967 Protection, while adult survival increased by 9% (Table 8).

The interpretation of these results is, however, complicated by the fact that the Danish Buzzard population is partially migratory (Holstein 1956, Salomonsen 1972). The migratory part of the population leaves the country in October (Salomonsen 1972), and so should largely have escaped shooting pressure in Denmark after the change in the start of the open season to 1st November in 1954. Therefore, a hypothesis postulating that legislative protection in Denmark has caused measurable increases in survival rates would predict that, for the migratory part of the population, this increase should

Table 6. Survival rate estimates for Buzzards based on four periods of different survival rates. Estimates based on 1) the total material of individuals ringed as pulli, 2) the material ringed as pulli and recovered in Denmark (data in Table 3), 3) ringed as pulli and recovered outside Denmark (data in Table 4), and 4) ringed as fully fledged (data in Table 5). Individuals recovered as shot are excluded.

		1)	2)	3)	4)
1920-53:	b_1	0.3290	0.3793	0.1667	
	s_1	0.7647	0.7656	0.7500	
1954-66:	b_2	0.4838	0.4265	0.5676	0.2991
	s_2	0.7431	0.7444	0.7414	0.8714
1967-77:	b_3	0.5360	0.5390	0.5367	0.5000
	s_3	0.8334	0.8346	0.8349	0.9136
1978-87:	b_4	0.2480	0.2684	0.2343	0.3773
	s_4	0.6951	0.7664	0.5162	0.7540

Table 8. Estimated survival rates and covariance matrix for Buzzards ringed as pulli. The estimates are for the model resulting from the analysis, i.e. with three periods of different survival rates (before 1967, 1967-77 and after 1977).

	b_1	s_1	b_2	s_2	b_3	s_3
	0.4133	0.7501	0.5360	0.8334	0.2480	0.6949
b_1	0.001452	0.000000	0.000000	0.000001	0.000002	0.000005
s_1		0.000902	0.000000	0.000001	0.000002	0.000006
b_2			0.002075	0.000009	0.000030	0.000109
s_2				0.000462	0.000019	0.000070
b_3					0.004203	0.000768
s_3						0.002792

have taken place as early as 1954. Accordingly, the data were split into recoveries from Denmark and recoveries from abroad (Tables 3 and 4). This splitting of data rests on a number of assumptions, the most important of which is that all individuals are either migratory or resident, implying, for example, that they do not become more resident with age. With respect to the latter, Nielsen (1977) has shown that the fraction of recoveries of adults from abroad is only slightly smaller than the fraction of juveniles (48% of juveniles vs. 43% of adults, difference not significant). Moreover, a tendency for increased residency with age should be discernible in the estimated survival rates.

Survival rate estimates for these two groups of recoveries are in accordance with expectations. For the recoveries from Denmark, estimated survival is higher after the

1967 Protection, while recoveries from outside Denmark show a high first year survival for the period 1954-66 (Table 6). For the recoveries from Denmark the null hypothesis is accepted but, if this result is disregarded and the analysis continued, pooling of data until 1966 shows that the period 1967-77 had significantly higher survival rates than before 1967 and after 1977 (Table 9). For the recoveries from abroad, the null hypothesis is rejected, and a significant difference is found between the periods before 1954 and 1954-66 (Table 10). These results suggest that survival rates increased following the 1954 change in the start of the open season. Further analysis shows that there was no significant change after 1967 but there was a highly significant decrease in survival rates after 1977 (Table 10).

Estimated survival rates for birds ringed

Table 9. Results of sequential Likelihood-ratio tests of differences between periods in survival rates for Buzzards ringed as pulli and recovered in Denmark. Survival rate estimates are given in Table 6.

	χ^2	df	P
H ₄ vs. H ₀	11.2722	6	8.03%
H ₄ - H _{3A}	0.3442	2	84.19%
H ₄ - H _{3B}	4.4310	2	10.91%
H ₄ - H _{3C}	6.3772	2	4.12%
H _{3A} - H _{2A}	6.3836	2	4.11%
H _{3A} - H _{2B}	6.6870	2	3.53%

Table 10. Results of sequential Likelihood-ratio tests of differences between periods in survival rates for Buzzards ringed as pulli and recovered outside Denmark. Survival rate estimates are given in Table 6.

	χ^2	df	P
H ₄ vs. H ₀	21.1854	6	0.17%
H ₄ - H _{3A}	8.5196	2	1.41%
H ₄ - H _{3B}	2.5196	2	28.37%
H ₄ - H _{3C}	11.5380	2	0.31%
H _{3B} - H _{2B}	9.4578	2	0.88%
H _{3B} - H _{2C}	10.7634	2	0.46%

as fully fledged and recovered in Denmark reveal a corresponding variation through the periods under consideration, though estimates of adult survival are somewhat higher (Table 6). The material is, however, sparser. The null hypothesis is rejected, but further analysis shows that this rejection stems from a significant decrease in survival rates after 1977 (Table 11). Changes in survival rates after the 1967 Protection are not significant. However, these changes are generally in agreement with the predictions, and first year survival rates 1954-66 for migrants are similar to those after 1967 for residents (Table 6). This is taken to suggest that first year survival actually increased by some 12% following escape from shooting pressure in Denmark.

Distribution of monthly mortality

Monthly distributions of recoveries from Denmark of individuals shot and recovered from other death causes (Fig. 3) were compared by Median tests (Siegel 1956). The relevant results are:

- 1) Following the 1954 Government Order, the distribution of individuals recovered as shot changed significantly ($\chi^2 = 12.54$ computed with Yates' correction), $df = 1$, $P < 0.0005$).
- 2) At the same time, the distribution of first year individuals recovered from other death causes also changed significantly ($\chi^2 = 6.88$, $df = 1$, $P < 1.0\%$). In both cases, recoveries were made later in the years after 1954.

Table 11. Results of sequential Likelihood-ratio tests of differences between periods in survival rates for Buzzards ringed as fully fledged and recovered in Denmark. Survival rate estimates are given in Table 6.

	χ^2	df	P
H ₃ vs. H ₀	12.98	4	2.67%
H ₃ - H _{2A}	3.22	2	19.99%
H ₃ - H _{2B}	7.87	2	1.95%

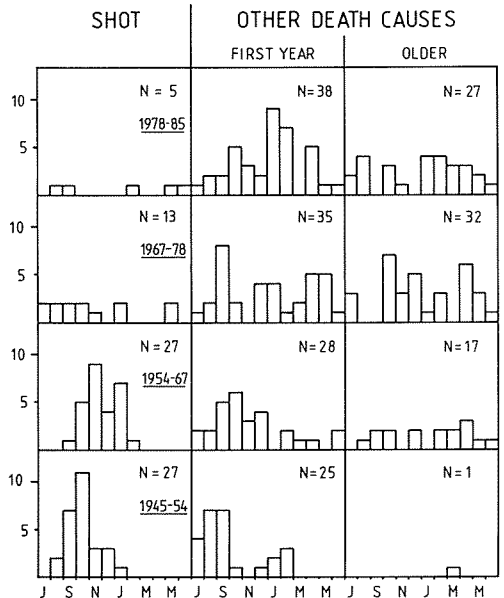


Fig. 3. Monthly distributions of recoveries of Common Buzzards either shot or recovered from other death causes in four different periods. Only recoveries from Denmark are included. Periods extend from 1st July of first year to 30th June of last year. For recoveries of shot individuals, age classes are pooled (no differences between 1st year and older were discernible).

- 3) Distributions of first year individuals 1954-66 and 1978-85 (the two periods of relatively stable population size) are significantly different ($\chi^2 = 4.71$, $df = 1$, $2.5\% < P < 5.0\%$). The period of population growth (until 1978) is intermediary and not significantly different from either.
- 4) There are no detectable changes in distributions of recoveries of older birds (1954-66 vs. 1978-85: $\chi^2 = 0.14$; 1954-66 vs. 1967-77: $\chi^2 = 0.50$; and 1967-77 vs. 1978-85: $\chi^2 = 1.47$). As shooting pressure affects individuals in their first autumn to a much larger extent, the relative constancy of distributions of recoveries of older birds is further evidence that the observed changes are caused by

changes and/or reductions in shooting pressure following changes in legislative protection.

Discussion and comments

Recoveries from Denmark of shot individuals suggest that shooting of this species did not cease until some years after the 1967 Protection (Table 12). In contrast to the period 1945-66, however, individuals that were shot in Denmark 1967-71 came mainly from regulation carried out near Pheasant pens. Comparison of the two periods, moreover, shows that in the period 1945-66, 45 individuals were recovered as shot and 65 from other causes of death (Danish recoveries only) while, in 1967-71, 14 were recovered as shot and 65 from other causes. This difference is significant ($\chi^2 = 4.69, P < 0.05$), and it is concluded that the 1967 Protection, notwithstanding the exemptions, did cause a significant reduction in the shooting pressure imposed on the species.

The interpretation of the partial analyses of recoveries from Denmark and from abroad is less certain. The number of recoveries of adults from abroad increased significantly after the 1954 change in open season dates, in spite of small numbers of recoveries before 1954, which is in excellent agreement with the predictions. Moreover, changes in first year survival were not observed for this group of birds after 1967, while recoveries from Denmark indicate increased survival after that year. The tendency for adult survival to show an increase after 1967 rather than after 1954 could be explained if adults migrate later in the year.

In a number of cases it has been demonstrated for partially migratory species that there is a genetical component involved in controlling whether or not to migrate (Berthold & Querner 1981, Biebach 1983, Berthold 1988). Thus, if there is a genetic component involved for the Buzzard, the results

Table 12. Age distributions of Buzzards ringed as pulli and recovered as shot in either Denmark (left) or abroad (right).

Year born	Recovered in Denmark								Abroad			
	Age	1	2	3	4	5	6	7	8	1	2	3
1945			2									
46		1										
47	2		1							2		
48	2											
49	3		1							1		
1950	1											
51	2											
52	3	1										
53	1									1		
54	1	2										
1955	3	2		1						1		1
56	1										1	
57	2											
58		1								1		
59	1				1							
1960												
61	3	1										
62												
63												
64										1		1
1965	6									3		
66	1											
67	1	1	1	1								
68	1									1		
69	2									1		
1970	4		1									
71	2											
72												
73												
74									1			
1975												
76												
77												
78												
79												
1980						1						
81												
82												
83	3											
84	1											
1985	1											
86												
87	1											

presented here strongly suggest that the 1954 change in the start of the open season caused selection in favour of the migratory part of the population. For a partially migratory population of Blackcaps *Sylvia atricapilla*, Berthold et al. (1990) were able to increase the frequency of migrants from 0.8 to 1.0 in three generations and, though this was done at considerably higher selection pressures than in the present case, it can be taken as a demonstration that such populations can respond very fast to changes in selection pressures.

It should be noted that the migratory part of the Buzzard population spends part of the year in Denmark. Some recoveries of migratory individuals will thus be included in the survival rates estimated for the resident part of the population; numbers of recoveries from those months are, however, low (Fig. 3). Moreover, survival rates for recoveries from Denmark and from abroad from 1954-66 are not significantly different, and so it remains speculative whether or not the increase was real. The overall trends in the material suggest that it was so but, whether or not this argument is accepted, it must be realised that the pooling of recoveries for survival rate estimation of partially migratory species may be difficult to justify.

The decrease in survival rates after 1977 (Table 6) is probably overestimated. When combined with the observed reproductive success, the estimated survival rates predict the population to be rapidly decreasing, even though its size has been very constant since that year (Jørgensen 1989). The probable reason for this underestimation is that the assumption of age independent survival after the first year only represents an approximation for the Buzzard, and that in fact survival is lower for second and third year individuals, too (Noer, in press). Although goodness-of-fit tests do not show significant deviations between observations and the model (App. I, but note the

discussion given there), this may be due to the relatively small data set. Investigation of this effect by treating earlier data as incomplete and comparing the estimated survival rates to those eventually observed confirms this tendency (Noer, unpublished). It should be noted that the significance level of the decrease in survival rates may be changed by future analyses of this species.

Sparrowhawk

Material

Recoveries of 901 Sparrowhawks ringed in Denmark were available. These recoveries stem from three different sources (Table 13)

Table 13. Sources of recoveries of Sparrowhawks in three different periods.

	Recovered		Recap- tured
	Ringed as:		
	Pulli	Juv.-ad.	
<i>1916-1944:</i>			
Zoological Museum, Copenhagen	12	6	1
P. Skovgaard, Viborg	71		
Total	83	6	1
<i>1945-1966:</i>			
Zoological Museum, Copenhagen	102	32	14
P. Skovgaard, Viborg	27		
Total	129	32	14
<i>1967-1987:</i>			
Zoological Museum, Copenhagen	451	122	54
P. Skovgaard, Viborg	5		
Game Biology Sta- tion, Kalø		3	
Total	456	125	54

but the material is rather heterogeneous. Before 1973, most Sparrowhawks were ringed either on Sjælland (Holstein 1950, Schelde 1960) or in West Jylland. In 1973 the Raptor Research Group of the Danish Ornithological Society initiated an intensive ringing scheme in Jylland, and the increased numbers of recoveries after that year originate from their work. When investigating the outcome of the 1967 Protection, the material is therefore not very balanced, especially as a much smaller fraction of the Sjælland and West Jylland population is resident (e.g. Schelde 1960). The analyses presented in this paper were preceded by separate treatments of the various parts of the country mentioned above. As far as comparisons could be made, all trends were convincingly similar. Accordingly, pooling of the total data set is considered justified.

Brood-sizes

From the beginning of the period under analysis, brood-sizes were significantly lower than those reported by Holstein (1950), and 95% confidence limits for the two first of the eight periods examined do not overlap (Table 14). No significant changes were found in brood-sizes between 1950 and 1979, but a significant increase

(no overlap of 95% confidence limits of mean) has taken place since 1980. This increase was also reported by Jørgensen (1989) and Brøgger-Jensen et al. (1988 and 1989). The average brood-size for the years 1980-85 is significantly different from all other periods between 1950 and 1979, but not different from those observed before 1950. The observed change in average brood-size was rather dramatic. The averages for 1980, 1981, and 1982 were 3.35 ($n = 110$), 3.46 ($n = 112$) and 3.72 ($n = 114$) respectively. These increases may have been influenced by a reduced number of younger birds breeding after the severe winters from 1978-79 onwards (Jørgensen 1989).

Survival rates

For the Sparrowhawk, protective legislation was introduced in 1922 and the open season prolonged by the 1931 Game Act (Table 1). The effects of the introduction of a closed season in 1922 cannot be evaluated (Tables 15 and 16), but the ratio between recoveries of shot individuals and recoveries from other death causes from 1922-31 is the same as it was before 1922. This is not so, however, after 1931 (Table 16). Even though the open season for the Sparrowhawk was prolonged, the ratio between recoveries of shot individuals and other

Table 14. Brood-sizes of Sparrowhawks. Distributions of brood-sizes (1-6), number of broods investigated (N), mean brood-size and 95% confidence limits of means given for 5-year periods. Periods are adjusted in relation to the reductions in the use of DDT from 1969 onwards.

Broodsize	1	2	3	4	5	6	N	Mean	95% c.l.
Period:									
< 1950	3	6	23	27	22	3	84	3.81	3.60-4.05
1950-54	4	5	7	6	1	1	24	2.92	2.36-3.47
1955-59	7	7	10	11	7	0	42	3.10	2.68-3.51
1960-64	7	14	19	18	11	4	73	3.33	3.17-3.48
1965-69	10	12	15	16	8	4	65	3.18	2.82-3.53
1970-74	28	24	29	40	27	9	157	3.26	3.02-3.50
1975-79	57	45	98	91	63	13	367	3.26	3.19-3.33
1980-85	54	95	135	177	181	40	682	3.67	3.57-3.77

Table 15. Age distributions of recoveries of Sparrowhawks ringed as pulli and recovered in Denmark before 1945. Individuals recovered as shot are excluded. Underlined entries indicate years in which change in protective legislation was effected (1922 and 1931). Asterisks indicate cold (*) and severe (**) winters.

Age	1	2	3	4	5	6	7	8	9	10
Year born										
1915		1							1	
16**	2	1								
17	1									
18	2	1								
19	1									
1920	<u>1</u>	<u>2</u>								
21**		1								
22										
23**										
24	1									
1925										
26										
27*										
28**										
29										
1930*	<u>1</u>	<u>2</u>								
31	1					1				
32	2	3					1			
33	1	1								
34	2		1			1				
1935										
36	1									
37	1									
38	1									
39**	1									
1940**										
41**	1	1								
42	2	1			1					
43*										
44										

Table 16. Age distributions of recoveries of Sparrowhawks ringed as pulli and recovered in Denmark before 1945. Shot individuals only.

Age	1	2	3	4	5	6	7	8	9	10
Year born										
1915	3	1								
16	4				1					
17	2		1							
18	2	1		<u>1</u>						
19	3	1								
1920	2				2					
21	<u>1</u>									
22										
23										
24										
1925	1	1								
26										
27	1									
28	1									
29										
1930	<u>2</u>									
31	1									
32										
33	2									
34										
1935										
36	1									
37	4									
38	1									
39										
1940										
41	1	1								
42	1									
43				1						
44	2									

death causes decreased. Comparisons between recoveries of shot individuals and those which died from other causes in the periods before 1922, 1922-30 and 1931-44 show that the decrease is significant ($\chi^2 = 6.87$, $df = 2$, $P < 0.05$). Furthermore survival rate estimates are higher in the period 1931-35. Before 1931, estimates are $\hat{b} = 0.5000$ and $\hat{s} = 0.5333$, for 1931-35 estimates are $\hat{b} = 0.6000$ and $\hat{s} = 0.6452$ (both

periods counted as complete). Due to the very sparse material, all of these estimates are both tentative and insignificant.

Because of the possible changes in survival rates for the species after 1930, recoveries from this period were not pooled with those from the period 1945-53. After 1967, shooting decreased abruptly as a mortality factor in Denmark (Tables 17 and 18). Recoveries of non-shot individuals outside

Table 17. Age distributions of recoveries of Sparrowhawks ringed as pulli and recovered in Denmark after 1945. Individuals recovered as shot are excluded. Underlined entries indicate: years in which change in protective legislation was effected (1954 and 1967), the start of population growth observed in the field (1971), the reversal of the population trend (1978) and the last year investigated (1987). Asterisks indicate cold (*) and severe (**) winters.

Age	1	2	3	4	5	6	7	8	9	10	11
Year born											
1945											
46**	1			1							
47	1	1									
48											
49	1	1						1			
1950											
51	2										
52											
53*	<u>2</u>										
54*	3										
1955**	2	1									
56	2		1								
57*											
58		1									
59	3		1								
1960	4										
61	2	1			1						
62**	3		1			1					
63	1										
64	5										
1965**	1			1							
66			1						1		
67	3		1								
68*	2			1							
69**	8	<u>1</u>									
1970	<u>2</u>				1						
71	6										
72	2	3		1		<u>1</u>					
73	6	5	1			<u>1</u>			1		
74	13	2	1	<u>2</u>	1	1	1			1	1
1975	11	2	<u>4</u>	2	3	1	1				
76	6	<u>3</u>	1	1	1			1	2		
77	<u>26</u>	10	6								
78**	14	2		1							
79*	10	2									
1980	30	3	3	1		2		<u>1</u>			
81**	24	1	2	1	1	1					
82	27	6	5	1	4						
83	23	10	2	2							
84**	38	11	5	<u>3</u>							
1985**	36	2									
86**	22	<u>4</u>									
87	<u>13</u>										

Denmark include a single individual recovered at a high age (21 years) (Table 19); this single recovery adds about 2-3% to the survival rate estimates given in the following. Recoveries of birds ringed as fully fledged are given in Table 20.

Survival rate estimation based on recoveries from Denmark and from abroad are in agreement with those for the Buzzard (cp. Tables 17 and 19), although the number of recoveries from outside Denmark is very low. Therefore, only survival rates based on the pooled material are presented in the following. Estimates are higher after both the 1954 postponement of the start of the open season and the 1967 Protection (Table 21). The Likelihood-ratio tests reject H_0 , while H_{3A} and H_{3C} are accepted (Table 22). The analysis is continued from H_{3A} , and H_{2A} is rejected while H_{2B} is accepted. Thus, the rejection of H_0 is due to the decrease in survival after 1978, and there are no significant effects of either the 1954 change or the 1967 Protection.

Data from a study area around Sorø, however, indicate that the Sparrowhawk population did not increase until after 1970 (cp. p. 36 and Fig. 7 below). Though the validity of extrapolating from this population to the total Danish population is uncertain, a large fraction of the recoveries stems from individuals ringed there. Survival of the species was therefore reinvestigated, using the periods: 1945-66, 1967-70, 1971-77 and 1978-1987. For these time periods, the increase in survival after 1970 becomes very pronounced (Table 21). H_0 is rejected very

convincingly, H_{3A} is accepted, while both H_{2A} and H_{2B} are rejected (Table 23). Accordingly, it is concluded that for the Spar-

rowhawk there were no immediate effects resulting from the 1967 Protection, though survival rates were high in 1971-77 (inclusive). In particular, changes in first year survival were pronounced, while changes in adult mortality were much less so (Table 24).

Distribution of monthly mortality

Comparison of monthly distributions of recoveries by median tests (Siegel 1956) reveals that the only significant difference is a change in the distribution of recoveries of shot individuals after 1953 (Fig. 4). The lack of significance in the monthly distributions of individuals recovered from other death causes may be due to small sample sizes, but inspection of Fig. 4 suggests that the distributions did not change. This is in contrast to the results for the Buzzard (p. 20) and for the Kestrel (Noer & Secher 1983).

Discussion and comments

The significant decrease in numbers of recoveries of shot individuals after 1931 is surprising when it is considered that the 1931 Game Act actually prolonged the open season for the Sparrowhawk. However, this result is in accordance with results for the Kestrel reported by Noer & Secher (1983). The Kestrel was protected in Denmark by the Government Orders of 1925 and 1928. This protection was enacted in 1931. Noer & Secher (1983) showed that the two Government Orders did not have any effect on survival rates and that survival rates increased after 1931, coinciding with a significant decrease in the number of recoveries of shot individuals. Thus, results for both the Kestrel and the Sparrowhawk suggest that legislative measures taken at different times do not receive equal attention, and that the 1931 Act was particularly heeded.

Table 18. As Table 17. Age distributions of Sparrowhawks ringed as pulli and recovered as shot in Denmark.

Age	1	2	3	4	5	6	7	8	9	10
Year born										
1945				1						
46										
47										
48	1									
49										
1950	2									
51	2									
52		1								
53	3									
54	1									
1955	3	1								
56	1									
57	2		1							
58										
59										
1960	1	1								
61	5	1	2	1						
62	3	1								
63		1	2							
64	3	1								
1965	3									
66	1									
67										
68	1									
69										
1970										
71										
72										
73										
74										
1975						2				
76										
77				1						
78										
79										
1980							1			
81	1									
82										
83										
84										
1985	2									
86	1									
87										

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Table 19. As Table 17. Age distributions of Sparrowhawks ringed as pulli and recovered outside Denmark. Individuals recovered as shot are excluded.

Age	1	2	3	4	5	6	7	8	9	10	..	21
Year born												
1945												
46												
47	2											
48												
49	1	1										
1950	1											
51	1											
52												
53	2	1										
54												
1955	3	1			1	1						
56	2	1										
57												
58												
59	1											
1960	1											
61												1
62	1											
63	1										1	
64												
1965	1											
66												
67												
68												
69												
1970	2											
71					1							
72		1										
73	1											
74					1							
1975	1	1										
76	1			1								
77	1	1										
78	3											
79	1											
1980	1											
81												
82												
83	1	1										
84	5	1										
1985	1											
86	3											
87	1											

Table 20. As Table 17. Age distributions of Sparrowhawks ringed as fully fledged and recovered in Denmark. Individuals recovered as shot are excluded.

Age	1	2	3	4	5	6	7	8	9	10
Year born										
1945										
46										
47										
48	1									
49										
1950										
51										
52										
53										
54	1									
1955	1									
56	1									
57	1									
58										
59	1	1								
1960										
61										
62										
63	2									
64	2									
1965	1									
66			1							
67	1									
68										
69	2	1								
1970	1									
71	1									
72										
73	1									
74	3									
1975	1									
76	1	1		1						
77										
78	1			1						
79	3	1								
1980	3									
81	2	2								
82	2									
83	4		1							
84	3									
1985	4									
86	1									
87										

Table 21. Survival rate estimates for Sparrowhawks based on four periods of different survival rates. Estimates based on A) the total material for pulli in periods before 1954, 1954-66, 1967-77 and 1978-87, B) before 1967, 1967-70, 1971-77 and 1978-87, and C) pulli + fully fledged in periods before 1967, 1967-70, 1971-77 and 1978-87. Individuals recovered as shot are excluded.

A			B		C	
1940-53:	b_1	0.3000	1940-66:	b_1	0.3151	0.2824
	s_1	0.6000		s_1	0.6600	0.6087
1954-66:	b_2	0.3208	1967-70:	b_2	0.1905	0.2501
	s_2	0.6750		s_2	0.7728	0.6667
1967-77:	b_3	0.4493	1971-77	b_3	0.4870	0.4781
	s_3	0.7363		s_3	0.7295	0.7224
1978-87:	b_4	0.2857	1978-87:	b_4	0.2858	0.2770
	s_4	0.5956		s_4	0.5959	0.5860

Table 22. Results of sequential Likelihood-ratio tests of differences between periods in survival rates of Sparrowhawks ringed as pulli. Pooled data from Tables 17 and 19 and survival rates from Table 21. Periods under analysis are: before 1954, 1954-66, 1967-77 and 1978-87.

	χ^2	df	P
H_4 vs. H_0	17.1596	6	0.87%
$H_4 - H_{3A}$	0.2260	2	89.32%
$H_4 - H_{3B}$	16.3188	2	0.03%
$H_4 - H_{3C}$	3.3480	2	18.75%
$H_{3A} - H_{2A}$	16.3188	2	0.03%
$H_{3A} - H_{2B}$	4.8720	2	10.75%

Table 23. Results of sequential Likelihood-ratio tests of differences between periods in survival rates of Sparrowhawks ringed as pulli. Pooled data from Tables 17 and 19 and survival rates from Table 21. Periods under analysis are: before 1967, 1967-70, 1971-77 and 1978-87.

	χ^2	df	P
H_4 vs. H_0	22.5050	6	0.12%
$H_4 - H_{3A}$	0.5948	2	74.27%
$H_4 - H_{3B}$	8.6934	2	1.29%
$H_4 - H_{3C}$	19.6466	2	0.01%
$H_{3A} - H_{2A}$	19.5410	2	0.01%
$H_{3A} - H_{2B}$	9.8486	2	0.73%

Table 24. Estimated survival rates and covariance matrix for Sparrowhawks ringed as pulli. The estimates are for the model resulting from the analysis, i.e. with three periods of different survival rates (before 1970, 1971-77 and after 1977).

	b_1	s_1	b_2	s_2	b_3	s_3
	0.2873	0.6945	0.4870	0.7295	0.2858	0.5959
b_1	0.002178	0.000000	0.000000	0.000000	0.000000	0.000001
s_1		0.002947	0.000000	0.000000	0.000000	0.000001
b_2			0.001735	0.000003	0.000004	0.000021
s_2				0.001673	0.000003	0.000017
b_3					0.000770	0.000281
s_3						0.001443

Compared to the other three species analysed it is striking that no immediate increase of survival rates can be observed for the Sparrowhawk following the 1967 Pro-

tection. This is hardly due to a too sparse material as 29 individuals were recovered from the 1967-70 cohorts (Tables 17-20). Instead, it can be taken to indicate that for

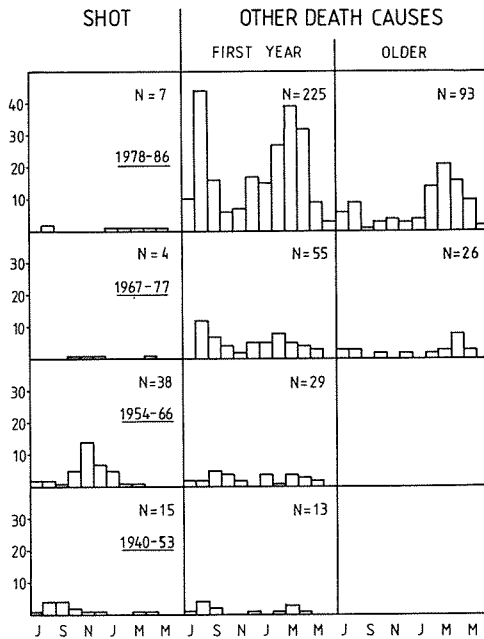


Fig. 4. Monthly distributions of recoveries of Sparrowhawk either shot or recovered from other death causes in four different periods. Only recoveries from Denmark are included. Periods extend from 1st July of first year to 30th June of last year. For recoveries of shot individuals, age classes are pooled (no differences between 1st year and older were discernible).

the Sparrowhawk factors other than the 1967 Protection caused the increased survival rates, but this is complicated by the sensitivity of the species to winter severity (e.g. Newton 1986, Brøgger-Jensen et al. 1988). Severe winters are indicated by asterisks in Tables 15 and 17, and it is seen that winters were unfavourable in the first years after protection. The winter 1969-70 was particularly severe, and this appears to be reflected in the recoveries from the 1969 cohort, 10 out of 12 of which were recovered during this winter.

The monthly distributions of recoveries of first year and older individuals after 1977 are very similar to those reported for British Sparrowhawks by Newton (1986). For first year individuals, there is clearly a

large mortality at the time of year when they become independent and mortality is also high during winter, in particular in the severe winters after 1977.

The latter is true for adults too (cp. Table 17 and App. I). The Sparrowhawk data are well suited for an analysis of winter mortality along lines similar to those developed for British Herons (North 1979, North & Morgan 1979), but such an analysis is considered outside the scope of the present treatment. Comparison of winter mortalities of different species show that while Kestrels and Buzzards are recovered in January-February, Sparrowhawks are recovered mainly in late February-March. This difference is significant (Median tests, $P < 0.01$) and commented in the Discussion (p. 46).

Goshawk

Material

Altogether, 586 recoveries of Goshawks were available for the present study. The majority of these, however, were ringed after the establishment of the Raptor Research Group of the Danish Ornithological Society in 1973. Older records are very sparse, the first being from 1942. With very few exceptions all were ringed as pulli. Thirty recoveries have been reported outside Denmark, mostly after 1975. All of these stem from Schleswig-Holstein or Scania, and they have been pooled with the recoveries from Denmark. The number of controlled individuals is also small (Table 25).

Brood-sizes

During the period 1950-1964 brood-sizes were low (Table 26) but, given the low population density of the species (see p. 36), this may have been caused by a high frequency of first time breeders (young/sub-adult

Table 25. Sources of recoveries of Goshawks in three different periods.

	Recovered		Recap- tured
	Ringed as:		
	Pulli	Juv.-ad.	
<i>1917-1944:</i>			
Zoological Museum, Copenhagen	3		
P. Skovgaard, Viborg	29		
Total	32		
<i>1945-1966:</i>			
Zoological Museum, Copenhagen	37		
P. Skovgaard, Viborg	3		
Total	40		
<i>1967-1987:</i>			
Zoological Museum, Copenhagen	469	1	44
Total	469	1	44

birds) in any breeding year. There is no evidence to suggest that the species has been affected by pesticides (Jørgensen 1989), though there is no data on the relative frequency of successful pairs for the periods before 1973. However, judging from Table 26, brood-sizes have not

changed since the mid 1960's and, from 1965 onwards i.e. some years before the start of the population growth, they were as high as earlier recorded (Holstein 1942).

Survival rates

Except for three individuals, all recoveries before 1940 were either shot during the hunting season or resulted from human persecution. Thus, the effects of legislative protection in the 1920's cannot be evaluated for this species. Due to the very small material from the period 1940-53 (Tables 27 and 28) the effects of the 1954 change cannot be tested either. Hence, analysis has been carried out using the estimation model with three periods (before 1967, 1967-77 and 1978-87) as described by Noer (in press). As for the other species, survival rates show increases after 1967 (Table 29). On the basis of the Likelihood-ratio tests, H_0 is accepted (Table 30) but, as survival rate estimates are in good agreement with those found for the other species, this could well be due to the smaller material. Survival rates immediately after 1967 are identical to those from 1973 onwards, indeed one of the oldest Goshawks recovered in Denmark derives from the 1967 cohort (Table 27).

The number of recoveries of shot individuals decreases after 1967 (Table 28).

Table 26. Brood-sizes of Goshawks. Distributions of brood-sizes (1-5), numbers of broods investigated (N), mean brood-sizes and 95% confidence limits of means given for 5-year periods. Periods are adjusted in relation to the reductions in the use of DDT from 1969 onwards. Due to small sample sizes data from the period 1950-64 have been pooled.

Brood-size	1	2	3	4	5	N	Mean	95% c.l.
Period:								
1945-49	1	2	2	1	0	6	2.50	
1950-54	5	2	1	0	0	8	1.97	1.66-2.28
1955-59	3	10	4	2	0	19		
1960-64	4	5	0	1	0	10		
1965-69	3	5	12	0	0	20	2.45	2.09-2.81
1970-74	10	15	18	13	0	56	2.61	2.33-2.89
1975-79	57	155	196	53	0	461	2.53	2.45-2.61
1980-85	99	227	355	88	1	770	2.56	2.50-2.63

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Table 27. Age distributions of recoveries of Goshawks ringed as pulli. Recoveries from Denmark and from outside Denmark (very few) have been pooled. Individuals recovered as shot are excluded. Underlined entries indicate periods of unchanged hunting legislation (changes effected in 1954 and 1967), the year in which the growth in the population decreased (1978), and the last year investigated (1987).

Age	1	2	3	4	5	6	7	8	9	10	11	12	13
Year born													
Before													
1945	7	3			1								
1945													
46	1												
47	1												
48													
49	3												
1950		2		<u>1</u>									
51	1												
52													
53													
54													
1955													
56	1												
57	1	1											
58	1												
59				1									
1960													
61													
62													
63	1	1											
64													
1965	1												
66													
67	1		1										
68		1											
69	1												
1970	2	3											
71	2												
72	3												
73		1		1									
74	4	2	3	<u>1</u>	1					1	1		
1975	7	6		1	2								
76	11	<u>2</u>					1	1					
77	<u>18</u>	1	5		3	1	1	2					
78	15	7	1	1		1			1				
79	17	8	7		1	1			<u>1</u>				
1980	20	4				1		<u>1</u>					
81	20	3		2	1	2							
82	21	3	1	2	1								
83	8	5	1	2	<u>1</u>								
84	10	3	7	<u>2</u>									
1985	16	3											
86	21	<u>5</u>											
87	<u>23</u>												

Table 28. As Table 27. Age distributions of recoveries of Goshawks ringed as pulli and recovered as shot.

Age	1	2	3	4	5	6	7	8	9	10	11
Year born											
Before											
1945	18	2	1								
1945	1										
46	1										
47											
48	1										
49	1										
1950	3	2	1								
51											
52											
53											
54											
1955											
56	2	1									
57	1										
58	1										
59	3										
1960											
61		1	1								
62	2										
63											
64											
1965											
66											
67											
68											
69											
1970											
71	1	1									
72											
73											
74											
1975											
76	1										
77	1										
78	1										
79	3	1		3	1						
1980											
81	5	2		1	1	1					
82	10	2		1							
83	4	5		1	1						
84	4	1									
1985											
85	5	1									
1985											
86	8										
87	2										
87	6										

Table 29. Survival rate estimates for Goshawks based on three periods of different survival rates (before 1967, 1967-77 and 1978-87).

		Other causes	Shot	Total
1940-66:	b ₁	0.3793		
	s ₁	0.5000		
1967-77:	b ₂	0.4818		0.4988
	s ₂	0.6388		0.6458
1978-87:	b ₃	0.4118	0.4435	0.4137
	s ₃	0.6837	0.7274	0.6932

However, it is seen that since the late 1970's the number of recoveries of shot Goshawks has again increased dramatically, this time caused by regulation of individuals under dispensation.

In order to improve estimation of survival rates after 1980, the two sets of recoveries were pooled (Table 29), but the decrease after 1980 is still insignificant. First year survival after 1967 is comparable to that of the Buzzard and the Sparrowhawk (Table 31).

Distribution of monthly mortality

Data sets for older records are too sparse to permit meaningful comparisons (Fig. 5). For the period 1978-85, control of the species was concentrated in July-September, coinciding with peak activity at Pheasant pens. Mortality from other death causes peaks in August-October for first year birds, while it is distributed evenly throughout the year for older birds.

Discussion and comments

Comparisons between numbers of shot individuals recovered in the different periods (Tables 27 and 28) reveal highly significant changes ($\chi^2 = 39.68$, $df = 2$, $P \ll 0.01$). Detailed comparison between the periods 1945-66 and 1967-77 (Tables 27 and 28) shows that after 1967 the number of shot

Table 30. Results of sequential Likelihood-ratio tests of differences between periods in survival rates of Goshawks ringed as pulli.

	χ^2	df	P
H ₃ vs. H ₀	4.4306	4	64.90%
H ₃ - H _{2A}	2.1632	2	33.91%
H ₃ - H _{2B}	1.8184	2	40.28%

individuals decreased significantly ($\chi^2 = 44.57$, $df = 1$, $P \ll 0.01$). Comparison between the periods 1967-77 and 1978-87 likewise shows a significant increase in numbers of individuals recovered as shot after 1977 ($\chi^2 = 10.27$, $df = 1$, $P < 0.01$).

The recoveries of shot Goshawks (Table 28) confirm a tendency already noted by Noer (in press) for the Buzzard (cp. Table 12). Amongst the recoveries of these two species and those of the Sparrowhawk (Table 18), the oldest recovery of a shot individual from the pre-1967 cohorts is 5 years. Initially, this might appear to confirm the general assumption that shooting pressure affects first year individuals more heavily than older ones. Calculations of survival rates based on recoveries of shot individuals, however, show that estimates for adult survival are far more heavily affected than estimates for first year survival. For the Buzzard, estimates based on shot individuals are $\hat{b} = 0.3043$ and $\hat{s} = 0.3913$, for the Sparrowhawk $\hat{b} = 0.3111$ and $\hat{s} =$

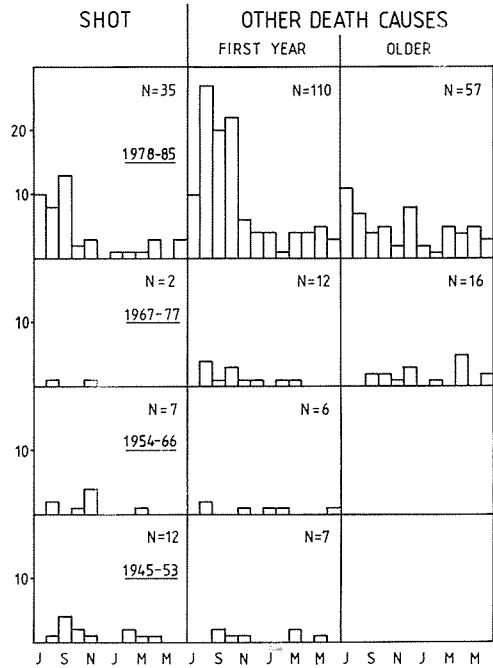


Fig. 5. Monthly distributions of recoveries of Goshawks either shot or recovered from other death causes in four different periods. Only recoveries from Denmark are included. Periods extend from 1st July of first year to 30th June of last year. For recoveries of shot individuals, age classes are pooled (no differences between 1st year and older were discernible).

0.3913, and for the Goshawk $\hat{b} = 0.2727$ and $\hat{s} = 0.2500$ (data in all calculations treated as complete). If it is assumed that learning is involved, then, as demonstrated

Table 31. Estimated survival rates and covariance matrix for Goshawks ringed as pulli. The estimates are for the model with three periods of different survival rates (before 1967, 1967-77 and after 1977). Note that this is the estimate used in the calculations of expected population growth, but not the model resulting from the statistical analysis.

	b_1	s_1	b_2	s_2	b_3	s_3
	0.3793	0.5000	0.4818	0.6388	0.4118	0.6837
b_1	0.008118	0.000000	0.000000	0.000000	0.000000	0.000000
s_1		0.012500	0.000000	0.000000	0.000000	0.000000
b_2			0.002661	0.000016	0.000024	0.000075
s_2				0.003510	0.000019	0.000059
b_3					0.001329	0.000520
s_3						0.001647

by Noer (in press), the fact that it is the estimates of adult survival that are by far the most biased implies that for these species more than one hunting season is needed before the necessary experience has been gained. Note that for the Goshawk, the age distribution of shot individuals after

1977 is identical to that for individuals recovered from other death causes (Tables 27 and 28, and cp. survival estimates in Table 29). This suggests that after a decade of protection the older individuals did not have the necessary experience to avoid shooting.

Discussion

Causes underlying the status improvements

Interpretation of the results

Summing up the evidence presented, no changes in reproductive success have been found that can explain the observed population growth. The secondary increases in brood-size for the Sparrowhawk occurred after 1980, i.e. after the population growth had ceased, and moreover these may have been partly due to a reduced fraction of first year individuals breeding (Jørgensen 1989) rather than to any increases in brood-size per se. Apart from the reduced brood-sizes for the Sparrowhawk in 1950-79, which influenced or possibly even caused the population decline, and the indications that brood-sizes of the Goshawk were low from 1950-64, there is no evidence that reduced reproductive success was the cause of the poor status of these species from 1960-70.

In contrast, there is much evidence that survival rates were high during the periods of population growth. For the Buzzard and probably the Goshawk, abrupt increases in survival followed the 1967 Protection. These results correspond to those found for the Kestrel by Noer & Secher (1983). For the Sparrowhawk, no increase was observed until after 1970, which is in good agreement with population trends. Even if these increases suggest that the improved survival rates were an important component of the population growth, it remains to be seen

whether they are indeed the sole explanation.

This question has been evaluated by means of computations of growth in age structured populations (by means of the Leslie matrix technique described on p. 13). Detailed information on reproductive success is given by Jørgensen (1989). However, almost no information has been published for one of the most important parameters in the population dynamics, namely, age at first reproduction. For this, it has been necessary to use figures published from other study areas.

Buzzard

Information on the status of the Buzzard before 1973 is sparse. Holstein (1956) estimated the total population at 1,500 pairs by 1955. Jørgensen (1989) accepted this estimate and judged that in 1965 the population size was 2,000 pairs. Although it is not stated on what evidence this figure is based, a slight increase in the population between 1955 and 1965 would be in agreement with the observed increase in survival after 1954 for the migratory part of the population. Accepting these figures, extrapolation from the 1955 and 1965 population sizes would imply that 2,118 pairs bred in 1967. Recent population estimates are 4,500-5,500 pairs by 1980 and 4,950 pairs by 1988 (Jørgensen 1989).

For the Buzzard, average brood-sizes

have been stable throughout the period 1945-88, but significant differences exist between brood-sizes in Jylland and the remainder of the country, 1.63 and 2.00 respectively (Jørgensen 1989). Population development has therefore been calculated separately for these two brood-sizes. According to Glutz von Blotzheim et al. (1971), some individuals breed at the age of two years. Therefore, population development has also been calculated separately for 0, 25 and 50% of the two-year old individuals attempting to breed. Results are given in Fig. 6. For a brood-size of 2.00, the population could by 1978 have reached a level of more than 4,000 pairs even if no second years bred. For a brood-size of 1.63, however, growth rates would be very much reduced, and the population level by 1978

would number only 2,500-3,000 pairs depending on the percentage of second year breeders. Note that, given the survival rates, the differences caused by brood-sizes of 1.63 and 2.00 are larger than those caused by 0 and 50% of two year olds breeding. Both populations have been stable over the past 10 years (Jørgensen 1989). How this is possible in spite of the very large brood-size difference is presently one of the most important unsolved problems in the population dynamics of Danish Buzzards.

The results presented in Fig. 6 show that the increase in survival rates can only explain the population growth for a brood-size of 2.00 (i.e. outside Jylland). This assumes, however, that the population size was 2,118 pairs by 1967. Dybbro (1976) esti-

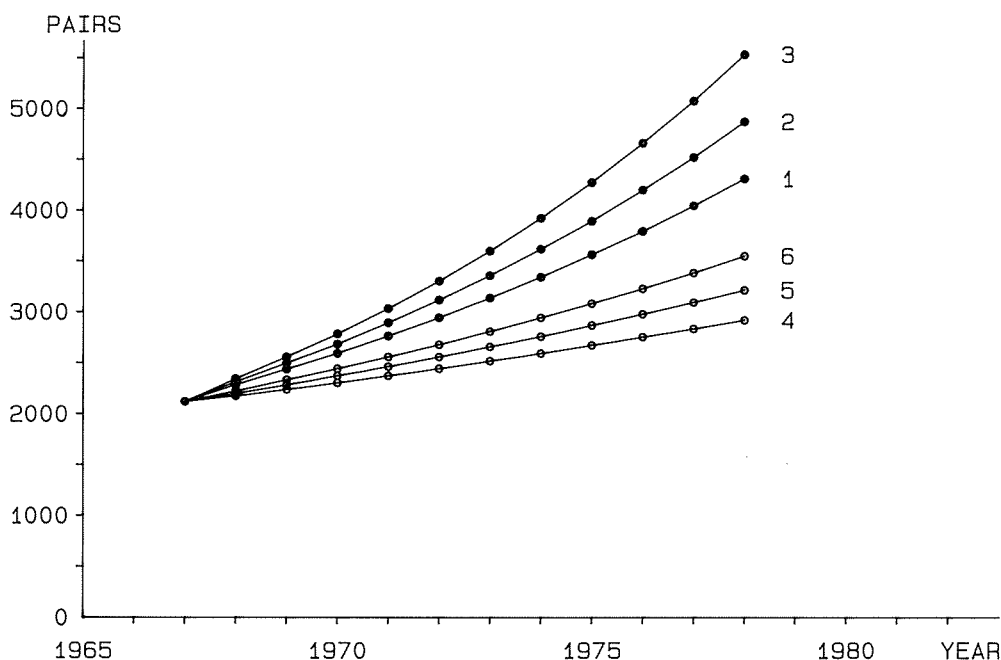


Fig. 6. Expected population growth of Common Buzzard 1967-78 based on the estimated survival rates. Data on reproduction and population development have been derived from Jørgensen (1989). Starting point is a population size of 2000 pairs in 1965. Since the population was estimated to be 1500 pairs in 1955 this corresponds to 2118 pairs in 1967. Percentage of successful pairs is 70.8 in all cases. Brood-sizes are 2.00 (1, 2 and 3) and 1.63 (4, 5 and 6) corresponding to populations on Sjælland and in Jylland, respectively (Jørgensen 1989). In all cases, it is assumed that no birds breed at the age of one year, and 100% breed at the age of 3 years. Different growth curves correspond to: 0% (1 and 4), 25% (2 and 5), and 50% (3 and 6) breeding at the age of 2 years.

mated the population size 1971-74 at 2,100-2,400 pairs, but Bomholt (1983) argued that this estimate was too low. Thus, the starting number used in the calculation is possibly too conservative. Bomholt (1983) judged the population to have grown by one third between 1970 and 1980. As this estimate was based on investigations in Jylland, the growth rate is in good accordance with the results for a brood size of 1.63 in Fig. 6.

As there are indications that the starting population size may have been too low and that the growth rate in Jylland is in accordance with expectations, it is concluded that the known facts about the growth of the Buzzard population could be explained by the observed survival rates 1967-77.

Population development after 1977 is not presented. With the survival rate estimates for this period the population would decline rapidly, in contradiction with the observed stability (see discussion on p. 22).

Sparrowhawk

There is no reliable information on the size of the total Sparrowhawk population before 1970-75. However, reliable information exists for a population at Sorø which was investigated in 1953-82 (Schelde 1960, Dyck 1983 and Jørgensen 1989). Although this population is rather small to be taken as representative of the overall development in Denmark, a large part of the recoveries concern birds ringed there. Accordingly, a simulation of the development of this population is considered relevant. Predicted and observed values are compared in Fig. 7. Although the increase in this population did not start until 1970, the evidence leaves open the possibility that growth actually did start in 1967 but was interrupted by the severe winters 1968/69 and 1969/70. The expected development is derived on the assumption that 50% of individuals aged one year breed, which cannot be too unrealistic in a low density popu-

lation such as existed in 1967 (with the corresponding stable age distribution, this would mean that about 17% of the breeding females were in their first year). The only figures on generation time that could be found in literature are those given by Newton (1986). In sharp contrast to the assumptions given above, he found that only 18% of the first year individuals bred, 45% of second years and 83% of the third years. These values would result in a population decline, even with the high survival rates of 1971-77, as with the (very similar) survival rates found by Newton (1986). However, Newton's ages at first breeding were found for a population that declined due to habitat reduction (Newton & Marquiss 1986) and are thus not representative for the situation in Denmark before 1980. Note that the implications here are that habitat reduction may affect population size through increased generation time, which is measurable within the sizes of the data sets under analysis.

The predicted population development fits the observed one convincingly, and it is concluded that the increase of at least this population can be fully explained by the increases in survival rates.

Goshawk

The Danish Goshawk population was estimated at 95-100 pairs in 1967 (Løppenthin 1967). During the years of the Atlas study the size of the population was estimated at 150-200 pairs (Dybbro 1976). No accurate counts, however, have been published before 1973, when the investigations by the Raptor Research Group of the Danish Ornithological Society were initiated (Dyck et al. 1981, Storgård & Birkholm-Clausen 1983a and b, Bomholt 1983). Accordingly, the comparisons only involve the period 1973-85.

Accurate numbers of breeding pairs for the southern parts of Jylland (10,700 km²) were given by Storgård & Birkholm-Claus-

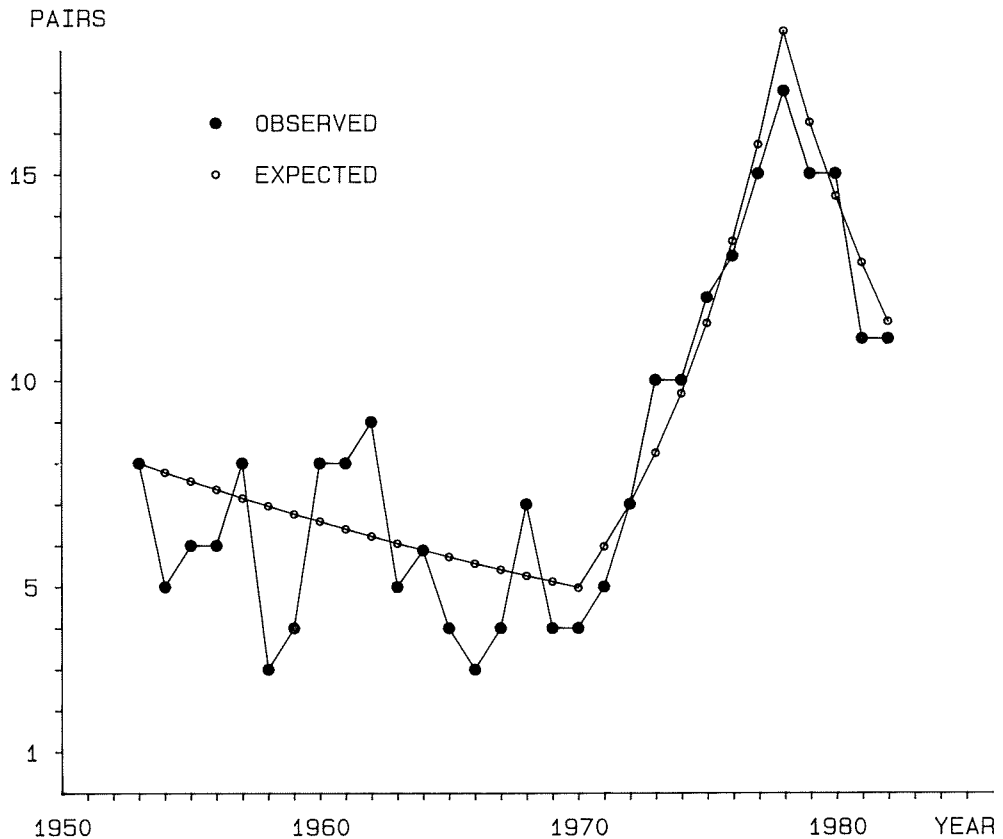


Fig. 7. Observed and expected population development of a Sparrowhawk population at Sorø, Sjælland, 1953-82. Expected growth has been calculated on the basis of estimated survival rates. Percentage of successful pairs is 62.4 (Jørgensen 1989), brood-size is 3.45 before 1980 and 3.80 after that year (both figures based on broods ringed in this area), and 50% of 1 year old females have been assumed to attempt breeding throughout the period.

en (1986) and Jørgensen (1989). These numbers are compared to expected numbers in Fig. 8. Data on reproductive success are derived from Jørgensen (1989), and the survival rate estimates used are those given in Table 26. With respect to age at first breeding, Jørgensen (1987 and 1989) stated that 10% of the breeding females in South Jylland were first years, while Nielsen (1986) stated that 25% of the (growing) population in North Jylland from 1977-86 were first year females.

Due to the gradually declining population growth in 1978-81 for the Goshawk in

South Jylland the expected population trends have been calculated separately for the periods of growth and decline. For South Jylland, it has been assumed that 25% of breeding females were in their first year in the period of population growth. With the corresponding age distribution this means that about 55% of the females breed at the age of 1 year and, as 25% of the breeding females were actually in their first year in North Jylland, this figure is assumed to be realistic. The population development in South Jylland after 1980 has been simulated using survival rate esti-

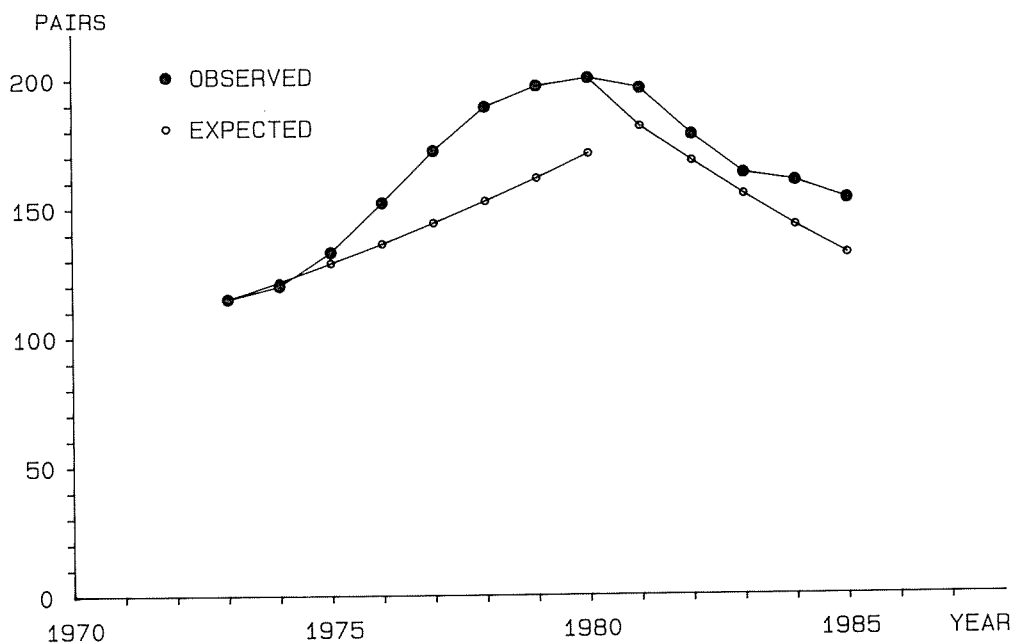


Fig. 8. Observed and expected population development of the Goshawk population in South Jylland, 1973-85. Expected growth has been calculated on the basis of estimated survival rates. Percentage of successful pairs is 77.10 and brood-size 2.60 (Jørgensen 1989). During the population growth period (starting 1973), 55% of 1 year old females have been assumed to attempt breeding; for the period of population decline (after 1980) 10%. The expected growth curve has been adjusted to the observed in 1980 in order to facilitate comparison of the negative growth rates.

mates from that period, even though they were not significantly different from those for 1973-70 and 10% of the breeding females were first year. For the population decline after 1980, observed and expected (negative) growth rates are in good agreement although for the period of population growth the predicted increase is somewhat lower than the observed (Fig. 8), even though the assumption that 55% of first year females breed may be too optimistic for this population. With the excellent reproductive data, this suggests that the estimated survival rates are too low. In particular, this could concern first year survival.

Further insight can be obtained for North Jylland, particularly because figures

for age-dependent reproductive success have been published by Nielsen (1986). Comparison between observed and expected population developments once again reveals that the predicted growth rate is too low (Fig. 9). There could, however, be more than one explanation for this result:

- 1) Survival rate estimates may be biased, – in particular, b may be too low (cp. Haukioja & Haukioja 1970),
- 2) the input survival rates are only estimates and thus they are not necessarily the true ones. Calculation of growth based on b and s , respectively + and – one standard deviation (roughly corresponding to 95% confidence limits), illustrates how large actual deviations

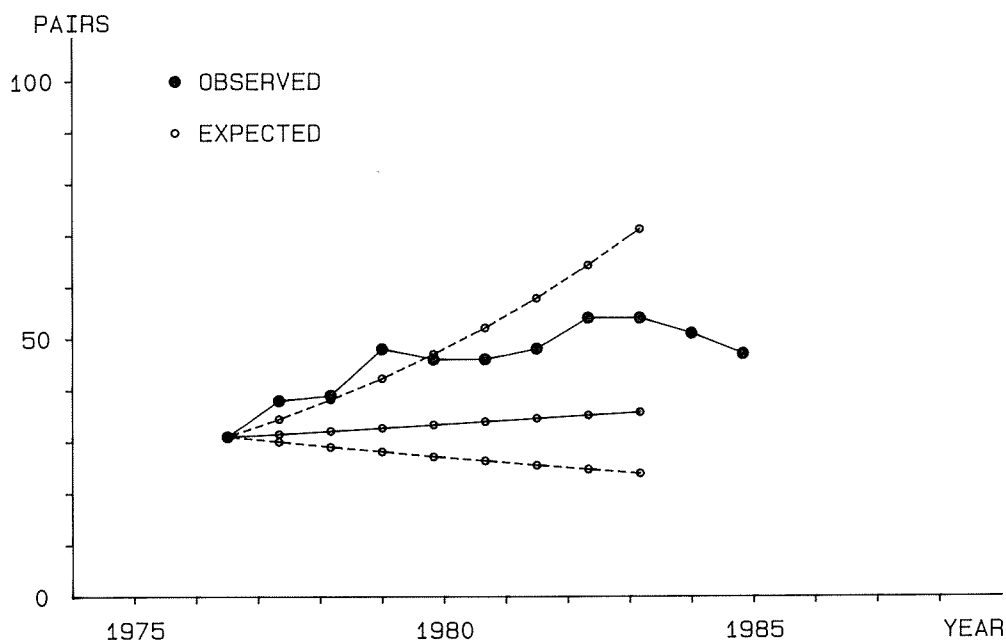


Fig. 9. Observed and expected population development of the Goshawk population in North Jylland. Expected growth has been calculated on the basis of estimated survival rates. Percentage of successful pairs is 54.7 for first year females and 75.7 for older individuals; brood-sizes are 2.17 and 2.63, respectively (Nielsen 1986). Of the 1 year old females 55% is assumed to breed. With the corresponding stable age distribution this is equivalent to 25% of breeding females being in their first year. Upper and lower expected curves are derived on the basis of survival rates \pm and -1 standard deviation, respectively.

- might be explained by random variation,
- 3) the population is not closed and immigration may take place. In particular, the high frequency of first year females in the breeding population and the possible emigration from South Jylland (see discussion on pp. 47-48) could support this, and
 - 4) confidence limits for predicted population growth would be even wider if uncertainty in reproductive parameters was also considered.

These difficulties in the interpretation show that the comparison of observed and expected population growth in order to check the reliability of survival rate esti-

mates as suggested by Lakhani & Newton (1983) is not necessarily efficient. It would be easy to demonstrate that estimated survival rates cannot be true, but it might be extremely difficult to show that this is caused by systematic errors in the statistical model and not by random variation in the estimates or other sources of error.

For the Buzzard and the Sparrowhawk it is therefore concluded that when the observed figures of reproductive success are combined with the estimated survival rates the population trends are described adequately. For the Goshawk, indications are that the estimated survival rates may be biased but, as shown, this bias is neither large nor grossly misleading. Hence, these results are interpreted to mean that the

changes in population sizes are explained by the observed changes in survival.

Causes of the increased survival rates

Restrictions on the use of DDT from 1969 onwards provide a very poor explanation of the findings. The secondary improvements of Sparrowhawk brood-sizes, which might be due to effects of these restrictions, came too late to be of any influence on the rapid recovery of the population which, at least on Sjælland, started abruptly in 1971 (Fig. 7). For the other species, no improvements in brood-sizes were found except possibly for the Goshawk in 1965-69 (Table 24). For the Sparrowhawk, moreover, eggshell indices were still low and DDE levels in addled eggs were still high by 1980 (Dyck 1983), in accordance with the long retention times of DDE in the environment (estimates of the half-life of DDE in soil vary between 12 and 57 years (Newton 1986) and measurements from West Germany indicate that DDE in Goshawk eggs declined by 50% in the four years following a DDT ban in 1971 (Conrad 1981)). Furthermore, the start of the Sparrowhawk population recovery is far too abrupt and early (starting the year after DDT was withdrawn from sale) to suggest any major influence (Fig. 7). Accordingly, it is concluded that reductions in DDT levels are unlikely to have influenced the population recovery even of the Sparrowhawk. This conclusion merely reiterates what has been found for Sparrowhawks in Holland (Opdam et al. 1987) and Great Britain (Newton 1979, 1981 and 1986, Newton & Hass 1984).

The fact that the status improvements were mediated through survival leaves open the possibility that either Aldrin (Fig. 1) or the 1967 Protection or both were causal factors. In principle, HEOD should affect survival of all age classes equally, in contrast to hunting which should mostly affect first year survival. The estimates are that

first year survival increased by 12% and adult survival by 8% for Buzzards ringed as pulli (Tables 6 and 8) and by 20% and 4% respectively for Buzzards ringed as fully fledged (Table 6). For Sparrowhawks, these increases were 20% and 4% for birds ringed as pulli (Tables 21 and 24), while no estimate could be given for birds ringed as fully fledged due to a too sparse material. For Goshawks, the increases were 8% and 14% (Tables 29 and 31), while for Kestrels ringed as pulli increases were 13% and 15% (recalculated from Noer & Secher 1983). Apart from the Sparrowhawk, therefore, these results leave open the possibility that age classes were equally affected and hence that reductions in the use of Aldrin could have contributed to the improved survival.

A number of other points, however, contradict this possibility. For the Buzzard, the Goshawk and the Kestrel (Noer & Secher 1983) the indications are that survival increased as early as 1967, since long-lived individuals appeared in that cohort for all three species. Thus, even though survival of the Sparrowhawk apparently did not increase until 1970, the increases were generally too early and abrupt in relation to the assumed gradual decrease in use of Aldrin (HEOD half-life in soil is reported to be 2.5 years by Newton (1986)). Neither were there observable effects when sale of this pesticide for spraying purposes was stopped in 1962/63 nor any indications that for example the Danish Sparrowhawk population decreased as rapidly as the British (Schelde 1960, Newton 1986, Newton & Hass 1984, and Fig. 7). No instances of mass death of birds of prey have been reported from Denmark, in contrast to for example Holland (Opdam et al. 1987), and reductions in the use of Aldrin cannot explain the changes in the distributions of monthly mortalities or the fact that no such changes were found for the Sparrowhawk, a species which is assumed to be sensitive to HEOD (Newton 1986, Opdam et al. 1987).

On the other hand, it is certain that the 1967 Protection removed a cause of mortality, and hence that at least some of the improvements in survival rates are due to this factor. Assuming breeding populations of the four species in question of 2,000 pairs (Buzzard), 1,500 pairs (Sparrowhawk), 100 pairs (Goshawk) and 1,500 pairs (Kestrel) by 1965, an increase in survival of 10-15% would roughly correspond to 700-1,000 Buzzards, 600-900 Sparrowhawks, 30-40 Goshawks and 700-1,000 Kestrels (these numbers being calculated on the basis of the corresponding autumn population sizes). This indicates that the total bag of birds of prey belonging to the Danish populations would be some 2,000-3,000 individuals. According to the Danish bag records, 10,000 birds of prey were bagged in 1965/66 and 7,000 in 1966/67 (Strandgaard & Asferg 1980). Although Strandgaard & Asferg (1980) argued that these figures were biased and possibly should be reduced by as much as 50%, even corrected figures are still in reasonable accordance with the numbers corresponding to the increases in survival, in particular when it is considered that the open seasons 1954-66 started on 1st November, when the bulk of the autumn migration of birds of prey has passed Denmark. Moreover, if it is assumed that the part of Danish populations that is migratory should be left out, the figures corresponding to the improvements of survival could be as low as 350-500 Buzzards, 400-600 Sparrowhawks, 30-40 Goshawks and 400-700 Kestrels.

Therefore, the numbers of individuals corresponding to the survival rate improvements could be accounted for by the 1967 Protection in itself. Although Aldrin was heavily related to the decline and subsequent recovery of the Dutch and British Sparrowhawk populations (Opdam et al. 1987, Newton & Hass 1984, Newton 1986), it does not seem to have played a measurable role for the Danish populations.

Reductions in numbers shot, moreover, can explain the changes in monthly distributions found for the Kestrel (Noer & Secher 1983) and the Buzzard (Fig. 3), though the fact that no such changes were found for the Accipiter species (Figs. 4 and 5) is more difficult to explain. Perhaps, this is caused by smaller numbers of recoveries or by different biological characteristics of the species. The fact that some of the estimates indicate similar increases in survival for all age classes could be explained if the learning processes involved also affect older individuals (Noer (in press), and see p. 33).

Accordingly, it is concluded that the total results presented here and by Noer & Secher (1983) are in general support of the hypothesis that for the Danish populations of birds of prey the 1967 Protection was the major cause underlying the recent status improvements. The reductions in the use of DDT and Aldrin only provide very inadequate explanations of the improvements. The mild winters 1972-76 have undoubtedly contributed, but in all cases survival increased some years before this period and, with the possible exception of the Sparrowhawk, there is no evidence that survival was enhanced after 1972.

It is emphasised that this conclusion does not state that pesticides have not been influencing populations of birds of prey in Denmark. Indeed, the presented materials would provide no background for such statements. It is merely concluded that withdrawal from sale of DDT and Aldrin is probably not the cause of the population growth, as this possibility is not supported by the presented data.

The strength of the conclusions

Since 1970, survival rate estimates based on recoveries of ringed birds reported by the public have been subject to increasing theoretical criticism (Cormack 1970, Brownie et al. 1985, Lakhani & Newton 1983, Lakhani

1985, 1987a, b, c, and in press). Essentially, this criticism states that estimates of survival rates may be subject to bias, in particular when based on older records where there is no information on numbers ringed, and on ringed pulli only. Because survival rates have been estimated in exactly this way in the present paper it is necessary to assess the strength of the conclusions very carefully.

The problems associated with the conclusions of the present work and that of Noer & Secher (1983) arise at two different levels (Noer, in press). At a general level, statements are made on causes of events where control and replication experiments cannot be made in a strictly scientific sense. At a more detailed level, the potential bias in the estimates means that both the survival estimates and the statistical testing, which is based on these estimates, could be misleading.

At the general level, the results presented here and in Noer & Secher (1983) represent a total of four cases where significant reductions of numbers of recoveries of shot individuals coincide with significant increases in survival rate estimates (Buzzards ringed as pulli: 1967; Kestrels ringed as pulli: 1931 and 1967; and, Sparrowhawks ringed as pulli: 1970). Of these, the increase in survival for the Sparrowhawk was delayed for 3 years. Corresponding results have been observed for five more data sets (Goshawks ringed as pulli: 1967; Buzzards, Sparrowhawks and Kestrels ringed as fully fledged: 1967; and, Sparrowhawks ringed as pulli: 1931). As all estimates for these two groups correspond closely, the lack of significance in the latter is taken to be caused by smaller sample sizes. Not counting the migratory part of the Danish Buzzard population which showed tendencies for increased survival after the postponement of the start of the open season in 1954, there is a total of 9 instances where reductions in numbers of recoveries of shot

individuals coincide with increases in estimates of survival rates. At the same time there are no instances before 1978 where one of these variates change without corresponding changes in the other. This is taken to be a very good indication of repeatability.

With respect to control experiments, it is possible to derive a partial test of the hypothesis that the 1967 Protection was the underlying cause of the status improvements. Jørgensen (1989) gives the known facts of population development of all species of birds of prey breeding in Denmark. The five species that have increased significantly in numbers since 1967 are the three species protected, the Kestrel, and the Marsh Harrier *Circus aeruginosus* (Table 32). Of these, the Kestrel was affected by shooting before the 1967 Protection (Noer & Secher 1983). For the Marsh Harrier, which leaves Denmark before the start of the open season, Jørgensen (1985) concluded that the major cause of the population increase was legislative protection in the winter quarters in France and Spain. For this species, coincidence between a significant reduction in number of recoveries of shot individuals and a corresponding significant increase in recoveries of individuals aged 2 years or more by 1970 (start of population increase) has been demonstrated by Jørgensen (1989). In conclusion, the species for which status changes have been observed are those, and only those, affected by shooting pressure. Though not the ideal experiment, this constitutes at least a partial control.

At the level of survival rate estimation, Lakhani & Newton (1983) argued that such estimates can gain in credibility if augmented with results from field investigations. Such results are presented in Figs. 6, 7 and 8, and the correspondance between expected and observed population sizes is considered to verify that the estimated changes in survival rates cannot be grossly

misleading. The only possibility that cannot be checked this way is that estimates of first year and adult survival are biased in opposite directions, resulting in no net bias in the calculations of population trends. However, the fact that estimates of first year and adult survival rates are positively intercorrelated (Noer in press, and Tables 8, 24, and 29) contradicts this possibility.

The considerations detailed above probably constitute all that can be done to check these results and conclusions. No cases have been found where checks indicate that the results and conclusions were

unlikely or liable to be wrong. Judging the strength of the total evidence, support for the 1967 Protection being the major factor underlying the status improvements is fairly strong, though it remains to be seen whether other hypotheses could explain these findings as completely and consistently.

Influence of shooting pressure on population sizes

If the 1967 Protection caused the population increases, the implication is that

Table 32. Changes in status of birds of prey breeding or having bred regularly in Denmark before and after the critical years 1967-70. After Jørgensen (1989).

Species with no or minor changes:

Osprey <i>Pandion haliaëtus</i>	Irregular before and after 1967
Honey Buzzard <i>Pernis apivorus</i>	600-700 pairs for "a long period"
Hobby <i>Falco subbuteo</i>	10 pairs before and after 1967
Peregrine <i>Falco peregrinus</i>	1 pair in 1967, extinct as a breeding bird since 1972
Montague's Harrier <i>Circus pygargus</i>	35 pairs in 1968 (350-400 in 1940), 40-50 pairs in 1984
Red Kite <i>Milvus milvus</i>	extinct before 1967, 6-8 pairs after 1980 (due to immigration)
White-tailed Eagle <i>Haliaëtus albicilla</i>	very irregular before and after 1967

Species with major changes:

Kestrel <i>Falco tinnunculus</i>	"low densities" before 1967, 2000-2500 pairs early 1970's, 1350 pairs 1987
Marsh Harrier <i>Circus aeruginosus</i>	80 pairs before 1967, 610 pairs in 1987
Sparrowhawk <i>Accipiter nisus</i>	Assumed 50-70% reduction before 1967, 3500-5000 pairs by 1980, 3000-3400 pairs in 1987
Goshawk <i>Accipiter gentilis</i>	95-100 pairs before 1967, 650 pairs 1987
Buzzard <i>Buteo buteo</i>	1500 pairs in 1956 (2000 in 1965?), 4500-5500 pairs 1980, 4900 pairs 1988

shooting pressure has had limiting effects on population sizes. The results presented are therefore of relevance in relation to discussions of the influence of shooting on population sizes. This necessitates some general comments.

Among Game Biologists, it is widely considered that shooting pressure does not affect population sizes of most hunted species. Even if shooting pressure is totally removed by legislative protection populations are not expected to grow because of the so-called "compensatory mortality". According to this theory, shooting removes a surplus of individuals that would otherwise die from other causes (e.g. Anderson & Burnham 1976). Evidence supporting the existence of compensatory mortality has for example been presented for North American Mallards *Anas platyrhynchos* by Anderson & Burnham (1976) and Nichols et al. (1984).

Fully compensatory mortality can only be expected for populations whose sizes are limited by other factors than shooting, e.g. resources (food, space) or predators. For birds of prey, therefore, the fact that the populations grew considerably in numbers in the years following the legislative measures implies that there has been no fully compensatory mortality. Indeed, the observed growth rates strongly suggest that compensatory mortality has been completely lacking after 1967. Alternatively, it would be necessary to assume that the limiting effects of other factors were relaxed simultaneously with the introduction of protection, but this argument would then have to be applied to all the three species treated here, the Kestrel (Noer & Secher 1983) and the Marsh Harrier (Jørgensen 1985 and 1989) and, accordingly, is considered untenable. Hence, it is argued that the population increases are in themselves very strong evidence that the 1967 Protection had positive effects, even for the Sparrowhawk, for which the effects were delayed 2-3 years.

This argument can be applied to several other species which were protected and subsequently increased in numbers, e.g. the Cormorant *Phalacrocorax carbo* (Gregeresen 1982) and several goose species wintering in Western Europe (Madsen 1987).

Essentially, the results and conclusions presented in this paper merely serve to lend empirical support to these arguments. The most substantial result is, therefore, the demonstration that improvements in survival rates after 1967 were sufficiently large to explain the total population growth, and that the numbers of individuals involved could correspond to numbers bagged, with the implication that the 1967 Protection could have been the sole cause.

Even if these populations did increase as a result of the 1967 Protection, this result is of limited relevance to the discussion of whether hunting in general affects population sizes negatively. The presence of compensatory mortality depends on a situation where the population is limited by factors other than shooting, and hence an evaluation of its importance to natural populations depends on how often this condition is fulfilled. The presented results show that this was not the case for the Danish birds of prey and, accordingly, it is only a small contribution towards a final understanding.

Factors presently limiting/ regulating population sizes

Even if shooting pressure affects the size of a population, protection can only be expected to cause increased survival for a limited period (Noer & Secher 1983). It has been shown above (pp. 9-10) how the extent of the secondary decrease of survival depends on whether the regulation of the size of a closed population is mediated through mortality or through reproduction. For territorial species such as birds of prey, it is argued that regulation through

reproduction might conceivably be mediated through increases in age at first reproduction (generation time) and/or the build up of fleeing populations. It has been shown (pp. 9-10) how this theoretically is reflected in the extent of the secondary decrease of survival rates as well. In this sense, therefore, the study of any secondary decrease in survival can potentially give information on the eventual limitation or regulation of the size of a population.

In practice, however, problems arise because survival rates estimated from ringing recoveries may be biased (Lakhani & Newton 1983, Lakhani 1985, 1987 a, b, c, and in press) and so the conclusions may be misleading. In particular, the criticism that has been levelled against survival rate estimates concerns incomplete data sets (Lakhani & Newton 1983), as in the present case. Moreover, there could be reasons to expect that survival is higher among individuals that hold territories than among individuals belonging to the fleeing population. Ringing recoveries are presumably made of individuals belonging to both of these groups, and so survival rate estimates represent an average taken over the total population. For these reasons, the following discussion should be considered as tentative, and the data sets eventually reanalysed.

Even if this part of the analysis is presently premature, the study of populations that increase and eventually stabilise as a result of for example conservation policies offers excellent opportunities to gain insight into the factors that regulate population sizes. The analysis of ringing recoveries may reveal not only to what extent regulation is mediated through mortality, but also the changes in both monthly distributions of recoveries and causes of death. Thus, it may be helpful in the formulation of hypotheses of the regulatory mechanisms. Accordingly, the following discussion

analyses the changes that can be observed in the ringing material, though it should be noted that ringing recoveries are likely to give information about key factors rather than about the often less conspicuous components of mortality that in the final analysis turn out to be the regulating factors. For this reason, more detailed follow-up studies should be planned in connection with legislative policies in the future.

Two important components of the habitat of birds of prey are foraging habitat and nesting places (e.g. Newton 1986, Newton & Marquiss 1986). In relation to the discussion of fleeing populations it should be noted that the build up of fleeing populations should only be expected if the latter of these factors is limiting the numbers of breeding pairs. Potentially, analyses of the possible existence of surplus individuals may also be indicative of the relative importance of these two environmental components.

Buzzard

Since 1978-80 the Danish Buzzard population has been very constant, totalling 4,500-5,000 territorial pairs. This constancy in itself indicates that the population size of the species is being regulated. There are no indications that reproductive success has been involved, as no changes in breeding performance have been observed (Jørgensen 1989). In contrast, the survival rate estimates after 1977 (Table 8) indicate that significant decreases took place. Therefore, the changes in population trends were in all probability mediated through survival. Although the estimated survival rates are too low to be realistic, probably due to age dependency of survival in combination with incomplete data (see notes on page 22), they can still be taken to suggest that there has been no increase in generation time or corresponding build up of a fleeing population. The decrease in

mortality in combination with the increase in the number of recoveries during winter (Fig. 3) indicates that winter mortality is presently limiting the population size. On the other hand, at present 5,000 breeding pairs share some 4,000 km² of woodland, and this indicates that territorial space is a limiting factor. How these factors operate in combination will have to await further studies, but inspection of Tables 3 and 4 suggests that the relative number of recoveries outside Denmark has been decreasing since the late 1970's. Perhaps, the increasing winter mortality since 1978 should be viewed in relation to an increased tendency for residency in connection with increased competition for territories. The increased frequency of recoveries of third year individuals after 1967 (Table 3) suggests that such competition could be a factor.

Kestrel

Although the Kestrel was not included in this study, it will be briefly commented. Results from this species give an excellent fit to the Haldane model (Noer & Secher 1983) and hence are likely to give the most reliable estimates for incomplete data. Estimates of survival rates after 1977 based on the model used in this paper (and data updated to 1987) are $\hat{b} = 0.3161$ and $\hat{s} = 0.5979$. Average brood-size since 1980 has been 4.4, and 83% of the breeding pairs were successful (Jørgensen 1989). Throughout the 1980's, the population has remained stable after a drastic reduction in the winter of 1978/79 (Jørgensen 1989). Substituting these values into the formula derived for the surplus population on p. 10 gives an estimate of a fleeting population at 43.6% of the territorial population or 30.3% of the total population. With an adult mortality of 40.2% and a stable population this means that 24.6% of the one year old individuals should breed. The species is sexually mature at the age of one

year (Glutz von Blotzheim et al. 1971), and recoveries confirm breeding at this age (Noer & Secher unpublished).

Status of the Danish Kestrel population is currently poor, with a total number of breeding pairs of 1,350 (Jørgensen 1989). It has been suggested that a reduction in foraging habitat and lack of nesting places are the underlying causes (Brøgger-Jensen et al. 1988, Jørgensen 1989). For a low density population of a species that potentially can breed at the age of one year, the expected frequency of 24.6% of the individuals breeding at this age is a low figure. Based on the discussion given for the Sparrowhawk above (p. 36), the results for the Kestrel therefore support the hypothesis that lack of suitable nesting places rather than lack of habitat presently limits growth of the Danish Kestrel population.

Sparrowhawk

The population size has been declining since the severe winter 1978-79. Jørgensen (1989) suggested that this decrease is due to the high frequency of severe winters from 1978-87, to which this species is sensitive (Newton 1986). The age distributions (Table 17, severe winters indicated), the corresponding survival rate estimates (Table 20) and the monthly distributions of recoveries (Fig. 5) support this explanation. Moreover, the temporal distribution of winter mortality differs between the Buzzard and the Kestrel on one side (most recoveries in January and the first half of February) and the Sparrowhawk (late February and March) on the other. This strongly suggests that scarcity of food is the ultimate cause. In Denmark, severe winters typically start in late December with heavy snow cover which generally thins during February while temperatures may remain low. Snow cover would mean that rodents are relatively inaccessible while passerines, which tend to flock in certain places, would

be accessible. Accordingly, the Buzzard and the Kestrel might be most severely stressed at the beginning of a severe winter while the Sparrowhawk might experience scarcity of food in the later parts. In support of this interpretation is the fact that birds of prey delivered for veterinary examination during winters generally have been very lean (B. Clausen, pers. comm.).

Given the sensitivity of the Sparrowhawk to severe winters and the declining (and therefore not stable) population, the indication is that the species is presently limited but probably not regulated. More detailed analyses of survival in relation to winter climate should be done for this species following methods used in the analyses of British Herons (Mead et al. 1979, North 1979, North & Morgan 1979, and Freeman & North (in press)) in order to unravel the details.

Goshawk

With the increased shooting of Goshawks in Denmark after 1977 (Table 26) this species has once more become controversial (Mikkelsen 1986, Jørgensen 1987, Brøgger-Jensen et al. 1988 and 1989 and Jørgensen 1989). It has been suggested that recent declines in certain regions are causally linked to increased shooting of the species (Jørgensen 1987, Brøgger-Jensen et al. 1988). This species will therefore be discussed at length.

As a result of the work of the Raptor Research Group of the Danish Ornithological Society the populations in Jylland – in particular those in the southern parts – are by far the most thoroughly investigated. Regional population trends have differed since 1980, populations in the southern parts having declined while those in the northern and north-eastern parts have been increasing (Fig. 10). Outside Jylland, estimates are: Fyn 50 pairs in 1980 (Bomholt 1983) and 51 pairs in 1987 (Jørgensen

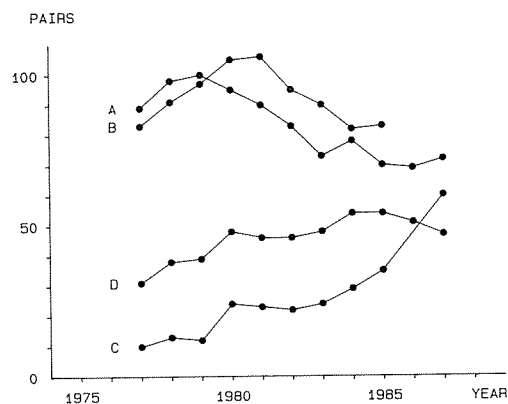


Fig. 10. Population developments for the Goshawk as observed after 1977 in four different parts of Jylland. A: South Jylland, B: Mid/West Jylland, C: East Jylland, and D: North Jylland. After Storgaard & Birkholm-Clausen (1986), Nielsen (1986) and Laursen (1987).

1989); Storstrøms County (South Sjælland) 35-50 pairs in 1980 (Bomholt 1983) and 60 pairs in 1987 (Jørgensen 1989); and North Sjælland 25 pairs in 1980 (Bomholt 1983) and 39 pairs in 1987 (Jørgensen 1989). The total Danish population was estimated at 500 pairs in 1980 (Bomholt 1983) and 650-680 pairs in 1987 (Jørgensen 1989). Although these figures vary in reliability, there is no published evidence that the total Danish Goshawk population has been decreasing since 1980. Rather, the evidence suggests that the increase has continued though at a lower rate.

Substantial decreases have only been documented for the southern half of Jylland (Figs. 8-10). Two hypotheses are of interest in relation to the decrease in this region. First, it may be due to the increased shooting of the species (cp. Table 28). However, given the lack of significant decreases in survival rates (Table 29) and the continuing increase of the population in the northern parts of Jylland, it is also possible that emigration from southern to mid and northern Jylland has taken place following the initial population growth in

the south (Laursen 1987). Summing up the evidence in favour of the first of these hypotheses, it is

- 1) present population densities are below 2 pairs/100 km², i.e. less than half of those in Holland, where 1,300-1,700 pairs bred in 1986 (Bijlsma 1988) and about two-thirds of those in West Germany (Arbeitsgruppe Greifvögel der Gro und Wog, 1989),
- 2) a significantly higher proportion of recoveries of shot individuals is found for birds ringed in southern Jylland, and
- 3) most recoveries of shot individuals are found in mid and western Jylland (Noer & Secher unpublished).

Directly in contradiction to this hypothesis are the following points:

- 1) While the age distribution of recoveries of shot individuals show that shooting affects all age categories, the (insignificant) decrease of survival rates only affects first year survival (Table 29),
- 2) ringing recoveries indicate that shooting is less intensive in South Jylland, where the population decline started earliest (Noer & Secher unpublished),
- 3) south Jylland is an area with many State forests and the density of Pheasant pens is much less there than for example on Fyn and in eastern Jylland. This is the reason why South Jylland was the main refuge area in Denmark before 1967 (Løppenthin 1967). Accordingly, if the decrease in numbers was due to control, the fact that the species declined in this part of the country and not in others would be paradoxical.

For the second of the two hypotheses, the following points are in favour:

- 1) Data presented by Jørgensen (1989) suggest that densities are at present rather homogeneous throughout the country. This is in accordance with the popula-

tion development in West Germany (though densities are 5 pairs/100 km² there) but in contradiction to the expected uneven distribution of regulation by shooting.

- 2) Since 1980, there has been a surplus of breeding females aged one year in the (growing) North Jylland population and low frequency (10%) in Mid and South Jylland. This is in agreement with the expectations if emigration was the cause,
- 3) movements of Goshawks ringed in South Jylland show a northward trend (Storgaard & Birkholm-Clausen 1983a),
- 4) after 1980, the trend in East Jylland suggests immigration (Laursen 1987), and
- 5) The Mid Jylland population increased for two years longer than South Jylland (Fig. 10).

Two points contradict this explanation:

- 1) The densities were only about 2 pairs/100 km² when the decline started, and
- 2) Emigration rate should not only increase during the period of population growth, but decrease correspondingly when the population declined. It is therefore difficult to envisage how emigration could lead to a decline in the population size.

In contradiction to both of these models is development of the population in South Schleswig and Holstein, just south of the Danish border. This population has declined by 30% since 1978, corresponding closely to the decline on the Danish side of the border. In Schleswig-Holstein, the decline came after a period of constant population size (Looft 1984).

Taking these pro et contra into consideration, the evidence suggests that emigration from South to Mid, East and North Jylland has taken place and that part of the changed trend in population growth in

South Jylland could be explained this way. The hypothesis that declines are due to shooting is less convincing and does not fit the facts so well, even though shooting may have had local influence in Mid and West Jylland. The Danish Goshawk population, therefore, reveals a complicated pattern where no single cause can convincingly explain the patterns of developments of sub-populations; exactly as for the populations in Rheinland-Westfalen (Arbeitsgruppe Greifvögel der Gro und Wog, 1989).

Discussion and conclusions

Summing up the evidence, the growth of the Buzzard and Sparrowhawk populations ceased following the severe winter in 1978/79. Evidence of the population size of the Kestrel is sparse but indications are that the population only increased for a few years after 1967 (Noer & Secher 1983) and that the population was considerably reduced in the winter 1978-79. The growth of the Goshawk population has apparently continued after 1980, though at a much reduced rate and with secondary declines in large areas. Thus, compared to the predictions three species have shown limited growth, but only for the Buzzard and (possibly) the Kestrel does the evidence suggest that population sizes are presently regulated. It is noteworthy that the results for the three analysed species and the Kestrel are much more heterogeneous with respect to times of changes and magnitude of decreases in survival rates than were the results for the period 1967-77. This supports the notion that one common factor caused the population increases.

The analyses of the ringing material strongly suggest that for the Buzzard, the Sparrowhawk and the Goshawk the changes in population trends have been caused by increases in mortality rates and not through decreased reproductive success. In particular, for these three species

no evidence has been found to suggest that increased generation time (i.e. the build up of substantial fleeing populations) has been involved in the decrease of the growth rates. For the Buzzard, there is evidence suggesting increased mortality at the age of sexual maturity (age class 3 in Table 4). For the Goshawk, the evidence suggests that emigration has taken place to less densely populated areas. Thus, build up of fleeing populations has not played a measurable role in the Danish populations. Only for the Kestrel has evidence suggesting an increased generation time been found, but this should be viewed in relation to habitat reduction or availability of suitable nesting places (Brøgger-Jensen et al. 1988, Jørgensen 1989). Since the build-up of fleeing populations is only expected when nesting places and not foraging habitats are limiting, the latter of these two possibilities is the most likely. This is supported by the rapid build up of local populations when nest-boxes are established (Bang 1986).

Increased mortality resulting from the severe winters 1978-87 has affected the Buzzard, the Sparrowhawk and the Kestrel strongly, for the Buzzard possibly because of an increased tendency for residency. Only for the Sparrowhawk, however, does the evidence actually suggest that this increase in winter mortality has been the ultimate cause affecting the population trends.

Reproductive success of Danish birds of prey has been studied in detail since 1973 (e.g. Brøgger-Jensen et al. 1988 and 1989, Jørgensen 1989). In this paper, results have been presented that very strongly indicate that the major part of the status changes of these species has been caused by changes in mortality rather than by changes in reproductive success. The implication is that such population trends cannot be understood in depth unless studies of mortality rates are included in future evaluations. As the validity of estimating survival rates from incomplete data sets is uncer-

tain, the inevitable corollary is that detailed, causal analyses will probably only be possible in retrospect. Studies of the age structure of breeding populations by collection of moulted feathers present a useful alternative that has hitherto been paid too little attention, but at present the interpretation of such results would probably require more insight into population dynamics than for example has been provided by the present study.

Since 1980, debate has arisen concerning the control of birds of prey by dispensation as allowed for in the 1983 Game Act (Mikkelsen 1986, Jørgensen 1987 and 1989,

Brøgger-Jensen et al. 1988 and 1989). The number of dispensations has been moderate throughout the 1980's (Noer, unpublished), and the evidence presented indicates that this control has not affected the populations measurably. The extent of illegal shooting of Goshawks is presently totally unknown and may have influenced Goshawk populations in some regions. However, restrictions in the opportunities for legal control would hardly change this situation for the better. There is no evidence either that illegal shooting has affected population sizes amongst other species of birds of prey.

Dansk resumé

Jagtlovsændringers indflydelse på overlevelse og statusforbedringer af danske rovfuglearter

Som følge af bestandstilbagegang blev de sidste tre jagtbare rovfuglearter – Musvåge *Buteo buteo*, Spurvehøg *Accipiter nisus* og Duehøg *A. gentilis* fredet i Danmark i 1967. Kort tid efter gennemførtes reduktioner i anvendelsen af visse pesticider, der var under mistanke for bl.a. at påvirke rovfugle negativt. Anvendelsen af DDT til landbrugsmæssige formål blev indskrænket fra 1969/70, og anvendelsen af Aldrin til sædbejdsning fra 1968/69. I begge tilfælde skete disse indskrænkninger i producentleddet og ikke ved direkte forbud mod anvendelse.

I løbet af 1970'erne viste flere arter af rovfugle markante fremgange i Danmark. Selvom denne fremgang for Musvågens og Spurvehøgens vedkommende kun varede til den hårde vinter 1978/79, er bestandsstørrelserne for de tre nævnte arter i dag mere end det dobbelte af, hvad de var i slutningen af 1960'erne.

Ud fra populationsdynamiske analyser af bestandsvæksten er det i princippet muligt at undersøge, hvor meget de forskellige lovmæssige og administrative tiltag har bidraget. Hvis fredningen var den vigtigste faktor, måtte det forventes, at årsagen til væksten var en forbedret overlevelse, – først og fremmest af unge fugle, fordi der nedlægges flest af disse. Hvis derimod indskrænkninger i DDT-anvendelsen var den væsentligste faktor, skulle bestandsvæksten være forårsaget af et forøget antal flyvedygtige unger pr. par, – fordi DDT først og fremmest har vist sig at påvirke fugles reproduktionsevne. Disse muligheder kan belyses ud fra resultater af ringmærkning af rovfugle, dels fordi der gennem alderen af genmeldte fugle fås oplysning om overlevelse, dels fordi der ved ringmærkning af flyvefærdige unger fås oplysning om kuldstørrelser.

Overlevelseshæregningerne er foretaget ud fra en udvidet version af den såkaldte Haldane-model. For de tre undersøgte arter kan markante stigninger i overlevelsen konstateres – især af første års individer – efter 1967. For Musvågen bliver denne stigning tydeligere, når der tages hensyn til en ændring af jagtsæsonens start fra

15.9. til 1.11 ved ministeriel bekendtgørelse i 1954. En del af den danske Musvågebestand trækker mod sydvest og forlader landet i september-oktober, og denne del må således forventes at have undgået jagttryk i Danmark mellem 1954 og 1966. Deles genmeldingerne op i hhv. danske og udenlandske, sker stigningen i førsteårsoverlevelse for genmeldinger fra udlandet allerede i 1954, mens den for fugle genmeldt i Danmark sker i 1967 (Tabel 3-12). Spurvehøgen viser først overlevelseshæstigninger efter 1970 (Tabel 17-24), muligvis pga. hårde vintre i 1968/69^{*} og især i 1969/70. Denne art viser de samme tendenser som Musvågen efter ændringen af jagtsæsonens start i 1954, men disse tendenser er ikke statistisk signifikante, og effekterne af 1954-bekendtgørelsen er derfor diskutabile. For Duehøgen (Tabel 27-31) er stigningen i overlevelse efter 1967 ikke statistisk signifikant, men da tendensen er identisk med den, der gælder for de andre arter, må dette tilskrives et mindre genmeldingsmateriale. Effekter af 1954-bekendtgørelsen kan ikke vurderes for denne art, ligeledes pga. et for lille materiale, men da Duehøgen er standfugl i Danmark, har der næppe været tale om væsentlige ændringer.

Der er ikke konstateret ændringer i Musvågens kuldstørrelser. Spurvehøgen havde nedsatte kuldstørrelser mellem 1950 og 1980 (Tabel 14), og Duehøgen havde muligvis en forringet reproduktion i begyndelsen af 1960'erne (Tabel 26). Disse ændringer falder dog ikke tidsmæssigt sammen med ændringerne i bestandsstørrelserne (f.eks. er Spurvehøgens kuldstørrelser først steget efter 1980, hvor bestanden atter var i tilbagegang), og de kan således ikke forklare disse.

Resultaterne betyder, at rovfuglenes bestandsforbedringer må tilskrives forbedret overlevelse og ikke forbedret reproduktion. Det indebærer, at indskrænkninger i anvendelsen af DDT næppe har været årsag til bestandsvæksten. Indskrænkninger i anvendelsen af Aldrin er heller ikke en sandsynlig årsag, dels fordi dette pesticid ikke har været bredt anvendt i

Danmark, dels fordi førsteårsoverlevelsen i en række tilfælde steg mere end voksenoverlevelsen. Fredningen i 1967 kan til gengæld forklare bestandsvæksten langt bedre. De beregnede overlevelsesstigninger skønnes at svare til højst 2.000-3.000 individer pr. år, og hvis ændringen af jagtsæsonens starttidspunkt i 1954 tages med i beregningsgrundlaget, reduceres dette tal yderligere til 1.000-2.000 individer pr. år. Det må anses for sikkert, at en dødsårsag forsvandt med fredningen, og antallet af individer, der svarer til overlevelsesstigningerne, er ikke større, end at det kan være fremkommet udelukkende som resultat af denne.

Det kan således konkluderes, at fredningen i 1967 med stor sandsynlighed var årsagen til den forbedrede status af visse rovfuglebestande.

Naturvidenskabelig metodik kræver, at resultater skal kunne gentages og at der udføres kontrol eksperimenter, hvilket i bred almindelighed skaber vanskeligheder, når effekter af lovmæssige tiltag skal vurderes. Samtidig har de senere års forskning vist, at overlevelsesberegninger på materialer som de anvendte er behæftet med en række potentielle fejlkilder. En nøje vurdering af konklusionerne er derfor påkrævet. Ved analyser af genmeldinger af danske rovfuglearter kan der i alt påvises 9 tilfælde, hvor signifikante reduktioner i antallet af genmeldinger af skudte fugle (som følge af jagtlovsændringer) falder sammen med beregnede overlevelsesstigninger. Der er ingen tilfælde før 1978, hvor den ene af disse to variable ændres uden tilsvarende ændringer i den anden. Dette kan tages som evidens for gentagelser. Samtidig kan det vises, at kun fem rovfuglearter har haft væsentlige bestandsforbedringer siden 1967 (Tabel 32). Dette er netop de fem, der har været påvirket af jagttryk (for Rørhøgens vedkommende i vinterkvarteret), hvilket kan opfattes som et kontrol eksperiment. Modellering af observerede bestandsudviklinger ud fra den fundne reproduktion og overlevelse beskriver ændringerne ret præcist (Fig. 6-9), hvilket indebærer, at de beregnede overlevelser må være rimeligt nøjagtige. Endelig kan der teoretisk argumenteres for, at selve væksten i bestandene viser, at der ikke har været kompensatorisk mortalitet, hvilket må betyde, at fredningen har haft indflydelse. Det kan derfor konkluderes, at en teori om at 1967-fredningen har været af afgørende betyd-

ning for bestandsvæksten er stærkt understøttet af de foreliggende kendsgerninger. Der er i øjeblikket ingen alternative hypoteser, der kan forklare disse resultater så fuldstændigt og sammenhængende. Det skal præciseres, at denne konklusion ikke betyder, at de rovfuglebestande, der yngler i Danmark ikke har været påvirket af pesticider, - blot at reduktioner i belastningen ikke har været årsag til bestandsvæksten.

Væksten i de undersøgte rovfuglebestande ophørte for Spurvehøgens og Musvågens vedkommende i den hårde vinter 1978/79, mens Duehøgebestanden på landsplan tilsyneladende er fortsat med at vokse gennem 1980'erne. Undersøgelser af denne periode er af stor betydning for forståelsen af, hvilke faktorer der begrænser/regulerer disse bestandes størrelse. Selv om de indkomne data er ukomplette, drages der alligevel en række foreløbige konklusioner.

For Musvågens vedkommende kan der påvises en voksende dødelighed efter 1978 (Tabel 6-11) sammenfaldende med, at væksten i bestanden hørte op. Samtidig ændredes den tidsmæssige fordeling af dødfundne fugle signifikant i retning af forøget vinterdødelighed (Fig. 3). Der er således næppe tvivl om, at en forøget mortalitet i de 6 hårde vintre i perioden 1978-87 har haft betydning. På den anden side har der gennem 1980'erne været ca. 5.000 ynglende par Musvåger i Danmark, hvilket antyder, at plads (territorier) kan have spillet en væsentlig rolle. Resultaterne antyder relativt færre genmeldinger fra udlandet i 1980'erne, og det er tænkeligt, at den forøgede vinterdødelighed skal ses på baggrund af en øget tendens til at overvintre på yngleterritoret, hvilket kan være forårsaget af forøget intraspecifik konkurrence om territorier.

Resultater, der viser, at Tårnfalken *Falco tinnunculus* har været påvirket af jagttryk i Danmark mellem 1945 og 1967, er tidligere offentliggjort af Noer & Secher (1983). Den langsigtede udvikling i denne arts overlevelse er behandlet på samme måde som for de tre andre arter. Resultaterne antyder, at kun ca. 26% af de 1-årige Tårnfalke har ynglet i perioden 1979-87. Dette tal må anses for lavt og kan understøtte formodninger om, at mangel på egnede redepladser udgør en begrænsende faktor for denne arts populationsstørrelse.

Spurvehøgen har vist tilbagegang, efter at be-

standens størrelse kulminerede i slutningen af 1970'erne. Denne tilbagegang skal sandsynligvis ses i sammenhæng med en række hårde vintre (Tabel 17-24).

Duehøgen har tilsyneladende haft en svagt voksende landsbestand i 1980'erne. Tendenserne er dog meget uens fra landsdel til landsdel.

Arten er gået tilbage i Sønderjylland og frem i dele af Øst- og Nordjylland (Fig. 10), mens der ikke er dokumenteret væsentlige ændringer for Øerne. Bekæmpelse af arten kan have virket begrænsende lokalt, men ser ikke ud til at have haft væsentlig indflydelse på landsplan.

Резюме на русском языке:

Влияние изменений охотничьего устава на переживание и улучшение благосостояния датских видов хищных птиц.

Вследствие понижения их численности, последние три вида хищных птиц, на которых в Дании была разрешена охота – сарыч *Buteo buteo*, перепелятник *Accipiter nisus* и ястреб-тетеревятник *A. gentilis* – с 1967 г. были защищены. Скоро после этого были введены ограничения применения некоторых пестицидов, подозревавшихся во вредном влиянии на хищных птиц. С 1969/70 г. было ограничено применение ДДТ для сельскохозяйственных целей, и с 1968/69 г. применение альдрина в качестве фунгицида для обработки семян. В обоих случаях ограничения применялись к производству этих средств, а не запрещали их применение.

В течение 1970-х годов несколько видов хищных птиц в Дании выказали значительный рост их численности. Хотя это повышение у сарычей и перепелятников длилось только до суровой зимы 1978/79 г., численности популяций всех трех видов теперь больше чем вдвое численности в конце 1960-х годов.

Исходя из популяционно-динамических анализисов роста популяции, в принципе возможно исследовать, сколько этому способствовали законные и административные мероприятия. Если запрещение охоты было важнейшим фактором, то следовало бы ожидать, что причиной роста было повышение переживания – прежде всего молодых птиц, так как из них больше всего убиваются. Если же наиболее значительным фактором были ограничения применения ДДТ, то рост популяции был бы должен объясняться увеличением числа летних птенцов за пару, так как выяснено, что ДДТ главным образом понижает способность птиц к размножению. Эти возможности можно выяснить результатами кольцевания хищных птиц, отчасти потому, что из возраста птиц, о которых получены возвраты, получаются сведения о их переживании, а отчасти потому, что пометка летних птенцов кольцами дает указание о численностях выводков.

Вычисления переживания произведены по расширенному варианту так называемой модели Халдэна (Haldane). У трех исследованных видов выяснились резкие повышения переживания, особенно однолетних особей, после 1967 г. У сарыча это повышение выражается более четко, когда принимается в учет отсрочка начала сезона охоты с 19 сентября на 1 ноября по министерскому постановлению от 1954 г. Часть датской популяции сарычей перелетает на югозапад и оставляет страну в сентябре-октябре, и можно предположить, что эта часть с 1954 по 1966 г. избежала охоты в Дании. При подразделении возвратов на датские и зарубежные, повышение переживания первого года по зарубежным возвратам уже начинается в 1954 г., а у птиц, о которых получены возвраты из Дании, в 1967 г. (Табл. 3-12). У перепелятника повышение переживания показывается только после 1970 г. (Табл. 17-24), возможно вследствие суровых зим 1968/69 и особенно 1969/70 г. После отсрочки начала сезона охоты в 1954 г. этот вид выказывает те же тенденции, как сарыч, но эти тенденции статистически незначительны, и эффекты постановления поэтому сомнительны. У ястреба-тетеревятника (Табл. 27-31) повышение переживания после 1967 г. статистически незначительно, но так как тенденция соответствует наблюдаемой у остальных видов, это может объясняться менее обширным материалом возвратов. Эффекты постановления 1954 г. для этого вида невозможно оценить вследствие недостаточного материала, но так как ястреб-тетеревятник в Дании является оседлой птицей, едва ли произошли значительные изменения.

Изменений численности выводков сарыча не обнаружено. У перепелятника с 1950 по 1980 г. численность выводков была понижена (Табл. 14), а у ястреба-тетеревятника возможно, что воспроизводство было понижено в начале 1960-х годов (Табл. 26). Однако, эти изменения не совпадают

по времени с изменениями численностей популяций (напр. численности выводков перепелятника возросли только после 1980 года, когда численность популяции снова понижалась), и они, следовательно, не могут этим объясняться.

Результаты означают, что увеличения популяций хищных птиц должны объясняться улучшенными условиями переживания, а не повышенным воспроизводством. Из этого следует, что причиной роста популяции едва-ли были ограничения применения ДДТ. Ограничения применения альдрина также не являются вероятной причиной, отчасти потому, что этот пестицид в Дании широко не применялся, а отчасти потому, что первогоднее переживание в ряду случаев повысилось сильнее, чем переживание взрослых. За то рост популяции гораздо лучше можно объяснить запрещением охоты в 1967 г. Вычисленные повышения переживания приблизительно соответствуют не больше 2–3.000 особям за год, и если в основании вычисления принимается в учет отсрочка начала сезона охоты в 1954 г., то это число еще понижается до 1–2.000 особей за год. Следует считать достоверным, что благодаря запрещению охоты исчезла одна из причин смертности, а число особей, соответствующее повышению переживания, не больше, чем оно могло быть в результате исключительно этого. Следовательно, запрещение охоты в 1967 г. с большой вероятностью может быть причиной улучшения благосостояния некоторых видов хищных птиц.

Естественно-научная методика требует, чтобы результаты могли повторяться, и чтобы производились контрольные опыты, что в общем создает затруднения, когда оценке подлежат эффекты законных мероприятий. В то-же время исследования последних лет показали, что вычисления переживания по таким материалам, какие применялись в этом случае, обременены рядом потенциальных источников ошибок. Поэтому необходима тщательная оценка выводов. Анализом возвратов о датских видах хищных птиц можно найти всего 9 случаев, где значительные понижения числа возвратов о убитых птицах (вследствие измене-

ний охотничьего устава) совпадают с вычисленными повышениями переживания. Нет случаев, в которых одна из этих двух переменных величин изменяется без соответствующих изменений другой. Это можно считать указанием повторимости. В то-же время можно указать, что только пять видов хищных птиц с 1967 г. выказали значительные изменения численности (Табл. 32), а именно те пять видов, которые были подвержены охоте (в случае камышевого луня – в зимнем полугодии), что можно считать контрольным опытом. Моделированием установленных наблюдений развитий популяций на основании вычисленного воспроизводства и переживания получается довольно точное описание изменений (Фиг. 6–9), из чего следует, что вычисленные переживания должны быть сносно точными. А наконец, теоретически можно привести доводы в пользу того, что рост популяций сам по себе указывает, что не было компенсирующей смертности, из чего следует, что запрещение охоты повлияло на него. Следовательно, можно вывести заключение, что теория о решительном значении запрещения охоты в 1967 г. для роста популяций сильно поддерживается наличными фактами. В настоящий момент нет никаких других гипотез, так же совершенно и связно могущих объяснить эти результаты. Следует уточнить, что этим не сказано, что гнездящиеся в Дании виды хищных птиц не были подвержены воздействию пестицидов, а только, что понижение этого воздействия не было причиной роста популяций.

Рост исследованных популяций хищных птиц прекратился у перепелятников и сарычей в суровой зиме 1978/79 г., а кажется, что рост популяции ястребов-тетеревятников общим числом для всей страны продолжался в течение 1980-х годов. Исследования этого периода очень важны для понимания того, какие обстоятельства ограничивают/регулируют численность этих популяций. Хотя собранные данные неполны, всё-таки возможен ряд предварительных выводов.

У сарыча можно установить возрастающую смертность после 1978 г. (Табл. 6 – II)

совпадающую с прекращением роста популяции. В то же время распределение по времени найденных мертвыми птиц заметно изменилось в направлении к повышенной зимней смертности (Фиг. 3). Поэтому едва-ли можно сомневаться в том, что имела значение повышенная смертность во время 6 суровых зим в периоде с 1978 по 1987 г. С другой стороны, в течение 1980-х годов в Дании было около 5.000 пар гнездящихся сарычей, что является признаком того, что места (территории) могут играть важную роль. Результаты указывают на сравнительно пониженное число возвратов из заграницы в 1980-х годах, и можно предположить, что повышенная зимняя смертность была связана с повышенной склонностью к зимовке на территории гнездования, что может быть вызвано более острой конкуренцией о территориях.

Результаты, показывающие, что обыкновенная пустельга Falco tinnunculus в Дании подвергалась охоте, в 1983 г. опубликовали Ноэр и Сехер (Noer & Secher). Долгосрочное развитие переживания этого вида было исследовано тем-же образом, как

для упомянутых трех видов. Результаты указывают на то, что только около 26% однолетней обыкновенной пустельги размножались в периоде с 1979 по 1987 г. Это число нужно считать низким, и оно может поддержать предположения о том, что недостаток удобных мест для гнездования является ограничивающим условием для численности популяции этого вида.

У перепелятника выказалось понижение после того, как численность этого вида в конце 1970-х годов кульминировала. Это понижение вероятно связано с рядом суровых зим (Табл. 17-24).

Численность ястреба-тетеревятника в общем по всей стране очевидно слегка повысилась в 1980-х годах. Однако, тенденция в разных частях страны очень неодинакова. В Южной Ютландии численность этого вида понизилась, в частях Восточной и Северной Ютландии повысилась (Фиг. 10), а на Островах не документировано значительных изменений. Местно, борьба с этим видом могла иметь ограничивающее влияние, но кажется, что в общем по всей стране её влияние было незначительно.

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Appendix

Goodness-of-fit tests

In principle, a total χ^2 goodness-of-fit test can be carried out by calculating expected values for each cohort and age class (conditional on numbers of recoveries within each cohort). Summing of the terms $(O_{ij} - E_{ij})^2/E_{ij}$ is done in the usual way (cells with expected values less than 2.0 are pooled with other cells) and, under the null hypothesis, the sum is distributed as χ^2 with $N(N-1)/2 - 2P$ degrees of freedom (where N is the number of investigated years, P the number of periods with different survival rates, and one additional degree of freedom is lost whenever a cell is pooled with another).

For the data sets presented, this test rejects the model for all three species, highly significantly for the Sparrowhawk and the Goshawk. This is not surprising, as it is generally agreed that survival rates are both age- and time dependent (e.g. Burnham & Anderson 1979, Anderson et al. 1981, Brownie et al. 1985). Since 1978, in particular, severe and mild winters have alternated and, when there is sufficient material, as in the cases of the Sparrowhawk and the Goshawk materials after 1973, this annual variation will be statistically significant.

The existence of this variation does not, however, answer the questions critical in the evaluation of the presented analyses. Comparing survival rates between periods – for example before and after protection – depends on comparing some average measure of survival within each period and, even if it can be shown that survival rates vary annually, the question of whether the survival rate estimates derived from the extended Haldane model are decisively biased still remains. Thus, total goodness-of-fit tests cannot be used to decide whether or not survival rate estimates

based on the Haldane model can be used for such comparisons. Instead, evaluation of this problem can be done by means of comparisons between predicted and observed trends in population size, as has been done above (pp. 34-40).

As the total goodness-of-fit test does not answer the question of whether survival rates estimated from the Haldane model represents a sensible measure of average survival within periods, partial goodness-of-fit tests have been done by pooling age classes within each period. In this way, individuals that have survived from one period into the next are treated as being recovered as adults at a younger age than they actually have obtained. Rather few individuals have been affected by this (cf. Tables 4, 6, 17, 19, 25 and 26). In the first set of tests presented, recoveries of individuals in their first year have been pooled over years within periods. This means that the number of degrees of freedom is the number of terms in the χ^2 -sum minus 1 minus 6 (the number of estimated parameters). Note that two additional degrees of freedom are gained this way because the number of expected recoveries of adults within a period can vary.

For the Buzzard and the Sparrowhawk, expected distributions have been calculated from survival rates corresponding to the hypotheses accepted. For these species the distributions presented were pooled from the tables giving recoveries of birds ringed as pulli from, respectively, Denmark and abroad. For the Goshawk, it was assumed that the acceptance of the null hypothesis was caused by the small numbers of recoveries before 1967, and the expected distributions were calculated from the same model as for the Buzzard. Moreover, in-

dividuals recovered as shot were pooled with those which had died from other causes. This was done because the age distributions of shot individuals and those recovered from other death causes were identical after 1970. Though the age distribution before 1967 is distorted by this pooling, the bulk of recoveries are from after 1970, hence this pooling improves the efficiency of the test.

It should be noted that throughout the tests entries with an expected number of recoveries less than 2.0 have been pooled, in accordance with the recommendations of White (1983) and Brownie et al. (1985). Goodness-of-fit tests are often weak and, even though Burnham (in press) has recent-

ly shown that the asymptotic power of such tests is only slightly reduced if numbers ringed are unknown (as in the present case), they should only be taken to demonstrate that the fit obtained by the models presented is satisfactory, – and not to prove that these models are necessarily correct.

The results of these tests have been taken by Noer (in press) to indicate that within each period the assumption of a constant, age-independent survival rate after the first year is reasonable. The assumption that survival rates are time-independent over years within each period is not checked by these tests, and they should thus be viewed as partial.

Appendix Table I. Buzzard. Underlined entries indicate pooled results for all older age classes. Test of observed and expected distributions with age classes pooled within period accepts the null hypothesis: $\chi^2 = 17.33$, $df = 15$, $P = 29.94\%$.

Age	1944-66		1967-77		1978-87	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1	98	98.0000	56	56.0000	47	47.0000
2	21	16.9399	14	11.7424	14	12.9292
3	11	11.5439	16	9.1838	10	8.7934
4	10	8.3687	6	7.1528	7	5.8196
5	2	6.1904	3	5.6486	4	3.8222
6	3	4.4474	4	4.2738	2	2.4874
7	0	3.2380	3	3.3091	4	4.2782
8	1	2.3553	3	2.5775		
9	4	5.2681	2	3.6311		

Appendix Table II. Sparrowhawk. Underlined entries indicate pooled age classes. Test of observed and expected distributions with age classes pooled within periods accepts the null hypothesis: $\chi^2 = 6.8705$, $df = 9$, $P = 65.06\%$.

Age	1945-70		1971-77		1978-87	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1	67	67.0000	74	74.0000	253	253.0000
2	10	7.8114	18	14.3487	60	56.2531
3	5	4.8761	7	8.8305	29	31.1172
4	2	3.2593	3	4.6166	12	16.7634
5	2	2.1459	4	3.6439	10	8.3510
6	3	4.1331			4	4.3873
7					2	2.2331
8					4	2.2294

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Appendix Table III. Goshawk. Underlined entries indicate pooled age classes. Test of observed and expected distributions with age classes pooled within periods accepts the null hypothesis: $\chi^2 = 6.1241$, $df = 8$, $P = 63.33\%$.

Age	1944-66		1967-77		1978-87	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1	52	52.0000	52	52.0000	219	219.0000
2	13	11.8750	17	12.3131	56	50.0633
3	3	4.7572	4	5.9957	25	31.2480
4	3	3.1750	2	2.4644	17	19.6048
5			2	2.0810	12	12.2165
6					9	7.7553
7					5	4.5273
8					2	2.5331
9					3	2.3906

It should be noted that other assumptions of the model, in particular the assumption of constant recovery probabilities, cannot be tested due to the lack of numbers ringed for older records. In principle it is therefore possible that the estimates have been influenced by this source of

error, though it is unlikely that the consistent association between reduction in numbers of recoveries of shot birds and increased survival rates – as well as the decreases of survival coinciding with the end of the population growth – could be explained this way.

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