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Korrespondens *Correspondence*

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Dynamics of a passerine bird community in a small deciduous wood, S Sweden, during 40 years

ANDERS ENEMAR, BERITH CAVALLIN, ERIK NYHOLM, INGA RUDEBECK &
ANN MARI THORNER

Abstract

The passerine bird community of a 13 ha nature reserve, consisting of a narrow valley with deciduous woods and open areas, was censused yearly from 1953 through 1992 by territory mapping. Its size, showing no significant trend, was on average 124±15(SD) territories, belonging to 20±2 species. The community has fluctuated significantly (range 103 to 158, CV=12%). Its stability was founded on the restricted fluctuations of the most abundant species. Out of the 39 stationary species, 19 (=95% of the community size) appeared there for more than 20 years, only 8 of which have been yearly present. *Fringilla coelebs, Phylloscopus trochilus, Sylvia borin,* and *Luscinia luscinia* were the most abundant species throughout. *Emberiza hortulana, Carduelis cannabina,* and *Anthus trivialis* disappeared, while *Sturnus vulgaris, Sitta europaea, Carduelis chloris,* and *Turdus pilaris* immigrated. The species turnover rate between successive years was 21.7±9.7%, the long-term rate being about 1%. The community structure changed gradually: taken together, the population sizes of residents and short-distance migrants increased, from 38 to 57% of the community size; the tropical migrants declined correspondingly. These two species groups showed an opposing and significant covariation.

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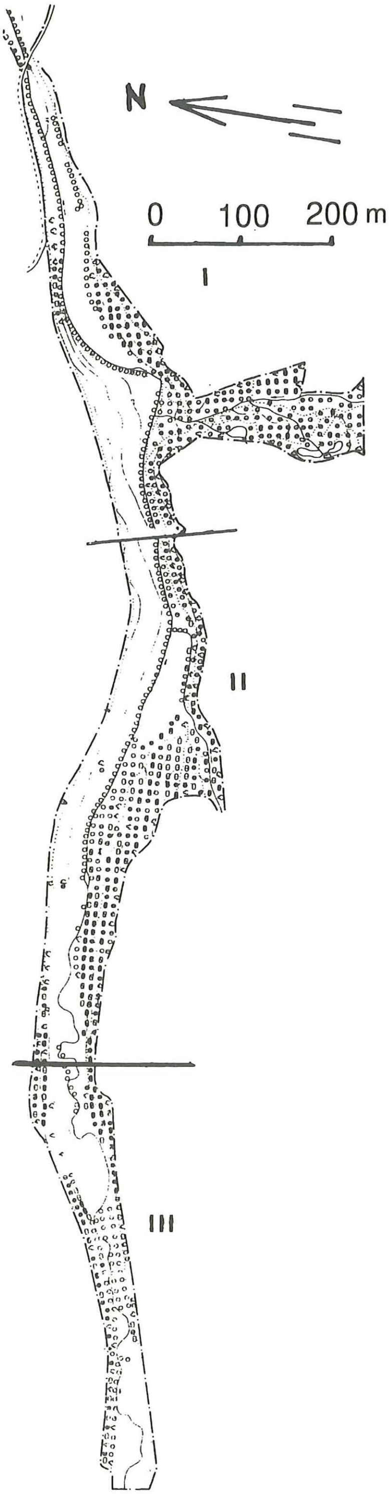
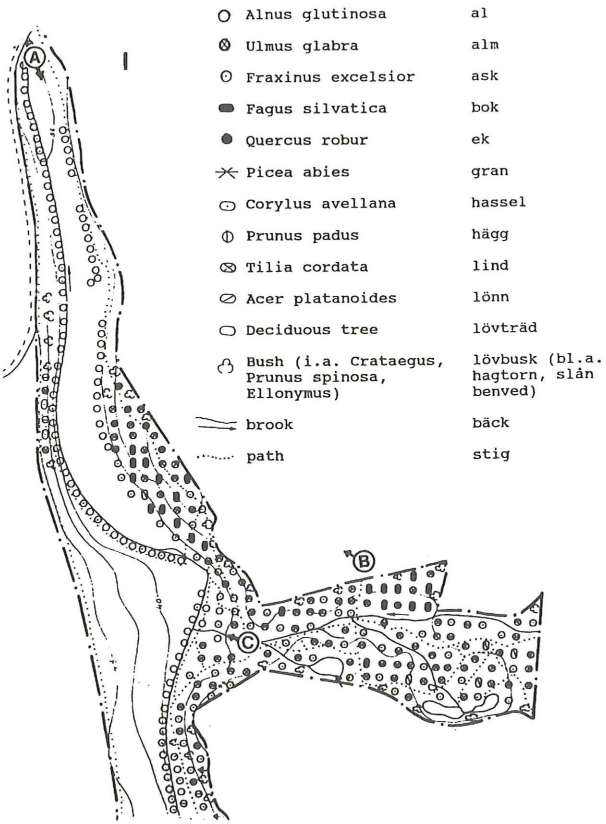




Introduction

The Swedish Ornithological Society made an effort in 1951 to start a national bird monitoring programme based on census work in a number of study plots in southern Sweden (Engström 1953). The local Scanian Ornithological Society organized the census work in the province of Scania (Skåne), among them a plot in Birdsong Valley, with one of the authors (A.E.) as census-taker as from 1952. The national programme was discontinued after some years, mainly due to the lack of proper instructions on how to carry out census work by territory mapping of a breeding bird community. The census work in Birdsong Valley was continued, however, and was soon combined with investigations to find reliable methods for mapping territories (Enemar 1959). The results of the study covering the ten years 1953–1962 have been published (Enemar 1966). The census work has been carried out during the breeding seasons without interruptions ever since.

In the 1950s the need for long-term census inves-

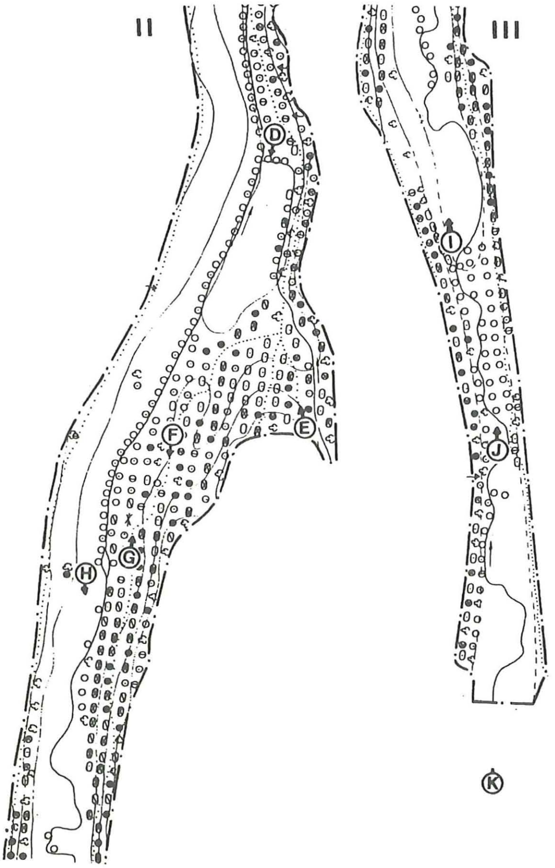


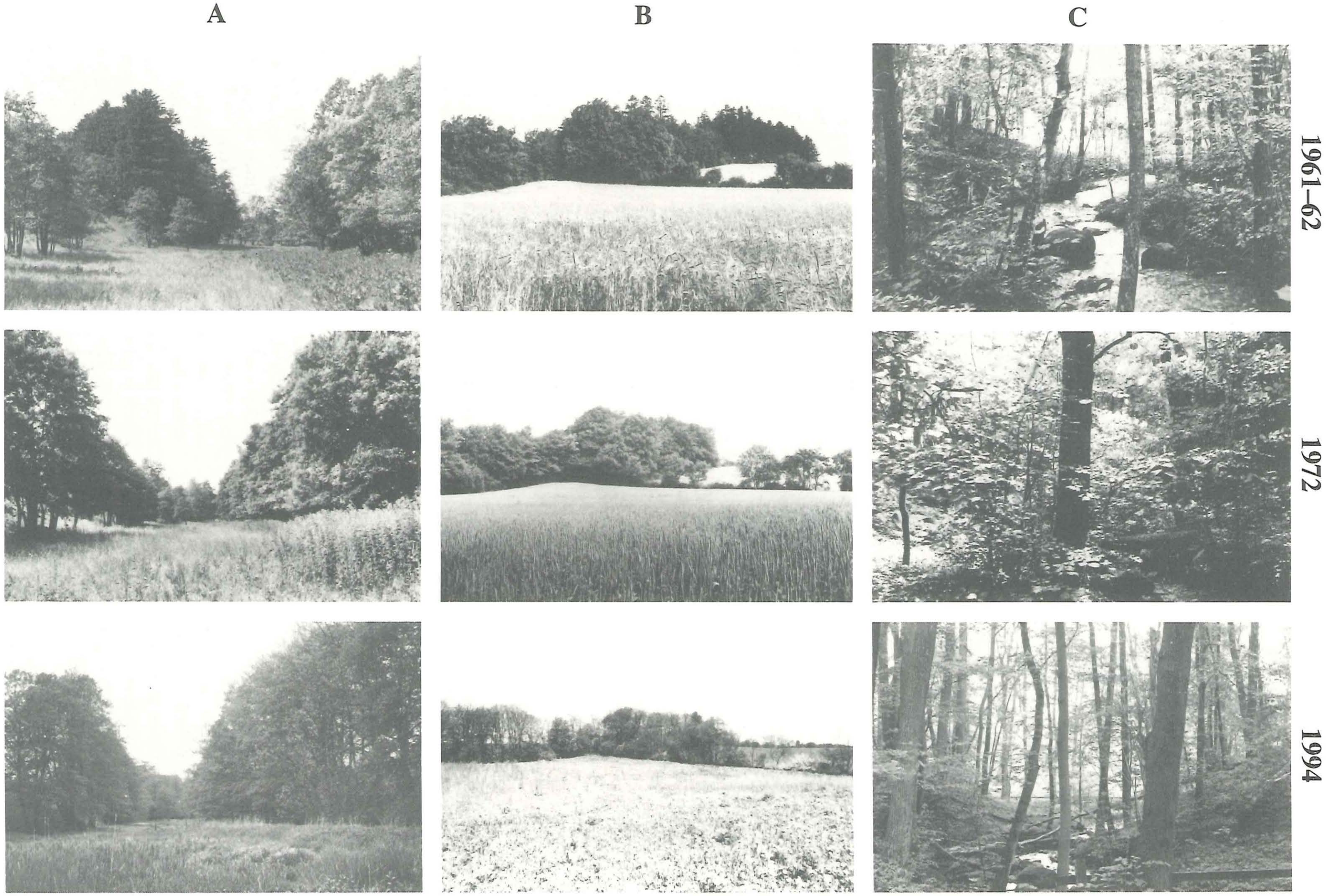
Fig. 1. Map showing the size and shape of Birdsong Valley (=the study plot) and indicating the distribution of wooded and of open, mostly grazed areas. The distribution of the different species of trees and some bush species are denoted by symbols which are seen on the three magnified sections of the valley (I, II, and III). Circles and arrows with the letters A to K show the locations and directions of the photographs presented in Fig. 2. (Map slightly modified after Malm et al. 1975).

Karta utvisande formen och storleken av Fågelsångsdalen (=provytan) samt utbredningen av trädbevuxen terräng och öppna områden, mestadels betade hagmarker. Förekomsten av olika arter träd och vissa buskar utmärks med symboler, vilka bäst syns på förstoringarna av dalens tre delområden (I, II och III). Cirklar och pilar med bokstäverna A till K utmärker läge och riktning på de fotografier, som visas i Fig. 2.

tigations was often emphasized among ornithological ecologists, with the honest conviction that they would provide important insights into the general features of the organization and dynamics of bird communities. These expectations have since then appeared somewhat exaggerated, to say the least. We are aware that our study plot is special – small and isolated as it is – and probably more suited for reliable census work than for the study of the regulating mechanisms of bird communities (if such an entity does exist from a functional point of view). We have always been aware that our results will probably contribute, if anything, to enhancing the complexity of the community problems rather than providing any solutions. In spite of this we have never found cogent reasons for giving up the field work (although we have never looked for any very energetically). Not anxious to conform our studies to the requirements set by the theories and paradigms of the ongoing bird community research, we have proceeded, driven only by our curiosity to see what will happen. After all, we are now able to describe the bird community of our study plot as it has appeared during the first 40 years since 1953.

The study plot

The study plot covers most of Birdsong Valley (Sw. Fågelsångsdalen), located about 8 km to the east of the town of Lund in the province of Scania in the very south of Sweden (55°43'N;13°18'E). It is a rather narrow valley which runs west-east and is surrounded by open farmland. The sides of the valley are in places quite steep, showing the slating which is a rather common geological formation of this area. The valley is therefore rich in lime and very fertile, thus supporting luxuriant vegetation with a rich herb flora. A winding brook flows gently at the bottom of the valley down to about twelve m below the level of the surrounding farmland.



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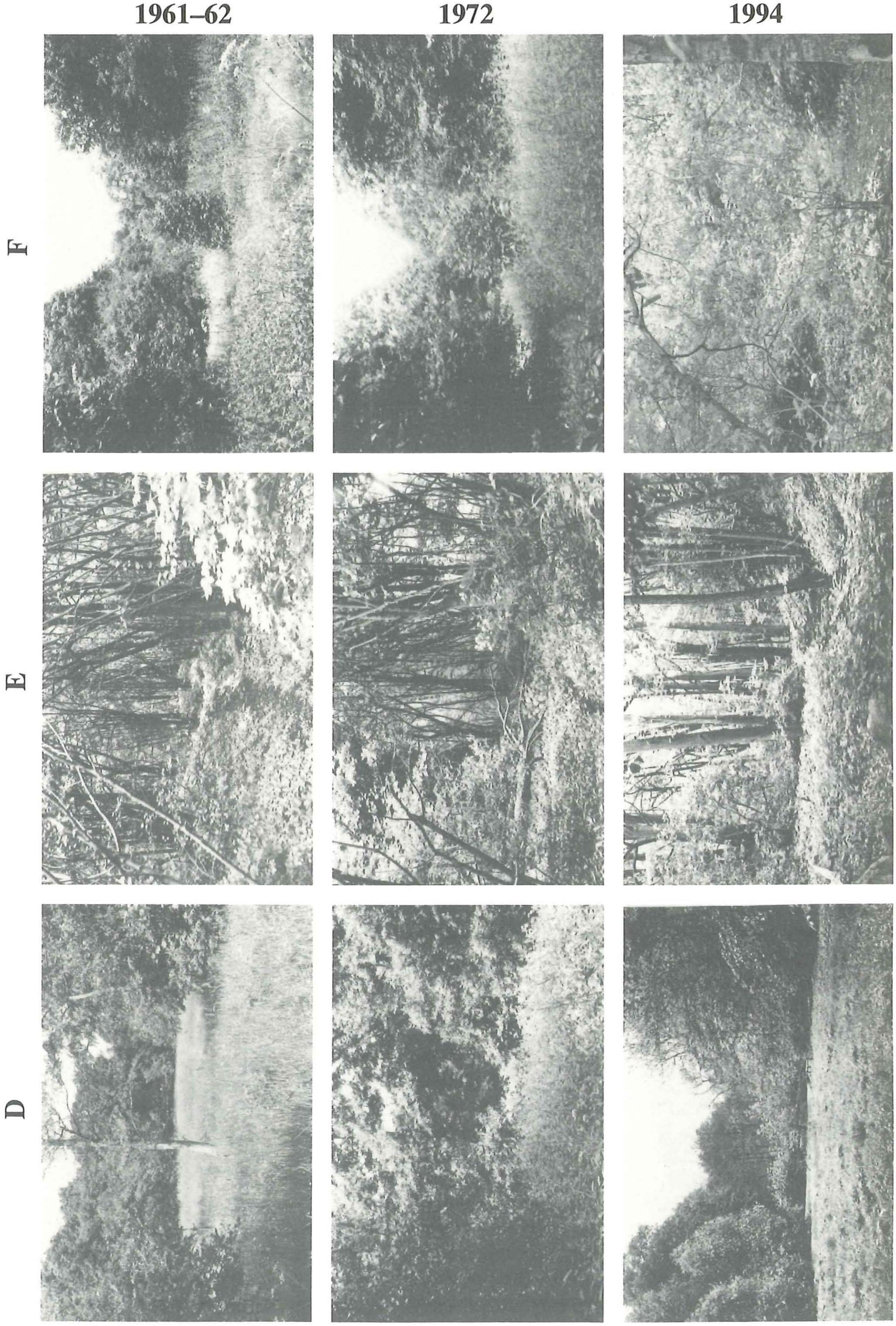

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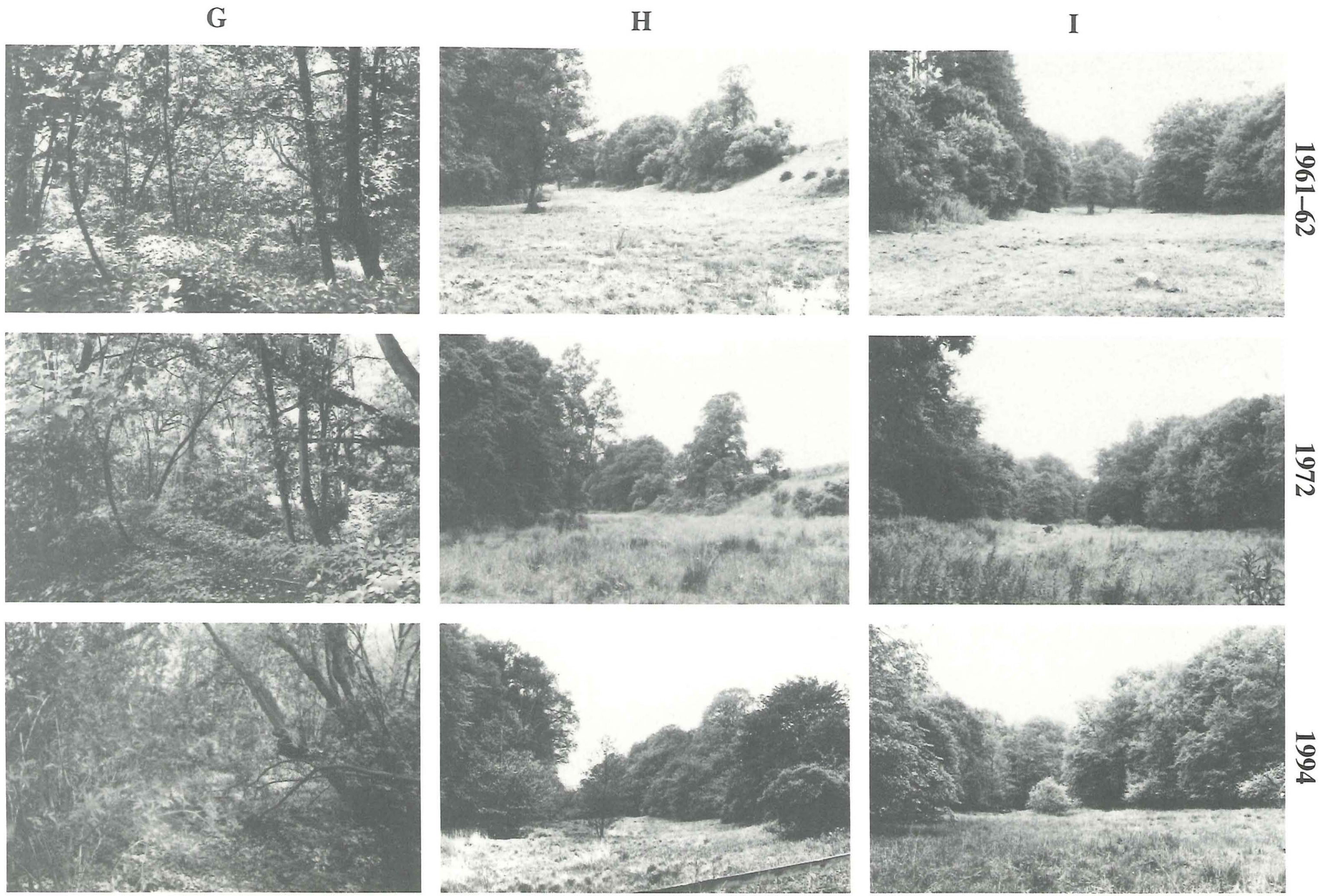

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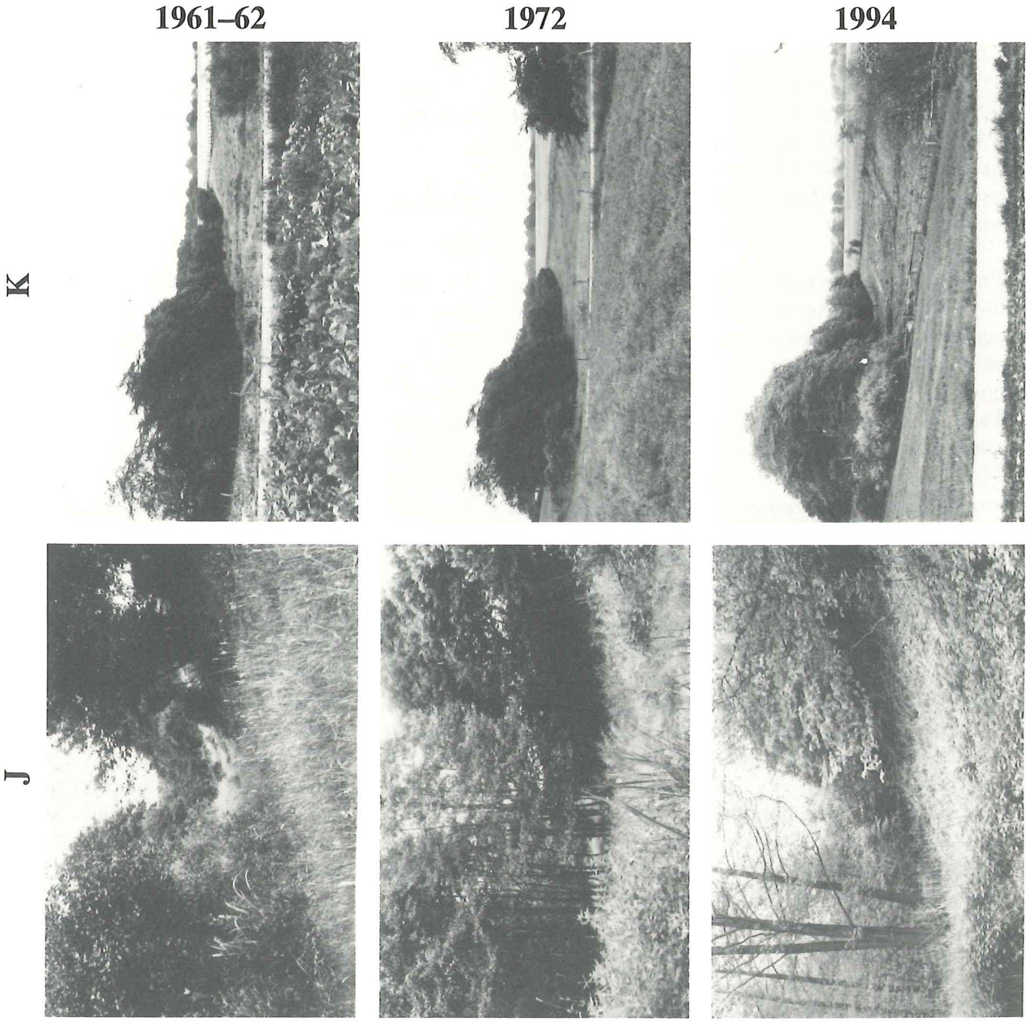


Fig. 2. (Pages 68–71.) Photographs showing 11 views (A to K) of the study plot in 1961/62, 1972, and 1994. The positions and directions of the camera have been the same all three years and are shown in Fig. 1. (The camera on position C was erroneously directed upstream instead of downstream along the brook in 1972.)

(Sid. 68–71.) Fotografier utvisande 11 vyer (A till K) i provytan från åren 1961/62, 1972 och 1994. Kamerans placeringar och riktningar finns utmärkta i Fig. 1. (Kameran riktades felaktigt uppströms istället för nedströms längs bäcken i position C år 1972.)

The study area covers about 13 hectares and is shown on the map of Fig. 1 where the distribution of open and wooded (trees and bushes) areas is indicated. The vegetation is dominated by several species of deciduous trees, which are indicated by symbols on the map. The latter, together with the photographs (Fig. 2), may provide a better general view of the appearance and characteristics of the valley than a wordy description.

A prerequisite for this long-term investigation was access to a study area which was protected from antropogenic influences. In fact, the valley was already granted the status of nature reserve in 1963. This means that the general structure of the vegetation as concerns the distribution of wooded and open areas has been preserved thanks to careful measures taken by the responsible authorities. Naturally, the habitat has nevertheless undergone a slow transformation but we have not tried to measure and describe this process. It appears from the photographs (Fig.

2), taken from selected positions in the valley indicated on the map (Fig. 1), that the habitat change has generally been fairly moderate from the 1960s up to 1994. However, the following events should be regarded as a complement to the photographs and as a background to the interpretation of the fluctuations of certain bird species populations.

1. The open areas were grazed in full mostly by cows until 1980. Grazing then decreased successively ceasing in 1986. It was resumed again in 1990 to protect the open areas from being invaded by bushes.
2. Two small clumps of spruces (*Picea*) (cf. Enemar 1966, Fig. 1) were removed in 1974.
3. Thickets of bushes have intermittently been removed from the grazed areas, especially in 1986 when a considerable clearing programme was undertaken in the western part of the valley. However, the bushes re-grew rather quickly, which means that the valley has experienced a number of such "bush cycles" in part of the open areas during the 40-year period.
4. Small glades in the wooded terrain have been closed by growing bushes and trees but new ones have been opened when fallen tall trees have been removed.
5. The village of Södra Sandby has expanded, and a number of detached houses (with their bird feeding tables) have been built closer to the southeastern boundary of the study plot but still separated from the latter by open agricultural fields.
6. A narrow path for strollers (and their sometimes free-running dogs) was prepared mainly in the wooded terrain soon after the valley was designated a nature reserve.
7. About twenty nest-boxes suitable for tits and flycatchers were erected in the middle of the 1950s at the two extremities of the valley by an ornithologist not belonging to the census team. These nest-boxes were not kept in good order and successively disappeared during the ensuing two decades.
8. As part of a special experiment, 60 nest-boxes were erected all over the valley before the breeding season of 1963 and removed in the autumn of 1966 (Enemar et al. 1972).

Our study plot is special in the sense that it is a luxuriant wooded island in an agricultural landscape. The impact of this kind of isolation on the species content has been the subject of many studies, especially in relation to conservation problems (e.g. Lynch & Whigham 1984, Opdam et al. 1985). Less interest has been paid to the effect on the fluctuation patterns of the species populations.

Methods

The census work

The bird community was censused by territory mapping during the breeding season. The investigation started in 1952. The reliability of the mapping technique was not carefully investigated until the seasons of 1956 to 1958, resulting in the conclusion that ten census visits to the study plot are required to count most territories (stationary males), as manifested by clusters of at least five registrations (Enemar 1959). The field work performed in 1952 was faulty in many respects and is therefore discarded. The results from the three seasons of 1953 to 1955 are useful from several aspects and are included in this study despite the fact that they are based on too few census visits. However, in 1970 recommendations for an international standard covering a mapping method were published (Anonymus 1970). They proved to be generally accepted by the ensuing census projects in many countries and were consequently adopted in our project. Thus all species maps analysed according to the first-mentioned technique have been re-evaluated. Consequently, the importance of simultaneous observations of neighbouring pairs has been carefully considered. Such observations are numerous on the species maps of the denser species populations in the valley. The reason is that the census-taker has regularly tried to hear once more a male that has been passed by before a new record was made (Enemar 1959). The re-evaluation of the species maps means that the previously published population numbers from the first ten-year period (Enemar 1966) differ somewhat from those presented here. The change in minimum cluster size from five to three registrations caused an average rise in the number of territories of 17±9 % (S.D., n=17).

The census-takers, the number of census visits, and the census periods are given in Table 1. The dates of the census periods differ somewhat between years, which may in some instances have influenced the recorded change in population numbers of certain species. On the other hand, the fact that the long sequence of years has been covered by only five experienced field ornithologists is an advantage. The conclusion is that the census results reflect, in a fairly reliable way, the long-term trends and other

Table 1. The census work in Birdsong Valley 1953–1992. AE=Anders Enemar, AMT=Ann Mari Thorner, BC=Berith Cavallin, EN=Erik Nyholm, IR=Inga Rudebeck, JS=Jan Samson, PG=Peter Gierow, SS=Sören Svensson.

Inventeringsarbetets omfattning i Fågelsångsdalen 1953–1992.

Year *År*	Census-taker *Inventerare*	Number of census visits *Antal inventeringar*	Period *Period*
1953	AE	6	15/5–21/6
1954	AE	4	19/5–12/6
1955	AE	5	24/5–19/6
1956	AE	12	20/5– 1/7
1957	AE	12	19/5–21/6
1958	AE	15	1/5–24/6
1959	AE	11	30/4–14/6
1960	AE	15	1/5–24/6
1961	AE	13	4/5–11/6
1962	AE	16	1/5–21/6
1963	AE,EN	14	3/5–21/6
1964	AE,EN	15	1/5–13/6
1965	AE,EN	14	14/5–13/6
1966	AE,EN,BC	14	14/5–21/6
1967	AE,BC,EN,JS	16	15/5– 4/7
1968	BC,EN	10	23/5–14/7
1969	BC,EN	15	23/5–28/6
1970	BC,EN	13	17/5– 2/7
1971	EN,SS	10	21/5– ?/6
1972	BC,EN	9	24/5– 2/7
1973	BC,EN	11	19/5– 2/7
1974	BC,EN	10	21/5–20/6
1975	EN,IR	10	23/5–15/6
1976	EN,IR	10	9/5–14/6
1977	IR	10	21/5–15/6
1978	IR	9	15/5–18/6
1979	BC,IR	10	15/5–12/6
1980	IR	9	15/5–12/6
1981	EN,PG	9	20/5–19/6
1982	IR,EN,AE	8	21/5– 9/6
1983	IR	12	29/4–12/6
1984	IR,BC	8	19/5–20/6
1985	IR	7	16/5– 4/6
1986	IR	10	17/5–14/6
1987	AMT	10	8/5–14/6
1988	AMT	10	16/5–16/6
1989	AMT	10	16/5– 6/6
1990	AMT	10	15/4– 8/6
1991	AMT	10	11/4–12/6
1992	AMT	10	3/4– 2/6

significant events in the community dynamics of the valley.

Calculations

Mathematical calculations and statistical tests are kept at a minimum in this paper. The problem is that the population numbers are not independent, as they stem from a time series (Järvinen 1979). This means that the population numbers of a certain year are partly dependent on the populations present in the preceding year, because a fraction of the latter will return to breed again in the same area. The derived indices or parameters are therefore useful, at best, first for comparisons with samples from similar study areas with the same statistical bias and, second, as fairly good descriptors of the community pattern.

If not otherwise stated, the statistical tests used are Student's t-test, analysis of covariance, and χ^2-test, following Bonnier & Tedin (1940).

The census results

The number of mapped territories of the different small passerine species in Birdsong Valley is found in Table 2. Apart from the small passerines only few species have regularly been stationary in the area: *Corvus corone cornix* and *Pica pica,* 1–3 pairs yearly, and *Columba palumbus,* 2–6 pairs yearly. The following species have settled in the area only occasionally during the 40-year period: *Dendrocopos major, Dendrocopos minor, Strix aluco, Falco tinnunculus, Anas platyrhynchos,* and *Ardea cinerea.*

So far, 39 species of small passerines have been stationary in the valley for at least one season, and 19 of these have been present in half or more of the 40 years. The latter are listed in Table 3. They make up 95 % of the total passerine community, which has fluctuated between 103 and 158 territories (nest-box years excluded) around an average of 124 territories.

The general trends in the fluctuations of the 19 species populations are presented in Fig. 3 as curves based on the moving averages of three seasons, together with the regression lines of the population sizes over time. The slope values (b), together with their level of significance (p), are found in Table 3.

Analyses and discussion

The qualities of the census material

The variation in population numbers and the community composition of study plots are usually inter-

Table 2. Number of birds (mapped territories) in Birdsong Valley 1953–1992. An asterisk (*) denotes the nest-box years. Note that the figures from 1953–1962 partly differ from those previously published (Enemar 1966) due to the re-evaluation of the species maps (see Methods).

Antal bofasta fåglar (karterade revir) i Fågelsångsdalen 1953–1992. Åren med holkar utmärks med en asterisk (*). Observera att siffrorna från säsongerna 1953–1962 delvis skiljer sig från dem som publicerats tidigare (Enemar 1966) beroende på att artkartorna omvärderats sedan dess (se Metod-kapitlet).

Year	1953	54	55	56	57	58	59	60	61	62	63*	64*	65*	66*	67	68	69	70	71	72
År	1973	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
Anthus	5	7	6	10	7	6	7	9	10	7	6	8	5	5	5	6	5	4	4	3
trivialis	3	2	3	6	5	4	5	7	3	2	6	3	5	7	3	4	3	–	–	–
Motacilla	–	–	–	–	–	–	–	–	–	–	1	–	2	1	–	–	–	1	1	2
alba	–	2	4	1	2	2	–	1	–	1	1	–	–	1	2	–	1	–	–	–
Troglodytes	1	2	1	–	–	1	–	–	2	2	–	1	1	–	–	1	1	–	2	2
troglodytes	3	6	7	7	8	7	–	–	–	–	3	3	–	–	–	–	2	9	11	9
Prunella	3	4	–	–	2	3	2	3	2	3	3	4	5	4	2	3	3	3	3	3
modularis	3	3	3	3	1	–	1	4	5	6	6	2	2	1	2	2	2	4	7	1
Erithacus	6	2	–	3	8	9	8	11	9	8	5	8	7	2	4	4	6	3	4	5
rubecula	3	4	5	7	1	1	1	4	4	3	4	5	1	–	2	2	6	5	10	6
Luscinia	9	13	7	17	14	15	16	14	13	10	10	13	13	16	15	12	14	13	12	10
luscinia	11	11	11	11	9	8	13	16	9	9	9	6	10	8	9	13	14	16	6	9
Phoenicurus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
phoenicurus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Saxicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
rubetra	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Turdus	7	7	5	7	9	7	7	7	8	9	6	8	9	6	11	8	14	8	8	11
merula	10	12	16	15	11	8	8	11	8	9	12	10	10	12	7	8	9	10	11	7
Turdus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
pilaris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	4	4	2	1
Turdus	–	–	1	–	–	–	1	1	2	2	1	2	3	–	–	–	–	1	–	–
philomelos	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	1
Locustella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
naevia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Acrocephalus	–	–	–	–	1	1	2	2	1	1	2	2	2	2	2	3	4	2	4	2
palustris	1	1	3	5	6	3	5	2	10	8	7	9	8	12	8	8	10	6	3	–
Acrocephalus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
scirpaceus	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hippolais	3	3	4	3	3	1	–	2	1	4	3	1	5	5	4	5	7	4	4	2
icterina	3	3	5	4	2	1	2	4	5	2	4	3	4	4	4	8	8	5	2	2
Sylvia	1	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–
curruca	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Sylvia	6	5	7	7	8	6	3	6	7	3	7	6	5	6	6	5	5	4	7	3
communis	–	2	5	3	6	4	4	3	6	1	3	2	4	–	5	6	3	2	1	3
Sylvia	16	14	16	18	19	14	13	14	16	12	13	9	15	11	14	12	14	11	11	9
borin	11	13	13	17	14	14	13	14	16	18	18	14	11	16	18	12	11	13	5	9
Sylvia	9	6	4	3	4	6	4	5	5	4	2	2	4	6	3	4	7	5	5	2
atricapilla	3	3	2	3	4	2	2	2	3	4	4	4	5	4	7	7	9	8	9	13
Phylloscopus	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	–	–	–	–
sibilatrix	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Year	1953	54	55	56	57	58	59	60	61	62	63*	64*	65*	66*	67	68	69	70	71	72
År	1973	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
Phylloscopus	23	22	20	20	23	23	17	18	13	13	17	15	13	11	16	14	12	11	10	11
trochilus	7	13	14	14	14	11	13	18	10	12	13	12	16	16	12	10	7	6	13	5
Regulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
regulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Muscicapa	1	1	1	–	1	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–
stricata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Ficedula	2	–	–	–	1	3	4	5	8	5	15	18	18	13	7	3	3	2	3	2
hypoleuca	2	1	1	–	–	2	2	4	2	3	4	2	4	3	2	3	1	1	–	3
Parus	2	1	4	4	5	1	3	2	3	2	2	2	4	2	4	2	3	2	4	3
palustris	1	2	3	2	3	3	3	3	1	1	2	2	1	1	1	2	–	1	1	1
Parus	1	3	4	1	3	3	2	4	5	3	6	4	7	5	3	1	3	3	2	3
cæruleus	5	3	4	5	3	5	2	6	5	2	4	3	6	6	6	3	3	4	11	5
Parus	2	2	3	4	7	7	8	10	11	9	9	10	19	16	9	7	6	7	10	5
major	7	10	10	12	10	12	14	14	10	4	12	8	9	15	8	7	7	9	13	14
Sitta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	2	1	3
europaea	2	1	–	–	1	1	–	–	1	1	2	–	–	–	1	–	–	2	2	–
Certhia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
familiaris	–	1	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	1
Sturnus	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1	2	2	1	2
vulgaris	6	5	8	8	4	6	3	8	8	5	10	4	3	3	–	1	1	1	1	3
Passer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
domesticus	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Passer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2	1	3	1
montanus	1	1	3	4	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Fringilla	17	19	14	10	14	12	12	13	17	17	18	22	17	15	19	17	19	15	12	15
coelebs	17	21	20	27	20	17	16	25	25	22	27	19	21	26	20	19	22	27	23	23
Carduelis	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	2	4
chloris	3	5	3	2	–	–	–	1	–	–	2	2	–	2	–	1	–	2	–	–
Carduelis	–	–	–	–	–	–	–	–	1	1	–	1	2	–	–	–	–	–	–	–
carduelis	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Carduelis	1	–	2	1	–	1	1	2	4	3	1	3	3	5	3	1	6	1	–	1
cannabina	1	–	1	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
C. cocco-	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
thraustes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Emberiza	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
citrinella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–
Emberiza	1	–	4	4	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
hortulana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Totals	116		103		132		110		139		127		162		132		139		113	
1953–1972		112		112		121		128		121		140		131		111		105		104
Totals	104		145		127		107		132		155		120		120		125		132	
1973–1992		125		158		112		149		113		113		137		122		138		116
Number of	20	17	17	15	18	19	17	18	21	23	19	21	23	18	21	21	22	22	22	23
species	22	23	23	22	22	20	17	21	19	19	23	19	17	17	21	22	21	22	19	19
Antal arter																				

Table 3. Average number (x), followed by standard deviation (SD), of those species of the study plot which have been stationary for 20 years or more. CV=coefficient of variation of x as a percentage, χ^2 = heterogeneity value, b = slope of the linear regression of the population size on time (cf. Fig. 3), p = level of significance. n = 40 for all species except for the *Parus* species, *Ficedula hypoleuca*, and Total community, where n = 36 (the four nest-box years excluded).

Medelantalet (x) karterade revir följt av spridningsvärdet SD för de arter i provytan som varit bofasta där i minst 20 av de 40 åren. CV = variationskoefficienten i procent, χ^2 *heterogenitetsvärdet som anger graden av olikhet i antal mellan åren, b=lutningsvärdet för regressionslinjen i Fig. 3, p=sannolikhetsvärdet. Antal år är 40 för alla arter utom för mesarna, svartvita flugsnapparen och hela beståndet, för vilka de fyra holkåren är fråndragna.*

Species/Art	x	SD	CV	χ^2	p<	b	p<
Anthus trivialis	4.9	2.4	50	46.8	0.40	–0.142	0.001
Troglodytes troglodytes	2.3	3.1	135	249.2	0.001	0.113	0.01
Prunella modularis	2.8	1.6	56	34.6	1.00	0.019	0.4
Erithacus rubecula	4.7	2.8	61	66.5	0.01	–0.063	0.2
Luscinia luscinia	11.6	2.9	26	30.1	1.00	–0.087	0.05
Turdus merula	9.2	2.5	27	25.7	1.00	0.079	0.02
Acrocephalus palustris	3.7	3.3	89	122.0	0.001	0.200	0.001
Hippolais icterina	3.5	1.8	51	40.8	0.80	0.046	0.1
Sylvia communis	4.4	2.1	47	38.2	1.00	–0.105	0.001
Sylvia borin	13.5	2.9	22	25.0	1.00	–0.063	0.2
Sylvia atricapilla	4.7	2.4	52	49.0	0.25	0.058	0.1
Phylloscopus trochilus	14.0	4.5	32	55.8	0.08	–0.270	0.001
Ficedula hypoleuca (36)	2.4	1.9	77	51.2	0.08	–0.016	0.547
Parus palustris (36)	2.2	1.2	53	21.8	1.00	–0.050	0.002
Parus caeruleus (36)	3.8	1.9	50	33.3	1.00	0.080	0.002
Parus major (36)	8.7	3.4	39	46.1	0.20	0.156	0.001
Sturnus vulgaris	2.5	2.9	118	126.7	0.001	0.117	0.01
Fringilla coelebs	18.8	4.5	24	41.6	0.75	0.265	0.001
Carduelis cannabina	1.1	1.5	135	77.8	0.001	–0.060	0.01
Total community (36) *Hela beståndet* (39 species/*arter*)	123.6	14.6	12	60.8	0.02	0.310	0.2

preted as a consequence of fluctuations in the bird numbers of the surrounding region or of mechanisms regulating the bird numbers at the community level within the plot, or both. A rather trivial factor at the local level is often a more or less radical habitat change within the study plot, such as logging or plantations. Fortunately, only few and limited human encroachments have taken place in our study area, which makes it all the more interesting, though not necessarily easier, to discern the factors operating behind the long-term trends shown by the studied bird fauna. On the other hand, as long as no experiments are made, it is not possible to reveal the causality behind the population dynamics. There are therefore reasons to raise the somewhat uncomfortable question: Is it at all worth while to publish the results of this entirely descriptive investigation? The basic requirement that must be met to answer this question in the affirmative is that the bird numbers have been estimated with the same, fair exactitude over many years. We believe that this is so because the same census technique and the same interpretation method were applied throughout, the shape of the study plot provided a minimum of borderline problems and the investigation was in fact long-term and performed yearly without interruptions.

Drawbacks to be remembered are the facts that the study plot is small and that it is special since it is an attractive island in the farmland. The significance of these points will be discussed further on.

It follows from the above that the census material does not permit analysis without restrictions. Probably the best information presented here concerns the long-term trends in the fluctuation patterns and

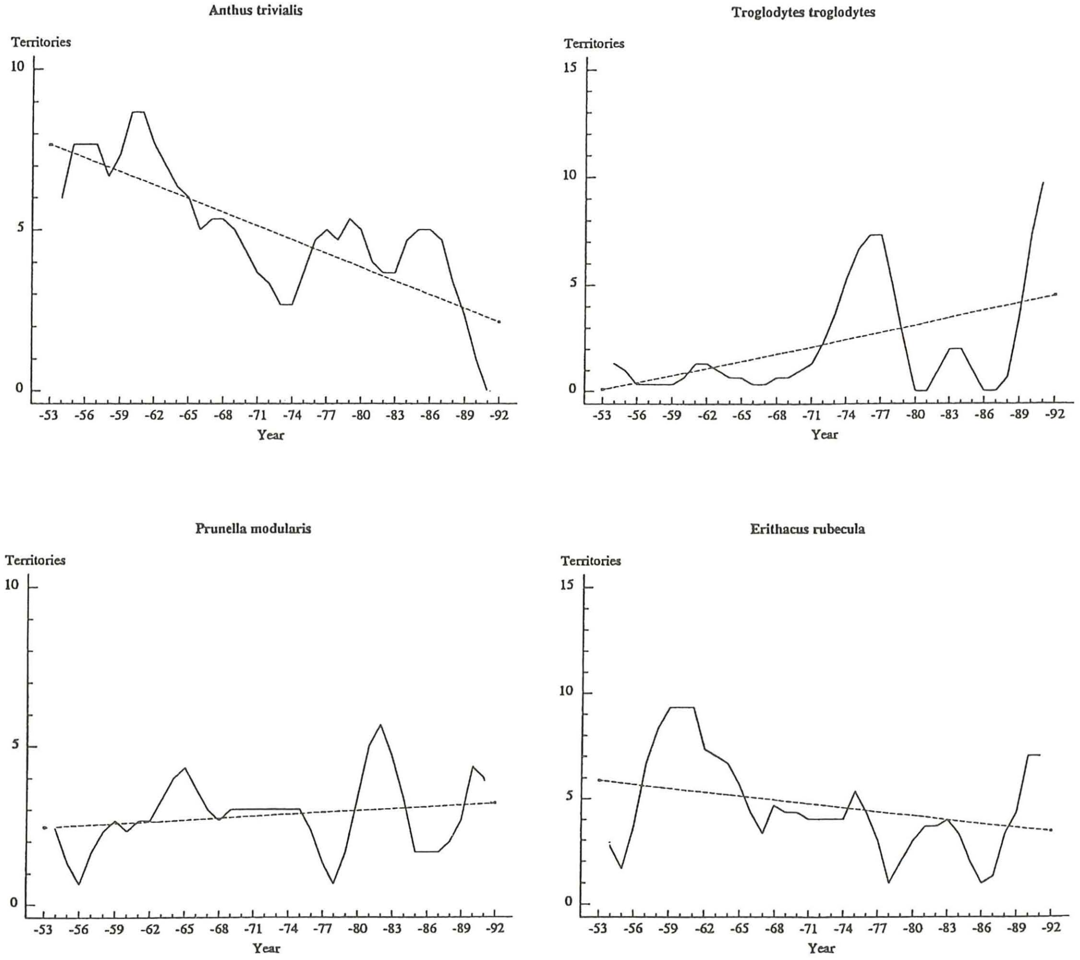


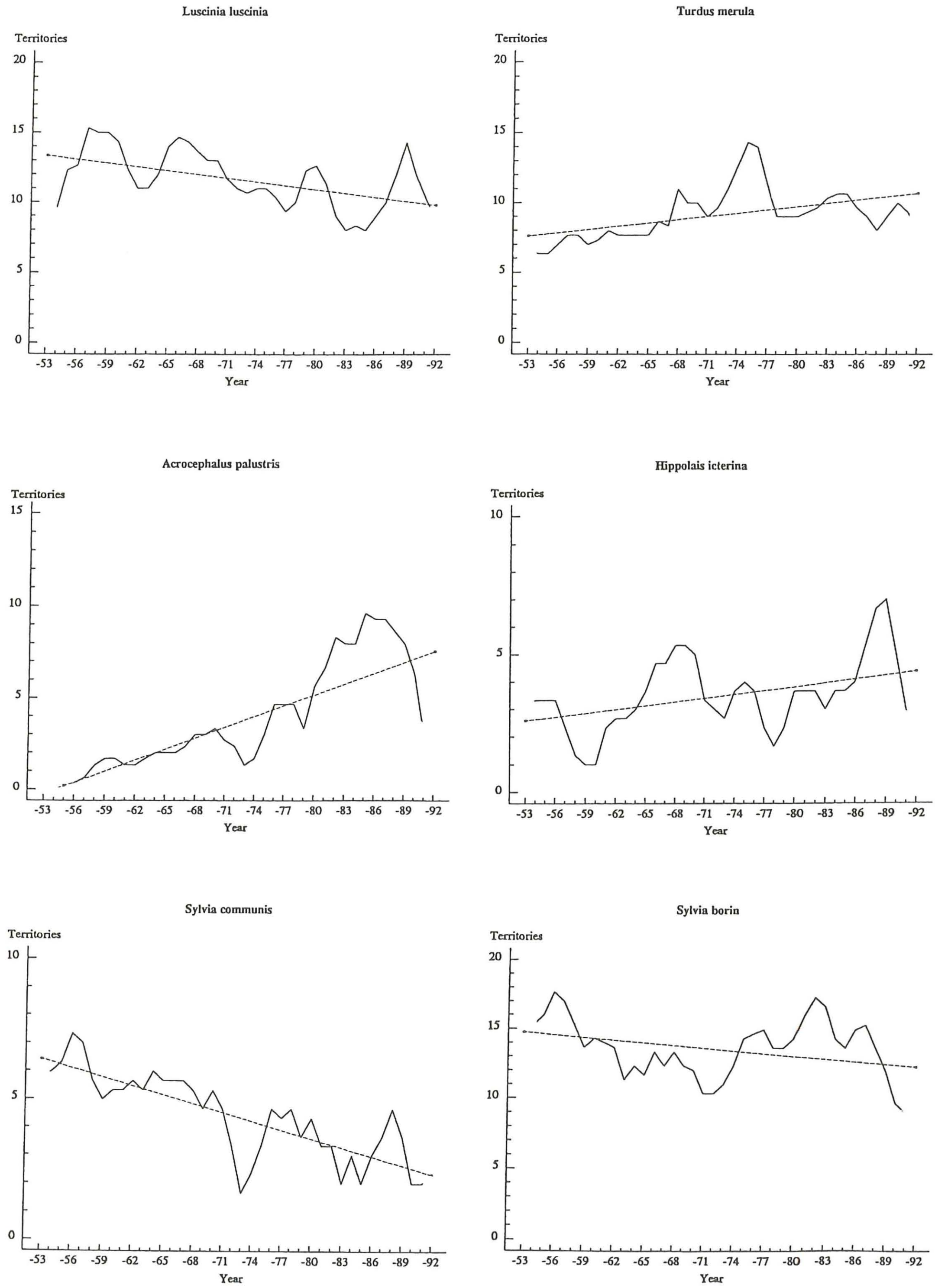
Fig. 3. (Pages 77–80.) The general trends in the fluctuations of the population sizes of the 19 most abundant species in Birdsong Valley, presented as curves based on moving averages of three seasons together with the regression lines of population sizes on time. The slope values (b) together with their level of significance (p) are found in Table 3. The nest-box years, 1963–1966, have been discounted when calculating the regression lines of *Ficedula hypoleuca, Parus major, Parus caeruleus,* and *Parus palustris.*

(Sid. 77–80). Diagram som visar den allmänna trenden i beståndsfluktuationerna för de 19 talrikaste arterna i Fågelsångsdalen i form av dels kurvor, som är baserade på s k glidande medelvärden över treårsperioder, dels s.k. regressionslinjer, som pekar ut medelriktningen i beståndsutvecklingen. Arterna återfinns i Tabell 3 tillsammans med hithörande statistiska data. Åren med holkar, 1963–1966, har uteslutits vid framräkningen av regressionslinjerna för svartvit flugsnappare, talgoxe, blåmes och entita.

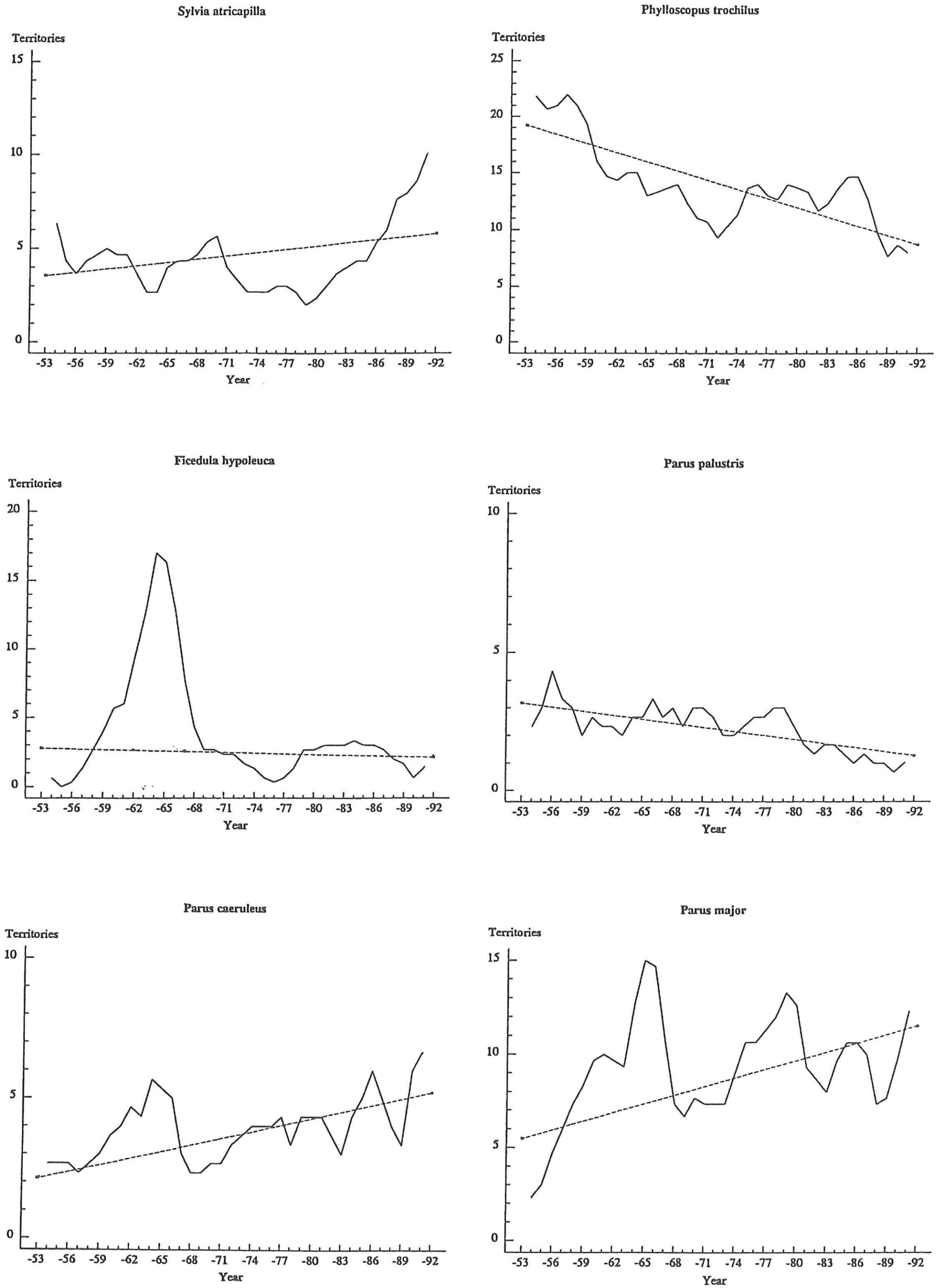
other population and community processes. This might be true even for the sparsely occurring species, as the long sequence of investigated years probably eliminates part of the "noise" caused by random events and occasional errors in the field work. Consequently, the analyses will be centered on the long-term category of processes and problems.

The species populations

Most of the analyses and discussions below will be restricted to the 19 species with average population sizes surpassing one territory. They are listed in Table 3. Some analyses concern the 24 most abundant species, which means that *Motacilla alba, Turdus philomelos, Sitta europaea, Passer montanus,*



Caption Figuttext p. 77



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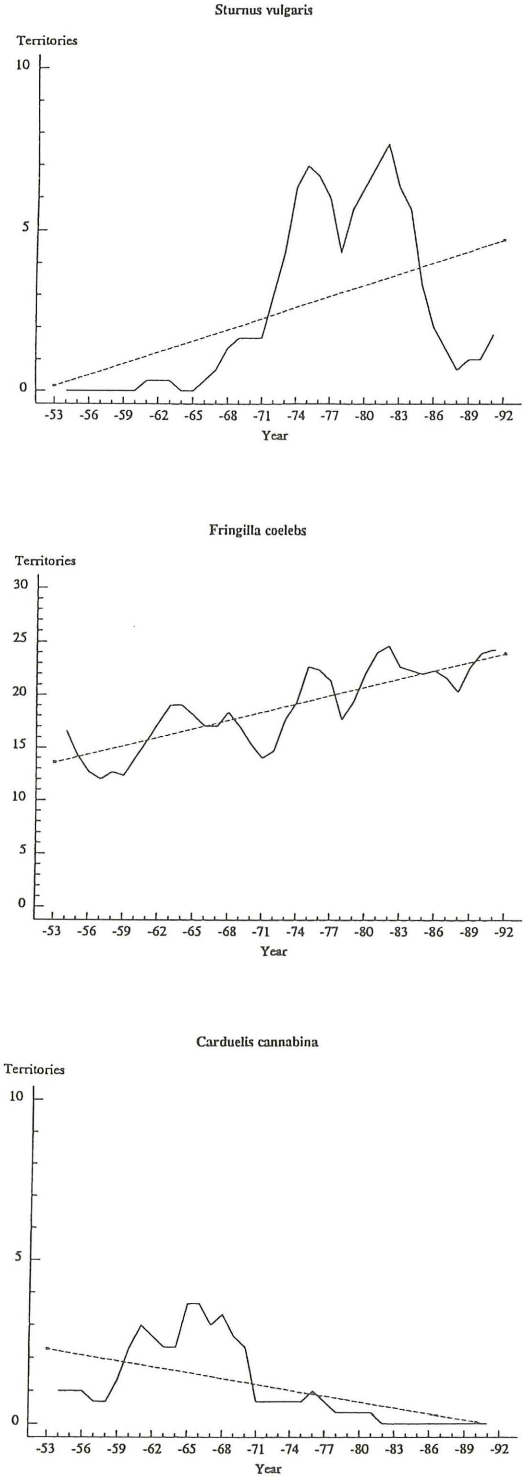
and *Carduelis chloris*, all with average populations of 0.5 to 1.0 territories, have been added to those of Table 3. These 24 species make up 98.5 % of the average community size.

The fluctuation amplitudes

By assuming that the yearly census results of the 19 species are considered as independent samples (which they are not), they can be subjected to a heterogeneity test (Table 3). The result indicates that only five of the 19 most abundant species varied significantly in population size. These are *Troglodytes troglodytes, Erithacus rubecula, Acrocephalus palustris, Sturnus vulgaris,* and *Carduelis cannabina,* all of which have been absent from the area for a varying number of years. The remaining species appear to be relatively stable with fluctuation amplitudes not extending beyond those expected due to chance only. A corresponding test on populations in more northern habitats revealed a higher proportion of unstable populations including e.g. *Phylloscopus trochilus* and *Prunella modularis* (Järvinen & Rajasärkkä 1992). Comparisons should be made with caution, however, because χ^2 could be misleading when the expected frequencies are small.

In general, species with high densities tend to be more variable than those with low densities (Wiens 1989b, with references). This pattern is said to hold in at least some bird communities (e.g. Holmes et al. 1986). This is also the case in Birdsong Valley according to the variation of the 24 most abundant species (Fig. 4). The absolute fluctuations expressed as SD-values increase with the average population sizes. On the other hand, the relation between the relative variations (the CV-values) and population size is reversed (Fig. 5), showing a significant negative regression of logCV on population size. This is partly due to the fact that every change in one territory is proportionally greater the smaller the populations are.

Because the CV-values are partly dependent on the sample size, they have to be recalculated to correspond to a common population size in order to make comparisons between species populations meaningful. Solonen (1986), applying the method presented by Svensson (1978), has adjusted the CVs to correspond to a sample size of 10 for the most abundant species of a bird community in southern Finland. After plotting the adjusted CV-values against population size, he found that the more abundant a species, the greater was its adjusted coefficient of variation (r=0.539, df=50, p<0.001). Fig. 6 shows corrected CVs plotted for the 24 most abundant



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species in Birdsong Valley. Here, the trend is quite the reverse. The adjusted CV decreases as the population increases. Solonen's study area mostly consists of luxuriant mixed forests with smaller open areas. It is highly fertile with a mosaic of diverse habitats and an abundance of edges. In other words, it does not differ significantly from the habitat of our investigation. On the other hand, more species were included in Solonen's analysis, also non-passerines. Excluding the latter, the regression remains positive and significant (r=0.39, df=35, p<0.02). It is likewise positive, let alone insignificant, when only the passerine species common to the two areas are considered (r=0.44, df=17, p<0.1). For comparisons, we calculated the adjusted CV-values from another study area in southern Sweden (Alerstam 1985). They show a significant and negative correlation with population size (r=–0.50, df=24, p<0.01), thus in agreement with the result from Birdsong Valley.

As seen in Fig. 6, the highest corrected CV-values are shown by those species of Table 3 which have varied significantly according to the χ^2-test together with five occasionally occurring species. The remaining ones have values between 25 and 42%, and interestingly, the corrected CV-values of these species are not correlated to their average population sizes.

Solonen (1986) suggested that the stability of his community was promoted by the presence of many less abundant rather than by a few dominant species. In contrast, the stability in our community is founded on the restricted variations shown by 14 species including the six most abundant ones (Fig. 6). This difference between the communities in southern Finland and southern Sweden, as demonstrated with the aid of the absolute species variations and expressed as their corrected CV-values, might be of significance and deserve a closer examination.

In this context, our bird community can be compared with those of two islands, where the bird fauna have been recorded over a long period of time, i.e. Farne Island, 29 years (Diamond and May 1977), and Skokholm, 34 years (Lack 1969). Wright & Hubbel (1983) have investigated the relationship between the CV-values and the proportion of years present for all species of these islands. The plotted curves appeared to be sigmoidal and nearly identical in shape to those predicted by a stochastic model. This model showed the proportion of time an (endangered) species was expected to be present in a reserve in relation to its CV. To quote Wright & Hubbel, "It is not surprising that species present in very few years should have high coefficients of variation of abundance. However, there is no statistical reason why species present in most or all years should necessarily have small coefficients of variation". Therefore, they found the agreement between the curves and the theory encouraging, even if it could not be accepted as a final proof. The corresponding and clearly sigmoidal curve based on all species in Birdsong Valley (Fig. 7) indicates that its bird community in this sense behaves as an island community despite the fact that it is surrounded by agricultural land and not by water.

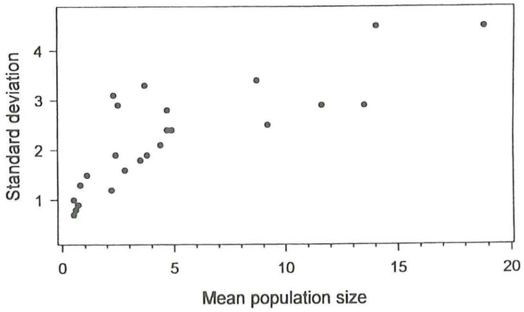

Fig. 4. The correlation between the fluctuations, expressed as the standard deviations (SD), and the mean size of the populations of 24 species in Birdsong Valley. The linear regression of SD on mean population size is y=1.4+0.17x, r=0.81, df=22, p<0.001.

Diagram som visar hur de absoluta beståndsfluktuationerna ökar ju större medelbestånden är för 24 arter i Fågelsångsdalen.

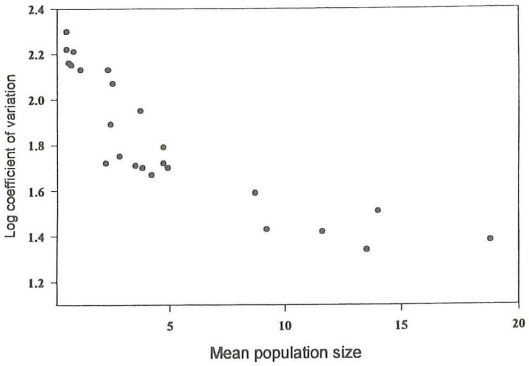

Fig. 5. The correlation between the coefficients of variation (CV) and the mean population size of 24 species in Birdsong Valley. The linear regression of logCV on population size is y=2.1–0.05x, r=–0.85, df=22, p<0.001.

Diagram som visar hur beståndsfluktuationerna, uttryckta som andel av medelbeståndet, minskar när beståndsstorleken ökar, allt för 24 arter i Fågelsångsdalen.

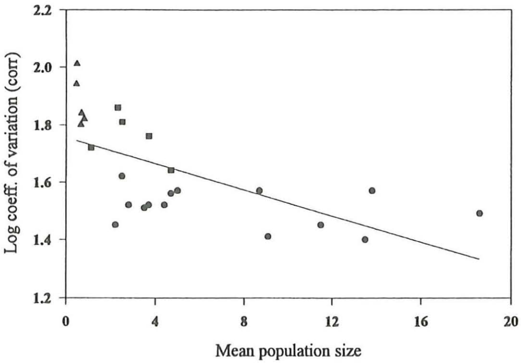

Fig. 6. The correlation between the logarithm of the coefficients of variation, adjusted to a common population size of 10, log CV(corr), and the mean population size of 24 species in Birdsong Valley. The linear regression of log CV(corr) upon mean population size is $y=1.8-0.02x$, $r=-0.41$, df=22, $p<0.001$. ● = the 14 species of Table 3 which did not fluctuate more than could be due to chance only according to the χ^2-tests. Note that their relatively low CV(corr)-values are independent of the mean population size. ■=the five species which according to Table 3 fluctuated significantly. ▲=five only occasionally territorial species.

Diagram som visar i princip samma sak som diagrammet i Fig. 4 efter vissa omräkningar i syfte att möjliggöra jämförelser med andra undersökningar.

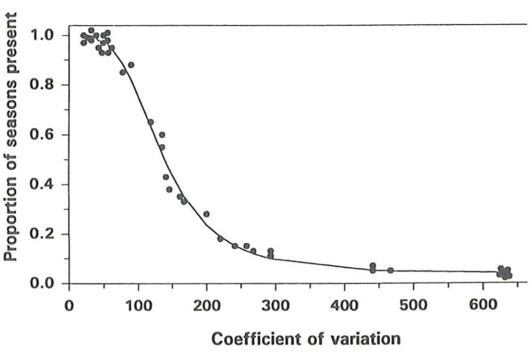

Fig. 7. The relationship between proportion of years present in Birdsong Valley and the coefficient of variation. The logistic equation best fitting the sigmoidal curve is

$$f(x)=[a-d]/[1+(x/c)^b]+d,$$

where a=symptotic maximum, b=slope parameter, c=inflexion point, and d=asymptotic minimum. The curve resembles those calculated for the islands of Skokholm and Farne Islands (Wright & Hubbel 1983).

Diagram som visar hur förhållandet mellan andelen år av närvaro i Fågelsångsdalen och fluktuationsstorleken för 24 arter följer en S-formad kurva. Denna liknar motsvarande kurva som upprättats för ett par öar utanför den engelska kusten.

The long-term trends of the bird numbers

The population numbers belong to a time series, and even small changes between years may build up trends which are significant over the whole or part of the investigated 40-year period. In this context we deal with the trends covering all four decades in the first place. They are presented for the most abundant species (Table 3) as fluctuation curves and regression lines in Fig. 3.

Three species, *Fringilla coelebs, Parus major,* and *Parus caeruleus*, show a steady increase in population size throughout the 40 years. This is true for the two *Parus*-species even when the effect of the nest-box years is eliminated. The three species have increased generally in southern Sweden during the last two decades, according to the mapping censuses and point counts organized by Sören Svensson (1992), which were started in 1970 and 1975, respectively. The population growth in Birdsong Valley may at least partly be a reflection of this trend. Also *Turdus merula* has increased significantly in number in the valley. Its population size peaked around 1975 followed by declining numbers, so far without reversing the long-term increasing trend. The species has not changed significantly in southern Sweden since 1975 according to Svensson (1993).

Sturnus vulgaris did not appear in the valley until 1962, but increased considerably during the third decade and then declined to a few pairs during the last ten years. The species has for a long time shown a negative trend in southern Sweden as well as throughout Scandinavia (Svensson 1992), and therefore the sudden "invasion" in the valley about 20 years ago was surprising. The decrease in numbers during the last decade is probably a consequence of the continuing and general decline of the Swedish population.

The dramatic fluctuations of *Troglodytes troglodytes* are since long known to be connected with variations in winter climate between years in NW Europe. The sharp rise in population numbers during the last few years is apparently a consequence of the high survival rate during the last five winters, which have been extraordinarily mild (Fig. 14).

Acrocephalus palustris shows a steady population growth from 1957, when it was first recorded in the valley. The immigration of the species in southernmost Sweden has been well documented since the 1940s (Wingstrand 1943, 1949, Cavallin 1979), and the behaviour of the population in the valley is certainly a reflection of this process. However, the numbers have dropped dramatically during the last three years (totally absent in 1992 and 1993), a fate which *A.palustris* shares with some other warbler species.

Phylloscopus trochilus and *Sylvia communis* show significant and declining numbers over the 40 years. This is in contrast to the general trend of these species in southern Sweden, where both have increased during the last two decades (Svensson 1992). A simliar pattern is shown by *Sylvia borin.* Its numbers declined significantly ($r=-0.49$, $p<0.05$) in the valley from 1975. When Svensson's point count project started in 1975 he documented a successive population growth. Its congener, *Sylvia atricapilla,* however, has shown a marked rise in number in the valley during the same time period ($r=0.88$, $p<<0.001$). This is in line with the trend in the surrounding landscape (Svensson 1992). He also noted that the population sizes of the three *Sylvia*-species dropped markedly in 1991. This was observed only for *S.borin* in Birdsong Valley. On the other hand, the point counts and the mapping censuses largely disagree in this respect in Svensson's own samples.

One of the dominant species, *Luscinia luscinia,* shows a slow and significant decrease in number with a clear low in 1991. Svensson (1992) also noted low numbers of *L. luscinia* in 1991, though otherwise revealing no trend. One of the most prominent events in the valley has been the successive decrease in number of *Anthus trivialis*, eventually becoming absent as from 1990 onwards. No less than five to ten territories were recorded in the valley during the first ten years. There has been no indication of a corresponding development in southern Sweden as a whole (Svensson 1992). Also *Carduelis cannabina* has abandoned the valley from being next to regularly present with two territories on the average during the first two decades. The last territory of this species was mapped in 1980. Its disappearance is probably a consequence of the general and persistent decrease which has occurred in southern Sweden since 1975 (Svensson 1992).

Another loser is *Parus palustris*, which has decreased from about three to one territory over the 40 years, a trend which is supported by the point counts but not the mapping censuses in Svensson's (1992) project.

Four species show only insignificant trends in their population sizes over the four decades. *Hippolais icterina* is represented by two fluctuation "cycles" with territory numbers varying from zero to eight. The population size of *Ficedula hypoleuca* (the nest-box years discounted) as well as that of *Erithacus rubecula* tend to decline in the valley. The latter species fluctuates wildly, which is characteristic of a species known to be sensitive to the winter climate (cf. *T.troglodytes* above). *Prunella modularis* also showed a fluctuation pattern reminiscent of that of *E.rubecula.*

Among those species which were irregularly present in the valley and therefore are not presented in Fig. 3, a few settled there for a limited sequence of years. *Carduelis chloris* and *Sitta europaea* were first recorded as territorial in 1964 and 1968, respectively. These species have then been only occasional despite the fact that they have increased considerably in southern Sweden at least from 1975 (Svensson 1992). *Motacilla alba* appeared in 1963 and has been recorded occasionally since then. A few pairs of *Parus montanus* bred in some nest-boxes (not erected by the census project) in the eastern part of the valley during a decade around 1970. *Emberiza hortulana* disappeared from the valley in the 1960s and was commented on by Enemar (1966). Three pairs of *Turdus pilaris* settled in 1988 and some pairs have appeared since then. This event might reflect the increase in the population size in southern Sweden during the last few years, as indicated by point counts and mapping censuses (Svensson 1992).

It is, needless to say, not possible to identify the factors causing the fluctuations of the species populations by only recording the bird numbers over a sequence of years. Good indications could be obtained in special cases, such as the conspicuous ups and downs of species which we know are sensitive to the climate in their north European winter quarters, where both extremely mild and harsh weather situations sometimes occur. Otherwise, due to the small samples, only the significant long-term trends are considered to reflect such events that within or outside the valley may be of importance for the population dynamics. The causation of these trends will be discussed mainly in the "Community" chapter below. Here some comments will be given upon possible habitat changes in the valley as factors of importance.

Even if the general structure of the habitat seems to have remained fairly constant (Fig. 2), less conspicuous changes in the habitat quality have of course occurred, such as those connected to the possibly increasing average age and, to some degree, the size of the trees. This might have paved the way for the increase in numbers of *Fringilla coelebs*, known as a successful inhabitant of climax forests. More nesting-holes accumulate as the trees grow older, which might explain the rising numbers of some hole-nesting species such as *Parus major* and *Parus caeruleus* (possibly favoured by increased(?) winter feeding in the region since the 1950s), as well as the immigration of *Sturnus vulgaris* and *Sitta europaea* from the end of the 1960s. The popping up of the "trunk-linked" *Certhia familiaris* during the last decade (four territories in 1993!) may depend on the same habitat change although the mild winters during the last few years may also have been of importance.

The previously mentioned growth and maturation of the deciduous trees may have affected the understorey (e.g. *Corylus, Crataegus, Prunus*) and the edge thickets of the valley, perhaps resulting in a quality decline for its inhabitants. If so, this might at least partly have caused the slow decrease of *Luscinia luscinia*, a typical understorey inhabitant, and the persistent and considerable retreat shown by *Phylloscopus trochilus*, which prefers forest edges and succession stages to mature woodland. It is more doubtful whether the decrease of *Sylvia communis* should be mentioned in this context, because this species is mostly tied to the open areas of the valley. And so are *Anthus trivialis* and *Carduelis cannabina*, whose disappearance cannot reasonably be related to a habitat change in the valley. According to Svensson (1992), the general population decline of *C.cannabina* is most likely due to changes in the structure of the farmland with an impoverished food supply as one of many consequences thereof.

The opposing trends shown by *Syliva borin* and *Syliva atricapilla* are also consistent with the surmised transformation of the wooded habitat. Although they overlap considerably in their habitat choice, the increasing *S.atricapilla* is the "tree-lover" of the two species (Rosenberg 1953), whereas the decreasing *S.borin* also settles in thickets without trees. On the other hand, according to experimental tests carried out by Garcia (1983), these species show a high degree of interspecific territoriality during the breeding season. The first arriving *S.atricapilla* should be able to oust its congener from localities acceptable to both species. Hence, part of the decline of *S.borin* in our study plot might be explained by the rising number of *S.atricapilla.*

It is possible that a moderate habitat change in Birdsong Valley has caused the long-term population development of some species in contrast to that established in the surrounding landscape. This is mere speculation, however, because the conclusion is only based on the knowledge of the ecology of the different species involved.

Interspecific competitive interactions at the community level might have been much more important than indicated above. These will be discussed in the following chapter.

The community

The field of community research – a mess of contradictory opinions

According to Wiens (1989a) who recently reviewed the rise and development of the bird community research in great detail (Wiens 1989a,b), the birds of Birdsong Valley form a community in the sense that it is an "assemblage of individuals of several species that occur together". But do such assemblages exist at all in any functional biological sense (Wiens 1980)? Opinions differ, to say the least, and many authors hesitate, based on various investigations, to accept the community as a rational concept (e.g. Underwood 1986). Opinions also differ among those who use the community concept as a starting point when studying the regulating mechanisms. Many scientists have emphasized that there are internal forces, such as competition and other interactions between species, which are balancing the community around some sort of equilibrium, while others have stressed the importance of environmental and climatic alterations and other "external" causes. The two sets of factors have been arbitrarily classified by Solonen (1986) as density dependent and density independent, respectively, and, of course, both of them will affect the structure and dynamics of the community.

The number of studies that describe the composition and dynamics of bird communities is considerable and still increasing, especially those covering long sequences of investigated years. There is now a need for more controlled experiments in the field (cf. e.g. Holmes et al. 1986, Brawn et al. 1987, Krebs 1991). On the other hand, many authors (e.g. Wiens 1983,1989b) still stress that our knowledge of bird communities is limited. Therefore, more descriptions are said to be of considerable interest, maybe first and foremost those that increase the knowledge of the long-term fluctuation patterns. Although there are good reasons not to do long-term studies, as mentioned by Krebs (1991), such investigations may contribute considerably to our understanding of the community as regards cyclic or unusual events which might be of importance. Therefore long-term census work should be encouraged (e.g. Wiens 1984, Wiens et al. 1986, Franklin

1989). Opinions differ also concerning the most suitable temporal scale in order to avoid misleading results (cf. Wiens 1977, Calder 1984, Weatherhead 1986). It has often been put forward that the appropriate time scale is certainly longer than the time span of a research grant. The present investigation more than fulfils this requirement (even if it has never enjoyed any grants).

The number of breeding birds of a study plot will always change between seasons. Therefore, a too short-term investigation can easily lead to mistakes when the aim is to describe the "true" or "average" community structure and behaviour (if there is any). Reasonably, the number of investigated seasons is not enough until fairly stable averages are discerned. Many published study plot censuses covering periods of about ten years have been considered long-term enough. Awaiting comprehensive analyses of this "long-term problem", the community data from Birdsong Valley will be presented not only for the 40-year period as a whole but also for each of the four ten-year periods. This may provide a preliminary idea of the reliability of the information based on 10-year periods. The more or less appropriate and partly interrelated community parameters most often used have been calculated (Table 4). As indicated in the table, the four nest-box years have been discounted for some parameters.

The size of the whole community

The size of the community has fluctuated significantly (Table 3) between 103 and 158 territories (nest-box years excluded). The average size does not differ from those of the four separate decades; nor do the latter differ among themselves (Table 4). The community shows an increasing, albeit insignificant, trend over the 40-year period, from around 115 to around 130 territories (Fig. 12). The changing trends of the separate decades differ in their directions and they are also insignificant. The coefficients of the density variation (the CV-values) are low throughout and furthermore in agreement with those characteristic of southern communities in northern Europe (Järvinen 1979).

The number of species

The average number of species remained relatively stable throughout the study although there is a significant difference between the first two 10-year periods (Table 4, $p<0.01$). This difference is questionable because some species may have been overlooked during the first three seasons of the first decade when relatively few census visits were made (see Methods and Table 1). This might also explain the higher coefficient of variation in the number of species, CV(S), of the first ten-year period compared to the three subsequent ones. The average value of the four periods, including the whole 40-year period, is significantly higher than the average of the nine southern study plots (plot B1=Birdsong Valley excluded) in Europe in Järvinen's (1979) review ($p<0.05$). The reason might be that our plot is an isolated "island" in the open farmland and therefore rather effective in attracting sparse species, when they happen to appear in the surrounding region during the spring migration. This promotes an increase in the variation of species richness. Moreover, it is a general experience that CV(S) is almost exclusively affected by the rare, so-called "in-and-out" species (Järvinen 1979).

The species turnover

So far, only eight species, i.e. about 40 per cent of the average total number of species (Table 3), have been stationary every year in Birdsong Valley. This indicates that a considerable species turnover has taken place. The latter has been calculated, as a percentage, according to the generally used formula $T=100(I+E)/0.5(S1+S2)t$, where I and E are the number of immigrating and emigrating species, respectively, S1 and S2 are the number of stationary species in the first and second season, respectively, and t is the number of years between the compared seasons. This method of describing the change in species composition between years has mostly been applied when studying island biogeography. As mentioned previously, the Birdsong Valley is an "island", surrounded not by water but agricultural land. Therefore we have chosen to adopt the same technique.

The species turnover between successive years ($t=1$) is shown in Table 4 as average values. This index is related to the CV(S) (Järvinen 1979) but, unexpectedly, the species turnover rate in our study area does not significantly exceed those of other plots in Europe. It varies between 4.4% and 50% and there is no significant trend over the 40-year period (Fig. 8).

According to Wiens (1989b), determining the turnover rates is not an easy matter due to a variety of problems. These are mainly due to (1) sampling errors arising when species numbers are established by one or few censuses only or at times separated by intervals of varying lengths, and (2) inclusion in the species lists of species which are not true members of the community. These errors are all negligible in

Table 4. Selected parameters of the bird community in Birdsong Valley given for each of the four ten-year periods as well as for the entire 40-year period.

Valda parametrar som karakteriserar fågelsamhället i Fågelsångsdalen, dels för var och en av de fyra tioårsperioderna, dels för de sammanhållna 40 åren.

	1953–1962	1963–1972	1973–1982	1983–1992	1953–1992
N	119.4±11.1	117.3±14.7*	127.2±18.7	127.8±12.8	123.6±14.6*
CV(N)	9.3	12.4*	14.8	9.9	11.9*
b	+2.072	–4.800*	–0.109	–0.982	+0.310*
r	+0.568, n.s.	–0.613, n.s.	–0.017, n.s.	–0.234, n.s.	+0.255,n.s.
S	18.5±2.3	21.2±1.6	20.8±2.0	20.0±2.1	20.1±2.2
CV(S)	12.6	7.6	9.6	10.5	11.1
T	20.5±8.8	20.0±7.4	18.7±6.5	27.4±13.6	21.7±9.7
H'	1.11±0.06	1.19±0.04*	1.16±0.04	1.15±0.04	1.15±0.05*
CV(H')	4.9	3.5*	3.8	3.5	4.5*
J'	0.88±0.02	0.89±0.03*	0.88±0.01	0.89±0.01	0.89±0.02*
CV(J')	2.4	2.9*	1.4	1.4	1.9*
V	0.68**	0.35*	0.29	0.98	0.73*
NewS	5	6	4	4	19
MaS	*Ph.trochilus* *S.borin* *F.coelebs* *L.luscinia*	*F.coelebs* *Ph.trochilus* *L.luscinia* *S.borin*	*F.coelebs* *S.borin* *Ph.trochilus* *L.luscinia*	*F.coelebs* *S.borin* *Ph.trochilus* *L.luscinia*	*F.coelebs* *Ph.trochilus* *S.borin* *L.luscinia*

*	The four nest-box years excluded. *De fyra holkåren frånräknade.*
**	The three first years (1953–1955) discounted. *De tre första åren (1953–1955) frånräknade.*
N	Number of mapped territories (mean±SD). *Antalet karterade revir (medeltal±SD).*
CV(N)	Coefficient of variation (100xSD/N). *Variationskoefficienten i procent.*
b	Slope of linear regression of community size on time. *Beståndsstorlekens genomsnittliga ändring per år.*
r	Coefficient of correlation of the linear regression above. *Korrelationskoefficienten för beståndsändringen.*
S	Number of stationary species (mean±SD) *Antalet bofasta arter (medeltal±SD).*
CV(S)	Coefficient of variation (100xSD/S). *Variationskoefficienten i procent.*
T	Species turnover rate, mean±SD of comparisons between successive years (t=1). *Artomsättningen, medelvärde±SD, baserad på jämförelser mellan varandra påföljande år.*
H'	Shannon's index of diversity (mean±SD). *Shannon's diversitetsindex (medelvärde±SD).*
CV(H')	Coeffient of variation of the diversity index (100xSD/H'). *Diversitetsindexets variationskoefficient i procent.*
J'	The evenness component of species diversity (H'/logS). *Artförekomstens "jämnhetsindex".*
CV(J')	Coefficient of variation of the evenness value. *"Jämnhetsindexets" variationskoefficient i procent.*
V	The variance ratio. *Varianskvoten.*
NewS	Number of new species after 1953. *Antalet nytillkomna arter efter 1953.*
MaS	The most abundant species listed according to population size. *De fyra vanligaste arterna ordnade efter populationsstorlek.*

our case, where the counted species are throughout represented by mapped territories at intervals of one year.

The relative turnover value in Birdsong Valley increases with increasing interval between the compared years, showing a close and linear relationship (Fig. 9). A similar increase of turnover rates was found by Abbott (1978), Jones & Diamond (1976) and also by Svensson et al. (1984), who analysed a 20-year census material from northern Sweden and discovered a peak for intervals of 13 to 14 years, after which a decline was observed. Our sequence of turnover values shows no tendency to peak so far.

The slope of the regression equation, 0.75% (Fig. 9), corresponds to the average increase in turnover rate following each addition of one year to the interval between the compared years. In theory, a total turnover (100%) is expected at intervals slightly exceeding 100 years. In other words, only few of the bird species present in the study area in the 1950s are expected to be found there around 2050, provided that the average number of species remains the same. However, the steady rise in the turnover with increasing interval, as shown in Fig.9, is expected to level off. The diagram indicates that this process may have started.

So far, only eight species (i.e. about 40 per cent of the average total number of species, Table 3) have been permanently breeding in Birdsong Valley, thus contributing nothing to the turnover of species and putting an upper limit to turnover rates, i.e. 60 per cent in our case. This level will be reached around the turn of the century according to the regression line of Fig. 9.

The described rise in turnover values with increasing interval between compared years is rather moderate (Fig.9), because the number of occasionally appearing species do not increase when intervals are protracted. As a consequence, when calculating the turnover rate between successive years by dividing the "interval turnover" by t, the result will of course decrease with longer intervals as demonstrated by Jones & Diamond (1976).

Obviously, most of the species turnover is caused by the occasionally occurring species which are stationary in the study plot for one or several years at a time. The turnover concept has therefore been considered "ecologically trivial" (Williamson 1983), and changes in total species number may be of little importance unless they reflect the "core" of the community, i.e. the appearance or extinction of species which will be or have been long-term stationary with no or only few absence seasons (Wiens 1989b). In Birdsong Valley, two such species have become extinct, *Emberiza hortulana* and *Carduelis cannabina*, and probably also the recently vanished *Anthus trivalis* (absent also in 1993). Three species have immigrated, *Sturnus vulgaris, Sitta europaea* and *Carduelis chloris*. The recently appearing *Turdus pilaris* (present also in 1993) probably belongs to the long-term immigrants. This means an "ecologically significant" or long-term annual turnover rate of about 1% (the number of immigrating and vanishing species (8) divided by the average total number of species (20.1) and the number of intervals (39)).

After the starting year of 1953, 19 *new* species have been *stationary* in the plot for at least one season, and they are rather evenly distributed over the four decades (Table 4). A clear decline might have been expected. On the other hand, the "island" character of the study plot and the dynamics of the north European bird fauna (Järvinen & Väisänen 1977, Järvinen & Ulfstrand 1980) may explain the documented steady supply of new species as well as making it likely that new species will settle during the fifth decade of the census work.

Other community parameters

The calculated community parameters, expressing species diversity and evenness with their coefficients of variation, are shown in Table 4. The indices of the four 10-year periods conform nicely, the only exception being the H'-value of the first decade, which is smaller than those of the subsequent two decades ($p<0.05$ and $p<0.01$). As this index is dependent on the number of species, the difference might partly be a consequence of the too few census visits to the plot during the first three years.

The four most abundant species, according to their average numbers during the 40 years, were also the most common ones during each of the 10-year

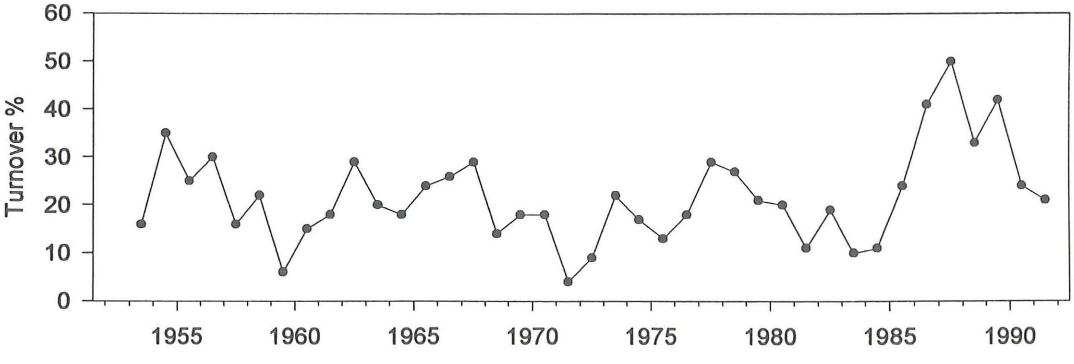

Fig. 8. The species turnover rate (%) between successive years in Birdsong Valley.

Artomsättningen i Fågelsångsdalen mellan på varandra följande år i Fågelsångsdalen uttryckt i procent av medelartantalet för de två jämförda åren.

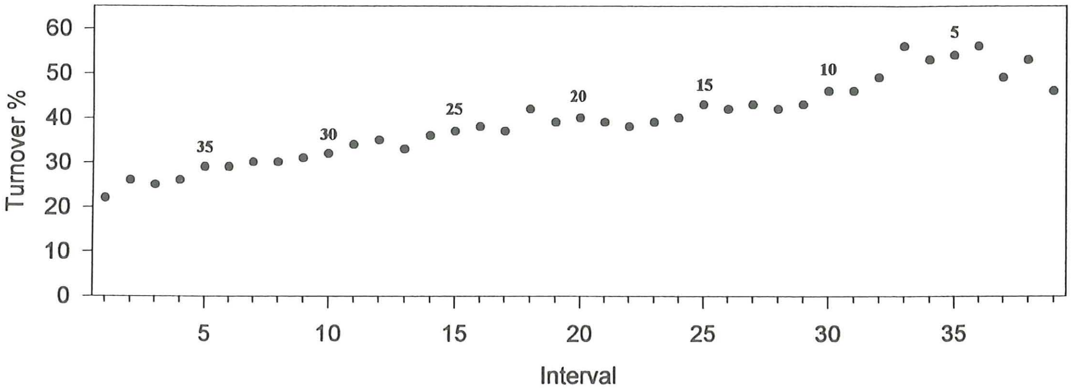

Fig. 9. The relation between the mean species turnover rate (%) and the interval (number of years) between the compared seasons. The figures above every five dots indicate sample size. The linear regression of the turnover percentage upon interval length is $y=24.2+0.75x$, $r=0.96$, $df=37$, $p<<0.001$.

Diagram som visar hur artomsättningen som medelvärde sakta stiger när intervallet mellan de jämförda åren ökar. Siffrorna ovanför vissa punkter anger det antal intervall som ligger till grund för beräkningen av medelvärdet. För det sista intervallet, 39 år, finns självfallet bara ett värde i den 40-åriga serien.

periods (Table 4). Only their abundance ranks have changed.

Taken together, the community parameters presented in Table 4 give the impression that the bird community of Birdsong Valley has remained rather stable throughout the 40-year period. Moreover, each of the successive 10-year periods tells largely the same story, which means that they have been long-term enough to give a "true" characterization of the structure and dynamics of the community. This is a consequence of the fact that the "ups and downs" of the bird numbers have been rather evenly distributed over the 40-year period as has the traffic of the "in-and-out" species (Fig. 8, Table 4). In spite of this, it is premature to conclude that the general structure of the bird community has totally escaped any radical change, as will be demonstrated in the following section.

Comparing the species fluctuations

The variance ratio test

Järvinen's (1979) variance test has been applied by calculating the variance ratio V to get an approximate idea of how the species fluctuations of the community are interconnected. (V=the ratio of the sum of the variances of the species densities and the variance of the sum of the species densities.) A V-value exceeding unity indicates that the species tend to covary negatively (compensatory fluctuations) whereas V less than unity suggests that the positive covariations predominate (parallel fluctuations). The results of this kind of test are not easily interpreted, as has been demonstrated by James & Boecklen (1984) and Schluter (1984), who also suggested more elaborate calculations in order to avoid misinterpretation.

The V-value of the 36 years (after discounting the four nest-box years) is 0.73, which should indicate a slight preponderance of parallel fluctuations in the community. Restricting the calculation to only the 19 regularly occurring species does not affect the ratio (V=0.74). The V-value does not deviate enough from unity to exclude the possibility that the species populations in general fluctuate independently. The established correlation matrix including the 19 regularly occurring species (171 species pair comparisons) reveals that only 62 pairs (36%) covary significantly, 28 of which show opposing (compensating) and 34 parallel fluctuations (Table 5). Obviously, the two types of covarying pairs of species tend to counterbalance one another, but no conclusion can be made as to the effect of this on the numerical value of V.

The variance ratios of the four ten-year periods differ a great deal (Table 4), although their numerical values are all less than unity, two of them considerably less. The V-tests thus indicate that parallel fluctuations prevail over opposing (compensating) ones. As far as the V-test can be considered trustworthy, there is apparently niche space enough in the valley to allow the population sizes to vary independently and for groups of species to react in a common way to environmental factors. In other

Table 5. Trends of species to fluctuate in parallel (+) or to opposing directions (–) from year to year. Bold symbols denote statistically significant trends ($p<0.05$). The species are listed in accordance with their grouping in the dendrogram of Fig. 10, with the species groups A and B separated.

Arternas tendens till samvariation (+) eller motsatt variation (–) från år till år. Feta symboler betyder statistiskt säker tendens (p<0.05). Arterna är uppradade på samma sätt som i gaffeldiagrammet i Fig. 10 med artgrupperna A och B åtskilda.

	A											B							
	Tm	Sv	Tt	PA	Pc	Er	PR	Fc	Ap	Hi	Sa	Fh	Cc	Ll	Sb	Pp	Sc	Pt	At
Turdus merula	:	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sturnus vulgaris	+	:	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
T. troglodytes	+	+	:	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Parus major	+	+	+	:	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Parus caeruleus	+	+	+	+	:	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erithacus rubecula	+	–	+	+	+	:	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunella modularis	+	+	+	+	+	+	:	.	.	.	.	.	.	.	.	.	.	.	.
Fringilla coelebs	+	+	+	+	+	–	+	:	.	.	.	.	.	.	.	.	.	.	.
Acrocephalus palustris	+	+	–	+	+	–	+	+	:	.	.	.	.	.	.	.	.	.	.
Hippolais icterina	+	+	–	–	–	–	+	+	+	:	.	.	.	.	.	.	.	.	.
Sylvia atricapilla	–	–	+	–	+	+	+	+	+	+	:	.	.	.	.	.	.	.	.
Ficedula hypoleuca	–	–	–	+	–	+	+	–	–	–	–	:	.	.	.	.	.	.	.
Carduelis cannabina	+	–	–	–	–	+	+	–	–	+	–	+	:	.	.	.	.	.	.
Luscinia luscinia	–	–	–	–	–	+	–	–	–	+	–	+	+	:	.	.	.	.	.
Sylvia borin	+	+	–	–	–	–	–	+	+	+	–	+	–	+	:	.	.	.	.
Parus palustris	+	–	–	–	–	–	–	–	–	–	–	+	+	+	+	:	.	.	.
Sylvia communis	–	–	–	–	–	+	–	–	–	+	–	+	+	+	+	+	:	.	.
Phylloscopus trochilus	–	–	–	–	–	+	–	–	–	–	–	–	+	+	+	+	+	:	.
Anthus trivialis	–	–	–	–	–	+	–	–	–	–	–	+	+	+	+	+	+	+	:

words, interspecific competitive interactions should not in general play an important role in the valley. There are, however, fluctuation patterns which indicate that such interactions should not be disregarded, as will be shown later.

Järvinen (1979) calculated the variance ratio of this community using Enemar's (1966) census results from 1953 to 1962 and found V=2.81, a surprisingly high value compared to those presented above. This discrepancy could be a consequence of the altered census results following the reevaluation of the species maps (see Methods). This has been checked by comparing the V-values of the old and new figures of the seven seasons of 1956–1962 (1953–1955 had too few census visits). In fact, the variance ratio decreases from 1.79 before to 0.68 after the reevaluation. This effect of the change from 5 to 3-clusters is surprising and deserves further investigation.

The cluster analysis

The degree of resemblance of the fluctuation patterns between the species populations has been the subject of a cluster analysis, according to the model developed by Cody (1974), to indicate the niche overlap among the species of a community. The correlation coefficients (r) have been calculated for all pairwise combinations of the 19 almost regularly occurring species and accepted as a measure of the degree of covariation. The character of the correlations (positive or negative), together with indicated signficance level, is shown in Table 5. The cluster analysis involves a successive pooling of species populations, which means the introduction of a problem especially in cases when a sparse species is added to an abundant one. The reason is that the fluctuation pattern of the new, pooled population is not equally affected by the original populations, which it should be. To compensate for this bias and following Enemar et al. (1984), the population numbers of all original species as well as the pooled "species" have been transformed into proportional values (P), according to the formula P=(X–Xmin)/(Xmax–Xmin), where X is the population size of a certain year, and the Xmax and Xmin are the peak and bottom values, respectively, of the investigated period. The P-values thus fluctuate from zero to unity for all populations. The resulting groupings of the species according to their "fluctuation relationships" are shown in the dendrogram in Fig. 10.

The dendrogram results in two groups of species, A and B, which covary negatively and significantly (r=–0.519). Group A is rather heterogeneous and consists of two unconnected species, *Hippolais icterina* and *Sylvia atricapilla,* one "dense" cluster of five species, and two species pairs. These three groups show insignificant covariation. Cluster B is more condensed compared to A and consists of one cluster and one species pair.

The dendrogram in Fig. 10 reveals two interesting facts. The first one is that all species which have increased significantly in number during the 40-year period (Table 3) are found in species group A of the dendrogram, whereas the decreasing ones are gathered in group B. The species which show only insignificant trends are divided between the groups in the same way, the only exception being *Erithacus rubecula*, which has landed in group A in spite of its weak and insignificantly decreasing trend. The second fact is that the majority of the species of group A are residents or short-distance (European) migrants with winter quarters in western or southern Europe, whereas most species of group B are long-distance migrants destined for tropical Africa. These two facts taken together suggest that factors operating outside the breeding season, such as the survival rates in the winter quarters and along the migration routes, are of dominating importance for the number of birds gathering to breed in the valley.

Three species, *Acrocephalus palustris*, *Carduelis cannabina*, and *Parus palustris*, are significant exceptions from the established relation between the wintering and migration ecology on the one hand, and the fluctuation pattern on the other. They disturb the interpretation above, unless the reasons for their allocation to "wrong" species groups could be found. Such reasons are in our opinion possible to trace. *A.palustris* is definitely a tropical migrant. In contrast to its fellow long-distance migrants, it has undergone a significant population increase in the valley. This is apparently a consequence of its well-known large-scale increase that cannot have anything to do with the winter conditions in Europe. The numerical value of the rising slope is next to that of *Fringilla coelebs*, to which *A.palustris* thus happened to be connected in the dendrogram. The short-distance migrant *C.cannabina* decreased significantly and landed among the declining tropical migrants in species group B, obviously without sharing the factors that may have depressed the population numbers of group B during the non-breeding season. As suggested above, the reduction of the population size is a reflection of a general decrease possibly caused by a persistent change in the structure of the farmland. The third "misplaced" species is *P.palustris*, a declining resident which could hardly have anything in common with the tropical migrants as concerns the cause of the decrease. In contrast, its two congeners have increased significantly in population size (Table 3) and may gradually have more or less ousted the *P.palustris* from the valley. It is known that this species is inferior to *P.caeruleus* in the competition for the nesting-holes, which are too narrow for *P.major*. Accordingly, the two small *Parus*-species show opposing fluctuations (r=–0.34, p<0.05). After all, the conclusion is that the three "misplaced" species do not provide justification for refraining from interpreting the dendrogram a step further.

Needless to say, the population fluctuation patterns in the valley are influenced by a large number of factors operating within as well as outside the breeding season. Some of them may be of little importance (e.g. random events, census errors) while others have a penetrating power. Unfortunately, the former may provide a "noise" that disturbs the analyser when trying to identify the latter. As mentioned above, the access to a very long-term series of observations of a constant quality may cause the principal factors to be revealed even in a noisy context. The construction of the dendrogram, as presented above, may be an example of this.

According to Fretwell (1972), many studies support the proposition that the non-breeding season is of primary importance in the regulation of bird numbers. It is known since long that the weather situation during winter time in Sweden and western Europe affects the population sizes of the resident species and the short-distance migrants. It is not surprising, therefore, to find that the five species at the top of the dendrogram are closely connected and that the two species next in line, *Erithacus rubecula* and *Prunella modularis,* covary nicely. It is reasonable to think that the tropical migrants are also affected by common factors in the non-breeding season, although possibly in a less homogeneous manner, due to the spread caused by the widely extended wintering areas and the protracted migration routes. The proposed interpretation of the dendrogram also conforms with the views presented by

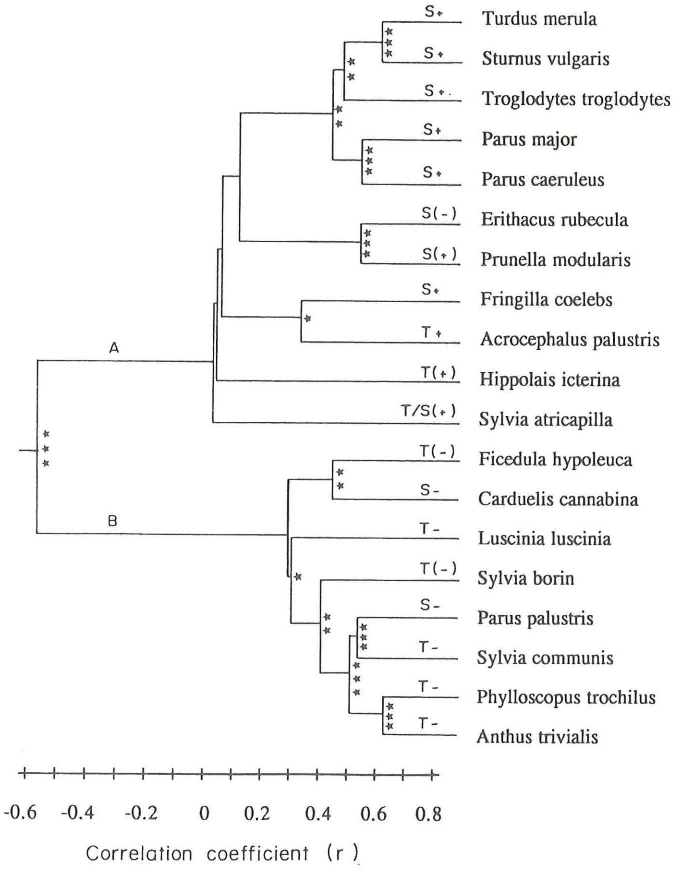

Fig. 10. Dendrogram showing the grouping av the 19 most abundant species according to the degree av similarity, expressed as the correlation coefficients (r), of their density fluctuations in Birdsong Valley 1953–1992. The derivation of the dendrogram (see text) unveils two "fluctuation groups", A and B, which covary negatively. S=residents and short-distance (European) migrants, T=tropical (African) migrants. These letters are followed by plus or minus signs to denote increasing and decreasing trends, respectively, in population size. The signs are within brackets when statistically insignificant (cf. Table 3). Level of significance of covariation is denoted by asteriscs (*, **, ***=p<0.05, 0.01, 0.001).

*Gaffeldiagram som visar hur de 19 talrikaste arterna i Fågelsångsdalen kan paras ihop med utgångspunkt från hur lika de har fluktuerat i antal (samvarierat) genom åren. Då samvariationen är statistiskt säker är detta markerat med stjärntecken, *, ju fler desto säkrare. Det hela resulterar i två grupper, A och B, som visar klar tendens att variera på ett motsatt sätt. S=stannfåglar och kortdistansflyttare (vinterkvarter i Europa), T=långdistansflyttare (vinterkvarter i tropiska Afrika). Dessa bokstäver åtföljs av plus- eller minustecken, vilket anger ökning resp. minskning i populationsutvecklingen. Tecknen har satts inom parentes, då trenden är statistiskt osäker.*

Alerstam & Högstedt (1982). They maintain that small land birds occurring at northerly latitudes, where Birdsong Valley is located, are mainly limited by the non-breeding niche space.

It is of course possible that factors operating during the breeding season have also been of some importance. As suggested above, a successive habitat alteration may have caused part of the successive change in the composition of the community, although it is hard to see how the habitat structure has in general improved for the resident and short-distance migratory species, while at the same time deteriorating for the tropical migrants. Competitive interactions may have been involved, as suggested for the *Parus*-species above. Such processes are not easily established through observations of pair numbers only, i.a. by recording opposing fluctuation patterns. According to the V-test, such patterns – although frequently occurring – do not dominate in the community. When examining the matrix (Table 5), it becomes clear that the opposing fluctuations predominate in the lower left square, where the species of group A (mainly residents and short-distance migrants) are compared with those of group B (mainly tropical migrants). Accordingly, the whole of species groups A and B show opposing and highly significant covariation (r=–0.52, p<0.001, Fig.10), indicating possible competitive interactions between the groups (cf. Järvinen 1980, Alerstam 1985). This fact provides some cues which will be dealt with further under the next heading.

In their 20-year study of the dynamics of the Swedish mountain birch forests, Enemar et al. (1984) found a corresponding grouping of the species in accordance with their wintering areas, although these species groups did not covary negatively. Other cluster analyses have revealed no or only few synchronic fluctuations related to common wintering areas (Holmes et al. 1986 (mapping 10 ha), Solonen 1986 (mapping 30 ha), Järvinen & Rajasärkkä 1992 (line transects), Hogstad 1993 (mapping 100 ha)). One reason for this lack of synchronic fluctuations may be that the investigated periods have not been long enough (16, 10, 8, and 12 years, respectively) to compensate for the background noise of stochastic and other origin. In contrast, Tomialojc & Wesolowski (1990) report, based on their ten years of extensive mapping censuses in the primaeval temperate forest of Bialowieza in Poland, a "significant negative correlation between changes in abundance of the whole group of tropical migrants and that of the residents", although such correlations were "extremely rare" in their data when the separate species were compared pairwise. They considered the reasons for the opposing fluctuations between the migrants and the residents as unclear. Finally, Morozov (1993) found that species with similar migratory habits tended to fluctuate in parallel in a south-taiga bird assemblage, although his conclusion was based mainly on variance ratio tests.

On the other hand, communities may of course differ as to the dependence of their species populations on the varying conditions in the winter quarters (cf. Hogstad 1993). Svensson (1985) and Holmes & Sherry (1988) stress that we know so little about the habitat events and the ecology of the migrants in the tropical/neotropical quarters that observed correlations concerning i.a. *long-term* population trends must be interpreted with great care. We agree, although we still believe that the changing conditions during the long wintering and migration periods could not be disregarded as important factors influencing the *short-term* population fluctuations in the breeding area.

Why have the residents and short-distance migrants been the winners?

As shown by the dendrogram in Fig. 10, most of group A consists of S-species (residents and short-distance (European) migrants) and most of group B of T-species (tropical migrants). In the following analysis, all S-species and all T-species are kept together, i.e. also those species are included that for specific reasons departed from their "migratory relatives" and landed in the "wrong" group in the dendrogram. These new S-species and T-species groups are negatively and significantly correlated (Fig. 11), a relation that might indicate that these changes are interdependent. How is it then, that the T-species tend to decrease in number when the S-species increase, and vice versa?

Herrera (1978) found that the proportion of tropical migrants in the passerine bird communities in Europe shows an increasing gradient from south to north. He concluded that the number of tropical migrants settling in the breeding area is dependent on the amount of available resources not used by the resident birds. Accordingly, the winter survival of the resident birds was the main factor determining the number of tropical migrants entering the breeding area. O'Connor (1981) found good support for Herrera's model when analysing the population fluctuations recorded by the Common Bird Census Scheme for farmlands in England. Similar views have been put forward also by Berthold (1990).

There are reasons to consider Herrera's interpretations when analysing what has happened in Birdsong Valley. We differ from Herrera in that we use the whole S-species group as "residents". The reason for this is, first, that there is no sharp distinction between the residents and the short-distance migrants, and second, that most short-distance migrants like the residents settle to breed in the valley before the tropical migrants arrive. Thus, the more of established territories of the S-species in the valley, the fewer T-species will be able to settle there, and vice versa, giving rise to the opposing correlation shown in Fig. 11. This model obviously involves an element of interspecific interaction.

The analyses of Herrera (1978), O'Connor (1981), and Berthold (1990) were based on community structure and dynamics recorded at the regional scale. It is easily suspected that the mentioned interplay between the species groups could hardly be possible to record within the community of such a small study plot as ours. However, the following facts may helped. First, the very limited spatial scale has been replaced by an extended time scale. Second, the community density has not changed significantly over the 40 years, which indicates that the (not necessarily saturated) carrying capacity of the valley has remained around a constant level. Third, the habitat ends where the fields start along the boundaries of the long and narrow plot. As a consequence, the established territories of most S-species cannot generally be expanded beyond the boundaries to compensate for possible losses to the arriving T-species. Most adjustments have to take place within the plot, with increased resistance to intruders as a consequence. Some support for this interpretation is provided by Reed (1982), who demonstrated increased interspecific territoriality on an island compared to that on the adjacent mainland.

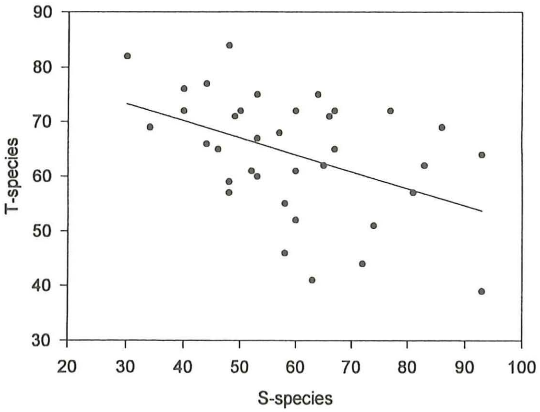

Fig. 11. The correlation between number of mapped tropical migrants (T-species) and residents and short-distance migrants (S-species) during the breeding season in Birdsong Valley. The negative correlation is significant ($y=82.7-0.31x$, $r=-0.45$, $df=34$, $p<0.01$).

Diagram som visar sambandet mellan antalet karterade revir av tropikflyttare (T-species) å ena sidan och av stannfåglar och kortflyttare (S-species) å den andra. Linjen visar hur i genomsnitt antalet tropikflyttare minskar i Fågelsångsdalen när den andra artgruppen ökar. Sambandet är statistiskt säkerställt.

The groups of S-species and T-species have shown diverging long-term trends (Fig. 12). The S-species have increased at the expense of the T-species from about 38% of the community in the early 1950s to about 57% 40 years later. Together with the "extinction" and immigration of some species, this is the most remarkable event that has happened in the valley.

The rising numbers of the S-species might have been caused mainly (1) by increasing recruitment to the plot due to a possible and successive habitat improvement and (2) by increasing non-breeding survival. It is well-known that the survival rate of many S-species is affected by the weather during the winter. This has been preliminarily investigated by plotting the yearly mean temperatures of the critical winter months (January, February, and March) in the neighbourhood of Birdsong Valley (the meteorological station at the town of Lund, (SMHI 1954–1993)) against the size of the S-species group the ensuing breeding season (Fig. 13). A significant and positive correlation was found. The milder the winter, the more of S-species territories in the valley. Moreover, according to the meteorological station of Lund the winter periods have become significantly milder from a mean temperature of about –1.5°C in the early 1950s to +1.5°C in recent years (Fig. 14). This trend is supposed to be representative for northwestern Europe (cf. Berthold 1990). Taken together, the information in Figs. 12, 13, and 14 indicates that the successively increasing size of the S-species group in the valley could be due to increased nonbreeding survival as a consequence of a successive amelioration of the winter climate. Other factors mentioned earlier could also be involved (intensified winter feeding in the region, increased reproductive output due to ongoing habitat change in the study area).

The declining trend of the T-species might have been caused by (1) increased mortality during migration and wintering, (2) decreased reproductive success due to a possible deterioration of the habitat, or (3) the increasing numbers of S-species already established in the valley when the T-species arrive (the "Herrera-effect"). We do not know anything about what has happened of importance in the present context in either Birdsong Valley or in the tropical winter quarters including along the migration routes. However, according to the recent account by Svensson (1993), none of the investigated tropical migrants have decreased in southern Sweden, as shown by point counts from 1975 through 1992. In contrast to what has happened in Birdsong Valley, some T-species have even increased, among them *Sylvia borin, Phylloscopus trochilus,* and *Ficedula hypoleuca*. This indicates that the down-trend of the T-species in our plot cannot simply be explained by a declining supply of returning birds in the spring. In our view, the "Herrera-effect" is responsible for most of the T-species' decrease.

The discrepancy between the results of the point counts (Svensson 1993) and our mapping may partly be explained by the fact that the mapping censuses only count the territorial males whereas the point counts also include the non-territorial or "floating" ones. The latter are expected to consist in part of T-species males which have been ousted from the high quality habitats (cf. also Wilcove 1988, Terborgh 1989). This has consequences for the methodology of regional monitoring programmes but they will not be treated further in this context.

It is temping to accept that interspecific exclusion contributes to shape the species composition of our bird community, as it allows a rather quick response of the one species group to the density change of the other. This means, however, that we must accept concepts as community saturation, carrying capacity and equilibrium, which all are, together with that of interspecific competition, controversial (cf. e.g. the reviews by Martin 1986, Wiens 1989a,b). The

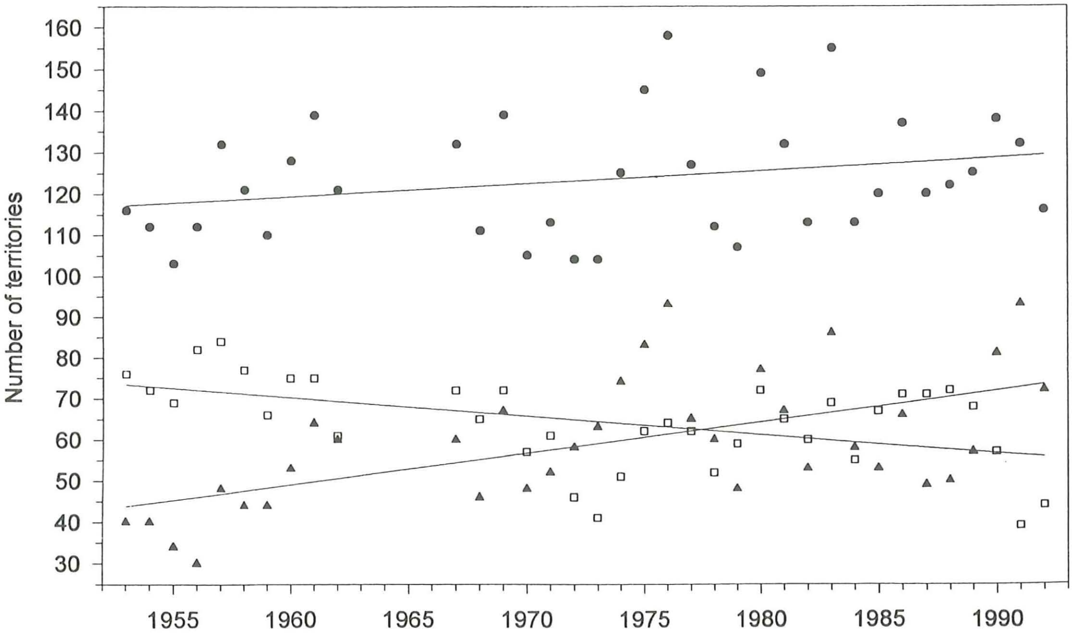

Fig. 12. Diagram showing the successive increase of the residents and the short-distance migrants (▲), and the simultaneous decrease of the tropical migrants (☐) in Birdsong Valley. The total community (●) remains at a relatively constant level. The figures of the four nest-box years are excluded. The equations of the regression lines are for ▲ $y=43.0+0.76x$, $r=0.58$, $df=34$, $p<<0.001$, for ☐ $y=73.9-0.45x$, $r=-0.50$, $df=34$, $p<0.01$, and for ● $y=116.9+0.31x$, $r=0.25$, $df=34$, $p<0.2$.

Diagram som visar hur stannfåglar och kortdistansflyttare (▲) ökat medan tropiska flyttare (☐) minskat under åren i Fågelsångsdalen. De genomsnittliga tendenserna är utmärkta med linjer och är statistiskt säkra. Hela fågelsamhället (●) har hållit sig ungefär på samma nivå, dvs den svagt stigande tendensen är icke statistiskt säker.

status of our community in these respects has not been established. The nest-box experiment mentioned above (Enemar et al. 1972) only indicated that the species populations in general fluctuate independently of each other in a probably unsaturated community. The variance ratio test described above does not contradict this view. Many census-takers have arrived at the same conclusion after mapping passerine bird communities (e.g. Rotenberry & Wiens 1980, Enemar et al. 1984, Svensson et al. 1984, James & Boecklen 1984, Alerstam 1985, Mountainspring & Scott 1985, Holmes et al. 1986, Hogstad 1993, Morozov 1993). On the other hand, many of the cited investigations have been short-term, perhaps too short-term, for the density changes caused by interspecific exclusion to be significantly conspicuous. This supposition is supported by the results from each separate 10-year period in Birdsong Valley, only the last of which shows a significant negative correlation between the groups of the T- and S-species ($r=-0.649$, $p<0.05$).

In contrast, the results of a large number of removal experiments indicate that the density in many communities may be at least near the limit set by the carrying capacity. The conclusions are based on the fact that new birds appear and settle in the vacated areas after the original territory-holders have been removed (cf. Edwards 1977, Mönkkönen 1990, with references). The design of the experiments and the interpretations are often directed to the intraspecific part of the competition problem, although interspecific exclusion has also been suggested or documented (e.g. Orians & Willson 1964, Hogstad 1975, Svensson 1978a, Garcia 1983).

The S- and T-species as competitors do not meet on equal terms. The T-species arrive in the valley when the S-species are already established and may even have started breeding. Although being first does not guarantee dominance in an interspecific conflict (e.g. Ulfstrand 1976, Svensson 1978a), the general experience is that a territory owner stands strong against an intruder. Therefore we think that an

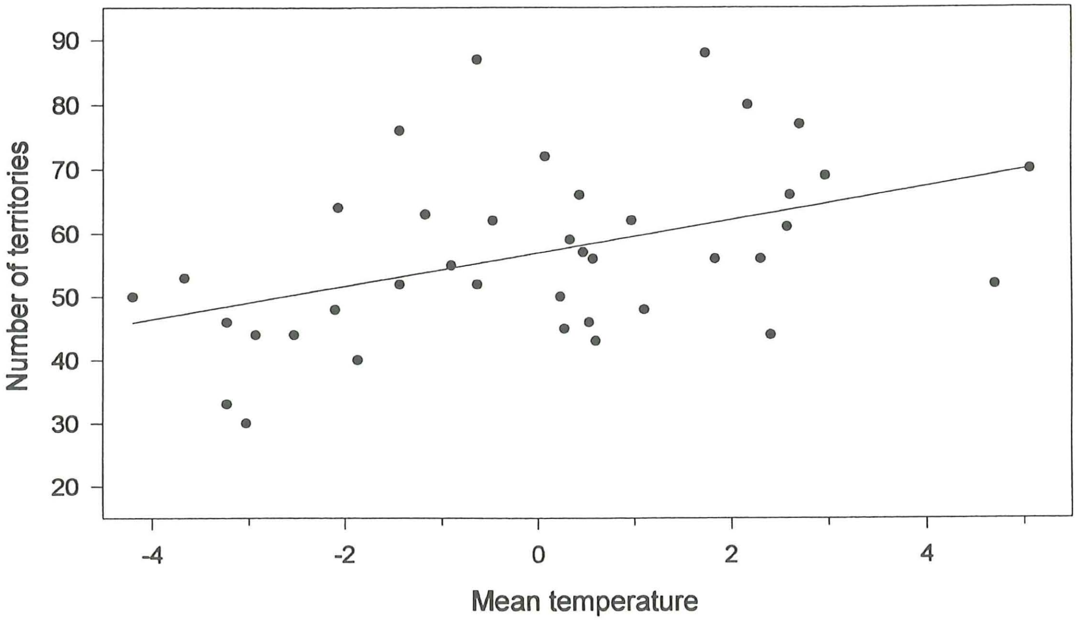

Fig. 13. The number of mapped residents and short-distance migrants (the S-species group) in the breeding season in Birdsong Valley as a function of the mean temperature of the preceding winter (Fig. 14). The correlation is significant (y=56.9+2.6x, r=0.44, df=37, p<0.01).

Diagram som visar sambandet mellan antalet karterade stannfåglar och kortdistansflyttare under häckningstiden i Fågelsångsdalen och medeltemperaturen under den föregående vinterperioden (Fig. 14). Linjen visar att ett statistiskt säkert positivt samband genomsnittligt föreligger: högre vintertemperatur följs av fler häckande par av artgruppen.

increasing number of territorial males of S-species in the valley prevents individuals of the T-species from settling there, all the more as the competitive interactions might have been intensified due to the shape and isolated status of the valley, as suggested above.

To sum up, the hypothesis best explaining the conversion of the species composition in Birdsong Valley is the one conforming with Herrera's (1976) model. The indicated successive amelioration of the winter climate together with a possible increase in winter food resources might have been followed by a concomitant increase in the winter survival rate of the residents and short-distance migrants. This scenario could have caused the documented successive rise in number of breeding pairs of this species group and presumably by competitive exclusion caused the likewise established successive decline in the number of breeding tropical migrants. The survival rate in the northern wintering quarters therefore seems to be one important, perhaps *the* most important, factor that has governed the long-term dynamics of the bird community of Birdsong Valley over the first 40 years of investigation.

Comparison with other long-term census investigations

The number of long-term study plot investigations based on territory mapping in wooded habitats is steadily increasing, and those covering about 20 years or more will be briefly mentioned here. A large number of them are "hidden" in large-scale bird census or monitoring programmes organized on a national basis, such as the Common Bird Census in Great Britain (Williamson & Homes 1964, O'Connor 1985) and the breeding-bird monitoring programme in Sweden (Svensson 1992). The published long-term studies of single plots mostly discuss the established changes of the bird numbers in relation to the often considerable habitat alterations in the plot. They may also discuss to what extent the plot reflects

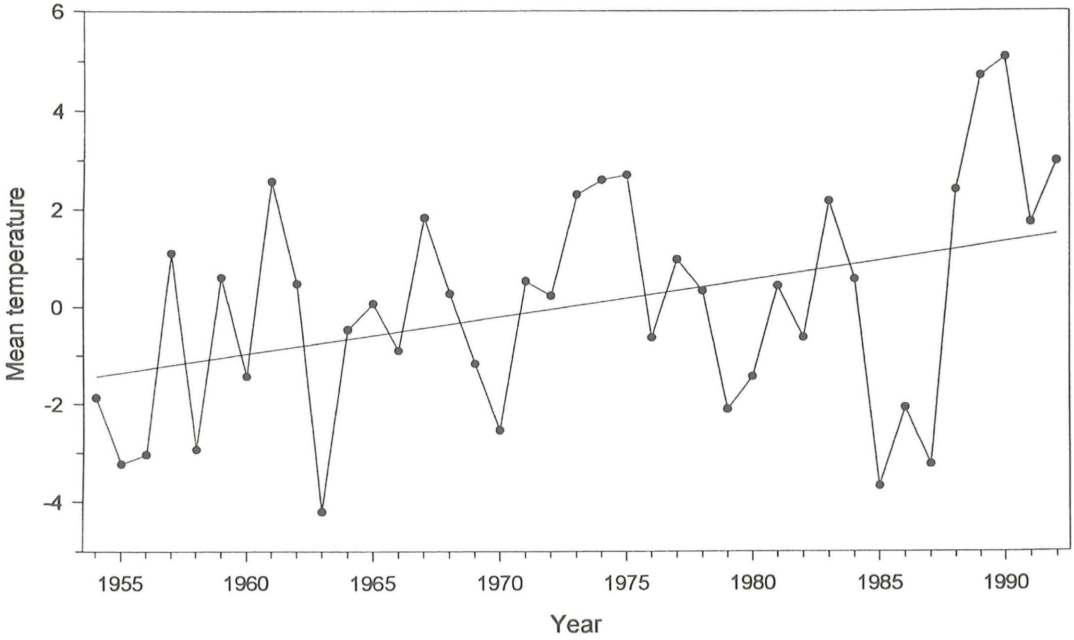

Fig. 14. The variation of the mean temperature of the winter periods, January through March, in the vicinity of Birdsong Valley 1954–1992. The increasing linear regression of the mean temperature upon time is significant (y=–1.51+0.08x, r=0.38, df=37, p<0.02).

Variationen i dygnsmedeltemperaturen för vinterperioderna, jan.–mars, i närheten av Fågelsångsdalen (den meteorologiska stationen i Lund) 1954–1992. Linjen markerar den genomsnittliga temperaturökningen under perioden, omfattande ca 3° från periodens början till dess slut, en statistiskt säker förändring.

the fluctuations taking place on a regional scale, less so the regulating mechanisms within the community, such as interactions between species populations. The latter problems have been considered to a greater extent in census studies of shorter duration. They have been referred to in various contexts above.

Kendeigh (1982) still has the "long-term lead" with the presentation of a 24 ha study plot in Illinois, censused over 50 years from 1927 through 1976. Like our study area, his plot is an island in a large area of farmland. A 23 ha plot in Connecticut (Askins & Philbrick 1987, Askins 1990) was investigated for 32 years. The fluctuation patterns of each of the long-distance migrants, short-distance migrants, and permanent residents were presented. There was no tendency to opposing trends between these categories as in the community of Birdsong Valley. A 6 ha plot in West Virginia was censused over a 36-year period, including 22 consecutive years (Hall 1984). The first 20 years of census results of the 10 ha plot in New Hampshire referred to above have shown that the species populations fluctuate largely independently of one another and that food was mostly limited except during the seldom occurring caterpillar irruptions (Holmes 1990).

Beven (1976) describes the breeding community of a British dense oak-wood plot of 16 ha over 27 years. Interestingly, he noted a decline in *Phylloscopus trochilus*, which he ascribed to the gradual habitat change involving increased maturity of the trees. This may have resulted in more nest holes, explaining the increase in number of nesting *Parus* species and *Sturnus vulgaris*. Other British oak-wood censuses are those of Price (1961, 40 ha, 34 years), which were restricted to the warblers only, and of Yapp (1969, 87 ha, 18 years), who used a transect census instead of territory mapping. In the Netherlands, Jansen & de Nie (1986) investigated a 50 ha mixed woodland plot by territory mapping over 30 years.

It is obvious that the earlier mentioned long-term census projects differ as to the precision in the census work and to the quality and constancy of the investigated habitats, facts that hamper fruitful comparisons. Some common experiences as well as opposing results seem nevertheless interesting. In the near future we can surely expect more of such information from the large number of long-term projects, which since long are going on all over the world.

Comparison with a similar study plot in the neighbourhood

Enemar (1966), referring mainly to the productive habitat of Birdsong Valley and the low coefficients of variation of its community, supposed that the study area was maximally populated or nearly so throughout the investigated 10-year period. He concluded that the area must be considered to be rather ineffective in showing the population fluctuations occurring in the wooded terrain of the surrounding landscape, at least as concerns the abundant species. A comparison between the fluctuation patterns in Birdsong Valley and a similar study area not very far away could be informative in this context. Moreover, Holmes et al. (1986) stress that replicate plots within the region are always necessary to distinguish regional from local causal factors. In fact, there is such an area, Borgen, near the town of Landskrona, located about 30 km to the northwest of Birdsong Valley. Its bird fauna was censused by Alerstam (1985) during the 11-year period between 1969 and 1979.

The Borgen area is of about the same size (12 ha) and structure as the Birdsong Valley. The census method was identical with that applied in our study. No habitat change of importance has taken place during the investigated period. A large number of nest-boxes were erected in 1973 and 1974. The community parameters were as follows (those of Birdsong Valley of the same period within brackets): community size (nest-box years discounted) 187 (123), density 15.6 pairs/ha (9.5), observed coefficient of variation 15% (16%), the same parameter corrected to common community size 20% (18%), the corrected CV of the 13 most common species (hole-nesters excluded) 24% (29%), average number of species 25 (22), its coefficient of variation 7.5% (8.1%), and the annual species turnover 10% (9%). The bird community of Borgen is thus 40% denser than that of Birdsong Valley and significantly richer (about three more stationary species). The presented community parameters indicate that the two study areas are of about the same stability.

The yearly sizes of the breeding bird communities covaried positively ($r=0.77$, $df=7$, $p<0.02$, nest-box years excluded) and so did the population numbers of the two most abundant species, *Fringilla coelebs* ($r=0.71$, $p<0.02$) and *Phylloscopus trochilus* ($r=0.77$, $p<0.01$). Reasonably, this coincidence between the two plots reflects a common response to the fluctuating supply of birds from outside, an interpretation which is contrary to the supposition above (Enemar 1966). An alternative, although less likely, explanation is that the carrying capacities of the two areas have changed between years in parallel and have been filled yearly to the brim with birds irrespective of the population variations in the region. Of the remaining 15 species (hole-nesters excluded), only *Troglodytes troglodytes* and *Sturnus vulgaris* covaried significantly. The large proportion of failing covariation probably depends on two factors; first that many species, especially in Birdsong Valley, are represented by only few pairs and therefore affected by random events, and second, that the period of comparison is relatively short. Of all species, only four show a weak tendency towards opposing fluctuations. The results of this comparison indicate that the wooded and productive "islands" of the kind represented by Birdsong Valley and Borgen are not normally saturated with birds to the extent that they become insensitive to the fluctuations of the bird community and its abundant species in the surrounding landscape.

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Sammanfattning

Småfågelfaunans sammansättning och beståndsväxlingar i ett litet lövskogsområde i södra Sverige. En 40-årsstudie.

Sveriges ornitologiska förening startade 1951 ett projekt i avsikt att bestämma det häckande fågelbeståndets täthet och förändringar genom upprepade inventeringar av ett antal provytor på olika håll i Sverige (Engström 1953). Skånes ornitologiska förening organiserade projektet i det egna landskapet, där en av provytorna blev Fågelsångsdalen med en av författarna (A.E.) som ansvarig. Det riksomfattande projektet avbröts snart, främst beroende på att goda riktlinjer för hur en provyta bör inventeras saknades. Fågelräknandet i Fågelsångsdalen fortsatte dock och kombinerades med särskilda studier i syfte att utröna, hur man med revirkartering kan erhålla användbara resultat (Enemar 1959). Revirkarteringen har sedan dess genomförts årligen utan avbrott, och de första 10 årens resultat har tidigare redovisats (Enemar 1966). Härmed presenteras resultatet av de första 40 årens arbete tillsammans med vissa analyser, som belyser möjliga orsaker till de registrerade händelseförloppen.

Provytan

Vår provyta är Fågelsångsdalen, belägen 8 km öster om Lund. Dalen är trång, löper i öst-västlig riktning med en ringlade bäck i botten. Den omges helt av åkermark. I de ställvis branta kanterna syns att berggrunden utgörs av kalksten, och dalen är därför näringsrik med en yppig växtlighet. Den inventerade ytan omfattar 13 ha, som omväxlande består av träd- och buskbevuxna delar och betade hagmarker (Fig. 1). Dalen avsattes som naturreservat 1963 och har därmed kunnat förbli i stort sett oförändrad genom åren. Den har fotograferats vid upprepade tillfällen från fasta punkter (Fig. 2). Fotografierna tillsammans med den schematiska presentationen av fördelningen av olika arter träd och buskar i Fig. 1 visar i stort dalens egenskaper som småfågelmiljö.

En förutsättning för det långsiktiga inventeringsarbetet har varit att inga stora ingrepp gjorts i miljön. Två små bestånd av gran togs bort 1974 och längs vissa kanter har buskagen avlägsnats och växt upp igen åtskilliga gånger. Några gläntor har växt igen men nya har öppnats, då större träd har fallit och tagits bort. Betning av hagmarkerna har fortgått med undantag för några år på 1980-talet. Ett 20-tal fågelholkar sattes upp i dalens båda ändar på 1950-talet av en intressent, som ej tillhörde inventeringsprojektet. Holkarna underhölls ej och blev så småningom obrukbara. Inom projektet hängdes 60 småfågelholkar upp över hela dalen för särskilda studier 1963–1966 (Enemar et al. 1972). Detta är anledningen till att dessa fyra år i det följande ibland räknas bort.

Fågelsångsdalen ligger som en långsträckt, frodigt bevuxen och attraktiv ö i ett omgivande "hav" av uppodlad slätt. Detta förhållande är förmodligen av betydelse för vad som händer och sker i dess fågelbestånd, något som kommer att skärskådas i det följande.

Inventeringsmetoden

Revirkarteringen har utförts enligt internationell standard (Anonymus 1970). Detta gäller såväl fältarbetet som sättet att tolka artkartorna. Under de första decennierna bearbetades dessa dock enligt de riktlinjer, som rekommenderats av Enemar (1959). Inför denna redogörelse har emellertid samtliga artkartor från denna tid omtolkats enligt de internationella reglerna. Därmed har storleken av vissa artbestånd ändrats jämfört med tidigare publicerade siffror (Enemar 1966). Den strikta tillämpningen av samma metod genom fyra decennier, tillsammans med det faktum att fältarbetet genomförts nästan uteslutande av endast fem erfarna fältornitologer (Tabell 1), betyder att det insamlade siffermaterialet är så homogent och av en sådan kvalitet i övrigt, att man kan förvänta sig, att i varje fall långsiktiga trender i fågelbeståndets utveckling skall ha blivit registrerade på ett tillförlitligt sätt.

Inventeringsresultaten

Antalet karterade revir för de små tättingarterna redovisas i Tabell 2. Av större arter har endast kråka, skata och ringduva varit regelbundna, medan större hackspett, mindre hackspett, kattuggla, tornfalk, gräsand och gråhäger häckat endast tillfälligt. Av de 39 småfågelarterna har endast 19 varit stationära i dalen i mer än 20 år. De är förtecknade i Tabell 3 och utgör i genomsnitt 95% av fågelbeståndet. Detta har varierat mellan 103 och 158 revir (holkåren frånräknade). Medelbeståndet för perioden omfattar 124 karterade revir.

De 19 arternas beståndsändringar genom åren visas i Fig. 3, dels i form av kurvor, baserade på glidande medelvärden över tre år, dels som linjer, vilka visar den genomsnittliga riktningen på beståndsändringarna.

Artbeståndens fluktuationer

Som framgår av Tabell 2 och diagrammen i Fig. 3 varierar de olika arterna betydligt i antal genom åren. Dock fluktuerar endast fem av arterna (gärdsmyg, rödhake, kärrsångare, stare och hämpling) mer än vad som kan förklaras av slumpen. Alla dessa har saknats i dalen ett varierande antal år. De talrikare arterna visar större antalsändringar genom åren än de fåtaligare (Fig. 4). Sätts dessa ändringar i relation till beståndsstorleken blir resultatet det motsatta (Fig. 5). Eftersom antalsvariationen genom åren för en enskild art delvis är en direkt följd av dess beståndsstorlek, är det nödvändigt att räkna om värdet på variationen till att gälla samma beståndsstorlek, när man vill jämföra olika arter. Resultatet av en sådan omräkning visas i Fig. 6. I stort gäller att variationen mellan åren minskar med ökande beståndsstorlek. Notera dock att variationen för de 19 talrikaste arterna (representerade av de runda prickarna) tycks vara stabil, dvs oberoende av beståndsstorleken.

För fågelfaunan på var och en av två öar utanför England har sambandet beräknats mellan det antal år, då en art funnits på ön, och dess relativa beståndsvariation. Detta samband visade sig följa en S-formad kurva, och samma blev förhållandet för "ön" Fågelsångsdalen, såsom visas i Fig. 7.

De långsiktiga trenderna i artbeståndens utveckling

Trenderna i artbeståndens utveckling illustreras i Fig. 3 och graden av deras statistiska säkerhet finns angiven i Tabell 3 (b- och p-värdena). Beståndsändringarna skall något kommenteras här och jämföras framförallt med resultaten av Sören Svenssons (1992, 1993) inventeringsprogram, vilket genomförts i södra Sverige under de senaste två decennierna. Bofink, talgoxe och blåmes visar säkra ökningar, vilket stämmer med utvecklingen i södra Sverige. Även koltrasten ökar, låt vara att den har i stort sett stått still under de senaste 15 åren. Gärdsmygen tillhör dem som ökat i antal, även om den uppvisar ett mycket oroligt variationsmönster. Detta är säkerligen en följd av artens känslighet för vädersituationen vintertid. Den kraftiga uppgången under de senaste åren står i samklang med flera milda vintrar i följd (se Fig. 14). Klimatfaktorer kan också vara en av förklaringarna till att trädkryparen i senare tid börjar att dyka upp oftare (ej mindre än 4 par 1993). Till vinnarna hör även staren, som dock ej börjar häcka stadigt i dalen förrän 1967. Den ökar sedan rejält under en period med negativ trend i Skandinavien. Arten ansluter sig dock till denna trend genom att gå kraftigt tillbaka under det senaste decenniet.

Bland långflyttarna visar kärrsångaren en säker ökning, vilken förmodligen speglar den kraftiga uppgång, som arten sedan länge visat i södra och mellersta Sverige. Annars är trenderna oftast negativa för långflyttarna, såsom lövsångaren, törnsångaren och trädgårdssångaren. I dessa fall står nedgångarna i motsats till resultaten från punkttaxeringarna i regionen (Svensson 1993). Ett undantag är svarthättan, som kraftigt stärkt sin ställning under senaste decennium. Till de säkra förlorarna i Fågelsångsdalen hör även långflyttarna näktergal och trädpiplärka, dock att denna tendens ej kan skönjas i Svenssons material. Samstämmighet råder dock för kortflyttaren hämplingen, en art som försvunnit från dalen och minskat även regionalt, och stannfågeln entitan, som halverat sitt lilla bestånd sedan 1950-talet.

Härmsångaren, svartvita flugsnapparen, rödhaken och järnsparven visar inga genomgående trender, vilket inte utesluter att de kraftigt varierar i antal, såsom klart framgår av diagrammen (Fig. 3).

Av de oregelbundet förekommande arterna, vilka uteslutits ur Tabell 3, har några tillkommit under perioden och är kanske på väg att bli årliga. Det gäller sädesärla, nötväcka och grönfink, av vilka de två sistnämnda tillhör de arter, som också ökat regionalt (Svensson 1993). Pilfinken var årlig i dalen under ett decennium från slutet av 1960-talet, vilket berodde på några holkar, som ej tillhörde oss. En liten koloni björktrastar finns i dalen sedan 1988, kanske en följd av konstaterad regional ökning. En art är borta sedan 1959, nämligen ortolansparven, vars bestånd ju sedan länge gått starkt tillbaka i landet.

Orsakssammanhangen bakom konstaterade beståndsändringar är som regel svåra att identifiera. Ibland kan dock hög sannolikhet nås, som då stränga vintrar i Nordeuropa följs av kraftiga nedgångar i bestånden av t.ex. järnsparv, rödhake och gärdsmyg. I sådana fall gäller det alltså faktorer, som verkar utanför Fågelsångsdalen. Som regel är dock artbestånden för små för att sådana analyser skall bli framgångsrika, eftersom risken då är stor att ren slump ligger bakom registrerade beståndsändringar. I det följande riktas därför uppmärksamheten vid analysen av processerna i fågelsamhället främst mot långsiktiga trender för grupper av arter.

En efterhängsen fråga i detta sammanhang är i vilken grad biotopändringar skett i Fågelsångsdalen under åren. Detta vet vi just inget om, men som framgår av Fig. 2 och beskrivningen ovan, har inga dramatiska förändringar ägt rum. Kanske har trädens medelålder och därmed höjd och grovlek ökat. Detta kan i så fall ha bidragit till ökningen av bofinken, den fullvuxna skogens invånare. Kanske har den stigande åldern hos träden medfört en ökning av antalet bohål i stammarna, vilket kan ha gynnat talgoxen och blåmesen och kanske legat bakom inflyttningen av andra hålbyggare, såsom stare och nötväcka. Det är möjligt att de alltmer uppvuxna träddungarna har påverkat undervegetationen negativt för arter som näkergal och lövsångare. De likaledes minskande bestånden av törnsångare, trädpiplärka och hämpling bebor dock dalens öppna områden och bör ej ha påverkats av nämnda förmodade miljöändring. Av artparet svarthätta och trädgårdssångare har svarthättan, den mest "trädälskande" av dem, ökat, medan den andra arten minskat. Detta kan också vara en följd av att svarthättan dominerar över trädgårdssångaren. Då arterna möts i konkurrens om revir, viker trädgårdssångaren undan.

Fågelsamhällets storlek och allmänna egenskaper

En ofta diskuterad fråga är hur länge en beståndsinventering skall behöva pågå för att utmynna i tillförlitliga resultat. Det beror självfallet på vad man önskar beskriva, eller vilka problem man vill lösa. Något generellt svar har ej givits. Därför har som bidrag till diskussionen den långa serien från Fågelsångsdalen delats upp i sina 10-årsperioder. I Tabell 4 redovisas dessa var för sig och tillsammans med den odelade 40-årsperioden. Där presenteras fågelsamhället med hjälp av allmänt använda parametrar. Man ser av siffervärdena, att några genomgripande olikheter inte är förhanden. En period om 10 år kan alltså vara tillräcklig, då det gäller att beskriva ett fågelsamhälles egenskaper. Men detta gäller icke alltid, vilket kommer att visas i det följande.

De fyra talrikaste arterna har varit desamma under samtliga 10-årsperioder. Det är endast ordningsföljden mellan dem som växlat. Dock har bofinken, med undantag endast för den första perioden och ett par av holkåren, stadigt legat i topp.

Som framgår av Tabell 2 och Fig. 12 har Fågelsångsdalens beståndstorlek varierat avsevärt under de 40 åren men utan att någon genomgående säkerställd tendens till ändring avtecknat sig. Inte heller 10-årsperioderna visar säkra ändringar.

Sammanfattningsvis kan sägas om informationen i Tabell 4, att Fågelsångsdalen uppvisat ett relativt stabilt bestånd. Detta gäller i stort även för 10-årsperioderna, vilket har sin grund i att uppgångar och nedgångar i artbestånden fördelat sig ganska jämnt över de 40 åren. Så har även varit fallet med "trafiken" av sporadiskt uppträdande arter. Men därmed är icke sagt att sammansättningen av dalens fågelbestånd varit i stort densamma genom åren. Tvärtom, en fortlöpande tydlig förändring har skett, vilket kommer att visas längre fram.

Antalet arter och artomsättningen

Antalet stationära arter har hållit sig runt 20 för hela perioden och alla 10-årsperioder utom den första, vars lägre antal säkerligen beror på ofullständiga inventeringar under de tre första åren.

Ett mått på artomsättningen har beräknats på följande sätt. Man lägger ihop antalet arter, som försvunnit resp. tillkommit det andra av de två år som jämförs. Summan uttrycks i procent av medelvärdet för de båda årens antal arter. Artomsättningens variation från det ena året till det andra visas i Fig. 8 och dess medelvärden finns i Tabell 4. Variationen är stor och svänger mellan 4 och 50%. En stor del av omsättningen beror på s.k. "in-och-ut-arter", dvs sådana som etablerar revir endast vissa år i dalen. Om man räknar ut artomsättningen med stigande intervall mellan de jämförda åren, får man det resultat som visas i Fig. 9. För de allt längre intervallen kommer de tillfälligt uppträdande arterna att spela mindre roll. Artomsättningen visar en konstant och låg ökning med stigande intervall. Lutningen på stegringen motsvarar en ökning av artomsättningen om 0.75% för varje ökning med ett år av intervallet mellan de jämförda åren. Om denna trend fortsätter, kommer de arter, som fanns i dalen vid undersökningens början, att sällan uppträda som bofasta omkring 100 år senare, alltså på 2050-talet. Förmodligen kommer dock den stigande trenden snart att avklinga och alltmer närma sig ett horisontellt förlopp och därmed upphöra helt.

Efter inventeringens början har 19 nya arter uppträtt i dalen, tillfälligt eller mera varaktigt. Som framgår av Tabell 4, har dessa nykomlingar fördelat sig ganska jämnt mellan de fyra 10-årsperioderna. Eftersom tillförseln av nya arter inte visat någon klar tendens att minska, är det inte osannolikt, att någon eller några nya arter kommer att dyka upp med varaktiga revir även under projektets femte decennium.

Jämförelse mellan artbeståndens variationer

Om man art för art jämför variationsmönstret genom åren med alla övriga arter, finner man att vissa arter tenderar att variera i takt, dvs de uppvisar olika grader av samvariation. Andra varierar mer eller mindre i otakt, alltså på ett motsatt sätt. Detta kan utläsas för de 19 talrikast förekommande arterna i Tabell 5. Med hjälp av diverse matematiska beräkningar kan arterna också paras ihop allt efter graden av samvariation. Resultatet av detta visas av "gaffeldiagrammet" i Fig. 10. Genom att slå ihop de samvarierande artparen och jämföra dessa summabestånds variation med övriga ensamma eller sammanslagna arter, växer så småningom ett gaffeldiagram eller "träd" fram. Av figuren framgår att före den sista sammanslagningen är arterna hänförda till endast två stora grupper, A och B.

Det intressanta med gaffeldiagrammet är att de flesta arter, som råkat hamna i grupp A, är stannfåglar eller kortflyttare (vinterkvarter i Europa), medan de flesta i grupp B är långflyttare till tropiska Afrika. Vidare kan man konstatera, att arterna i grupp A som regel har ökat i numerär under 40-årsperioden, medan däremot arterna i grupp B har minskat. Detta antyder, att det är överlevnaden i vinterkvarteret och under flyttningen som betyder mest för hur många som kommer att häcka i Fågelsångsdalen påföljande säsong. Denna tolkning ökar i trovärdighet, om man kan finna orsakerna till varför några få arter enligt indelningen ovan hamnat i fel grupp i diagrammet. För det första kan man bortse från de felplacerade arterna härmsångare och svarthätta, eftersom dessa är endast mycket löst anknutna till grupp A. Däremot "stör" kärrsångaren mönstret i denna grupp. Arten har dock sedan ett par decennier förstorat sitt utbredningsområde, vilket kan tänkas ha överflyglat effekten av andra beståndspåverkande faktorer. Hämplingens position i grupp B är en följd av att artens bestånd minskat allmänt i Sverige. Entitans nedgång kan kanske förklaras av de andra mesarnas ökning. Som konkurrent om bohålen med liten öppning får entitan stå tillbaka för blåmesen. Trots de nämnda "felplaceringarna" finns det enligt vår mening inte någon anledning att förringa värdet av de signaler som gaffeldiagrammet enligt ovan ger.

Självfallet påverkas de olika arternas numerär av en mångfald faktorer. Därtill kommer att slumpen spelar stor roll, isynnerhet för alla artbestånd, som med nödvändighet blir små i en så liten provyta som Fågelsångsdalen. Denna störning kan skymma sikten, då det gäller att urskilja även genomgående och betydelsefulla trender i variationsmönstren. Till detta bidrar säkert också de misstag, som ibland görs under inventering och utvärdering. Men man har anledning att förmoda, att ju längre en observationsserie är, desto större blir möjligheten att ur virrvarret av siffror sålla fram väsentlig information. Vad gaffeldiagrammet visar kan vara ett exempel på detta.

Många forskare anser, att överlevnaden i vinterkvarteren spelar den största rollen för de häckande beståndens fluktuationer. Som närliggande exempel härpå kan kortflyttarna rödhake och järnsparv utpekas, båda känsliga för vinterklimatet. Som framgår av Fig. 3 och 10, samvarierar dessa båda arter vackert.

Naturligtvis får händelser i provytan under häckningstid, såsom ovan berörda ev. miljöförändringar, inte frånkännas sin betydelse. Därtill kommer att arterna kan påverka varandra. Ett par möjliga exempel har nämnts tidigare. I detta sammanhang bör uppmärksammas, att de båda artgrupperna A och B enligt gaffeldiagrammet (Fig. 10) varierat på ett motsatt och statistiskt säkerställt sätt. Detta antyder, att ett konkurrensförhållande av något slag råder mellan de båda artgrupperna, vilket skall skärskådas närmare i följande avsnitt.

Varför är stannarna och kortflyttarna vinnarna i Fågelsångsdalen?

Om man slår ihop alla stannare och kortflyttare (S-arterna) och på samma sätt samlar alla tropikflyttare (T-arterna) och sedan jämför de båda gruppernas fluktuationer, visar det sig, att dessa är motsatta. När S-arterna ökar, minskar T-arterna, och vice versa (Fig. 11). Denna relation mellan artgrupperna har påvisats av Herrera (1978), som fann att i Europa ökar andelen T-arter i fågelsamhällena successivt norrut, medan andelen S-arter alltså minskar. Han gör sannolikt att det är S-arterna som "bestämmer". T-arterna fyller ut det utrymme, som blir kvar sedan de tidigare anländande S-arterna etablerat sina revir. Av stor betydelse skulle därmed S-arternas överlevnad mellan häckningssäsongerna vara. Detta har bestyrkts av O'Connor (1981), som fann att efter stränga vintrar i England med stora förluster för S-arterna, ökade andelen T-arter den påföljande häckningsssäsongen.

Herrera's och O'Connor's studier är baserade på regionala inventeringar. Det verkar i förstone osannolikt, att den beskrivna relationen mellan de båda artgrupperna skulle kunna bli tydlig i en liten provyta som Fågelsångsdalen. Följande fakta kan ha bidragit att så ändå blivit fallet. 1. Ytans litenhet har kompenserats med en mycket lång inventeringsperiod. 2. Ytan har som miljö varit i stort sett konstant (Fig. 2) och dess totala fågelinnehåll har icke ändrats genomsnittligt genom åren (Fig. 12). 3. Provytan är en isolerad och attraktiv ö i jordbrukslandskapet, vilket innebär att provytans miljö upphör vid provytans gränser. Därmed kan flertalet S-arter inte utvidga sina revir utanför gränserna för att kompensera sig för förluster till inträngande T-arter. Regleringen måste ske inom provytans gränser, och därmed borde mottrycket öka.

S- och T-arterna har inte endast uppvisat motsatta fluktuationer, deras långsiktiga trender är också motsatta (Fig. 12). S-gruppen har ökat från 38% av totalbeståndet i början av 1950-talet till 57% i början av 1990-talet, medan T-arterna uppvisat motsvarande nedgång. Vid sidan av att vissa arter försvunnit under de 40 åren och några har varaktigt flyttat in, är denna ändring i fågelsamhällets sammansättning det mest anmärkningsvärda som hänt i Fågelsångsdalen.

S-arternas fortlöpande ökning kan ha orsakats av förbättrad häckningsframgång men även, och kanske framförallt, på ökad vinteröverlevnad. Av Fig. 13 framgår att det finns ett positivt samband mellan medeltemperaturen för vintern (uträknad för tiden januari–mars med data från väderstationen i Lund) och storleken av S-arternas bestånd den påföljande häckningssäsongen. Ju mildare vinter, desto fler revir av S-arter i dalen. Fig. 14 visar dessutom att medeltemperaturen för vintern har stigit med inte mindre än tre grader under de 40 åren. Detta kan mycket väl vara en förklaring till S-arternas stigande trend under samma tid. En bidragande orsak till vissa S-arters förbättrade överlevnad kan vara en förmodad ökning i vinterfågelmatningens omfattning i takt med tätorternas snabba tillväxt under senare decennier.

T-arternas tillbakagång kan ha många orsaker, t.ex. försämrade förhållanden i vinterkvarteren. Att så skulle vara fallet är mindre troligt, eftersom Svenssons (1993) resultat från de regionala punkttaxeringarna visar, att de tropikflyttare, som förekommer i Fågelsångsdalen, uppvisat antingen konstanta eller ökande bestånd under de senaste 18 åren. Förklaringen kan därmed misstänkas ligga i dalen och bestå antingen i att biotopen förändrats till dessa arters nackdel, eller i att det tätnande beståndet av S-arter försvårat för T-arterna att erövra plats för revir. Vi anser att det sistnämnda alternativet, som bygger på Herrera's ovannämnda hypotes, ligger närmast till hands. Det är viktigt att komma ihåg, att S- och T-arterna inte konkurrerar på lika villkor. När T-arterna anländer till dalen, har många S-arter redan etablerat revir. Det är en allmän erfarenhet, att en revirägare står stark gentemot en revirlös inkräng-ling.

Den enligt vår mening mest sannolika förklaringen till den fortlöpande förändring av artsammansättningen i Fågelsångsdalen, som skett under 40 år, är att stannarna och kortflyttarna gynnats främst av de allt mildare vintrarna. Det ökande antalet överlevande har kunnat tätare befolka den tomma dalen om våren, vilket i sin tur försvårat för de senare anländande tropikflyttarna att etablera sig där.

Jämförelse med en liknande isolerad provyta i grannskapet

I redogörelsen för de första tio årens inventeringar i Fågelsångsdalen (Enemar 1966) framkastades tanken, att dalen är mindre lämplig som mätare av olika arters beståndsvariationer i regionen. Detta skulle bero på att dalen som en isolerad, frodig och därmed attraktiv ö i åkerlandskapet årligen skulle fyllas "till bredden" med fågel, och detta i stort sett oberoende av variationen i vinteröverlevnaden. Detta skulle gälla främst de talrikt förekommande arterna. Hur det förhåller sig därmed, skulle man i viss grad kunna klargöra genom en jämförelse med en liknande provyta i grannskapet. Detta är nu möjligt, beroende på att Alerstam (1985) startade samma typ av inventering 1969 och fortsatte i 11 år i provytan Borgen utanför Landskrona, ungefär 30 km nordväst om Fågelsångsdalen. Storleken är 12 ha, med omväxlande lövblandskog med rik undervegetation och öppna områden samt med genomströmmande bäckar. En jämförelse med motsvarande period i Fågelsångsdalen visar, att de flesta värden bland dem, som återfinns i Tabell 4, ligger på samma nivå för båda ytorna. Den största skillnaden är att Borgen har nästan dubbelt så hög fågeltäthet som Fågelsångsdalen, vilket delvis förklaras av att andelen öppen mark i Borgen är mindre.

De olika artbestånden i de båda provytorna tenderar att samvariera. Det gäller med stor statistisk säkerhet för de båda talrika arterna bofink och lövsångare, men även för stare och gärdsmyg. Av de 15 jämförda arterna visar endast fyra svag tendens till motsatta fluktuationer. Eftersom många artbestånd är små och den undersökta perioden endast 11 år, kan slumpprocesser ha påverkat åtskilliga fluktuationer. Att överensstämmelsen mellan de båda bestånden ändå är så relativt god, antyder att provytorna i icke ringa grad speglar de beståndsvariationer, som sker i regionen, och att ovannämnda farhågor framstår som något överdrivna. Resultatet av jämförelsen betyder emellertid inte, att bestånden i Fågelsångsdalen och Borgen skulle utgöra tillförlitliga stickprov ur den omgivande regionens fågelbestånd i samma biotop. Orsaken ligger i deras egenskap av isolerade och attraktiva biotop-öar. De problem, som sådana provytor ger upphov till som delar i regionala inventeringsprogram, skall icke närmare behandlas i detta sammanhang.

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The wintering of Blackcaps *Sylvia atricapilla* (L.) in Sweden

THORD FRANSSON & BENGT-OLOV STOLT

Abstract

A total of 688 winter observations of Blackcaps in Sweden were compiled for an analysis of distribution, trend in numbers and winter survival. During the last 30 years wintering Blackcaps have been observed annually, with a maximum of 72 individuals reported during the winter 1982/83. The number of reports of wintering Blackcaps increased markedly from the 1960s to the early 1980s. Some possible explanations for this increase are discussed, including a new migratory habit in continental Blackcaps to move northward during autumn. Early winter observations occur over almost the whole country. In northern Sweden, nearly all the Blackcaps (98%) disappeared during the course of the winter, indicating a high mortality. In the southern part of the country, the decrease from November to March was 69%, which means that in this area about one out of three Blackcaps survived the winter, if we assume losses to be mortality. For the country as a whole, the decrease was 72% for males and 81% for females. The habit to feed at bird-tables is widespread. Some Blackcaps were stationary for longer periods, and 19 birds stayed for more than three months.

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Introduction

The migratory behaviour of European Blackcaps *Sylvia atricapilla* is highly diversified. Among the different migration routes described (cf. Berthold & Schlenker 1991) a newly developed autumn migration behaviour, directed WNW from continental Europe towards wintering areas in Great Britain, has attracted much attention (cf. Berthold & Terrill 1988, Berthold et al. 1992). Recently, northward autumn movements from continental Europe towards Scandinavia have been described (Fransson & Stolt 1993). After this finding we decided to compile all available information about the winter occurrence of Blackcaps in Sweden in order to analyse the following questions: 1) How regular and widespread is the occurrence of Blackcaps in Sweden during the winter?, 2) Is there an increasing trend in the number of wintering occurrences, as described from England (Leach 1981) and Belgium (Fouarge 1980)?, and 3) To what extent do birds survive the winter at northern latitudes?

Material and methods

Observations of Blackcaps made in Sweden during winter (November–March) were collected by searching the literature, and by distributing requests to all regional committees of the Swedish Ornithological Society.

The Swedish Ornithological Society has a system with 30 regional committees covering the country (see Tyrberg 1992). The system has been successively built up during the last 30 years. In the journals of the regional ornithological societies the committees publish annual lists of birds for which reports are wanted, and summaries of the reports received. During spring 1993 we sent to the committees a request for all reports on Blackcaps found during the months November–March. In our request, we also asked for observations of the birds' behaviour and on the food taken by them. By the end of October we had received answers from all the committees. In this analysis, we have included observations up to and including the winter 1992/93, even if some observations from the last winter are missing.

Swedish journals with ornithological reports were checked, as well as a number of handbooks and other published faunistical reports. There are certainly some gaps in our survey of the literature, but we believe we covered most of the faunistical reports published during the last hundred years. Important journals are *Fauna och Flora* starting from 1906, *Vår Fågelvärld* from 1942, and a rapidly growing number of regional ornithological journals started during the 1970s and 1980s.

In the present study, we define the northern and the southern part of Sweden as the areas north and south of latitude 61°N, respectively. In order to provide an idea of the general weather situation in southern Sweden in different winters we have compiled, from the official annual publications of SMHI (Swedish Meteorological and Hydrological Institute), the mean January temperatures at Örebro (59°17'N 15°13'E) for the years 1911–1993. We believe that the temperature at this site reflects the situation in southern Sweden fairly well.

Results

Annual occurrence

Our survey resulted in a total of 688 winter observations of Blackcaps from Sweden. Only three of the birds were reported before 1950 (Fig. 1). Observations of Blackcaps have been reported every winter since 1957/58. The number of birds observed increased to a maximum value during the winter 1982/83 when 71 individuals were seen. This is the highest number recorded so far. During the last ten years the number of reported Blackcaps varied between 58 and 18, with the lowest number reported during the winter 1988/89 (Fig. 1). The last winter (92/93), which was incompletely covered, had again one of the highest numbers observed.

The January mean temperature at Örebro (59°17'N 15°13'E) varied without any obvious trend (Fig. 1). During the early 1970s there were some mild winters. The winter 1982/83, when the largest number of Blackcaps was observed, coincided with a mild January. A few years later, during the winter 1986/87, the coldest January since 1911 occurred (Fig. 1). This unusually cold winter was followed by six mild winters, but with a relatively low number of Blackcaps. However, a small increase in the number of wintering Blackcaps is evident during the last three years.

Although the majority of the Blackcaps were recorded in southern Sweden, as many as about 20% of the observations were made in the sparsely populated northern part of Sweden. The first report from this area was in 1964/65. After a peak during the winter 1981/82, the annual number of observations in northern Sweden fluctuated between five and eleven.

Sex ratio

Information about sex is available for 510 birds (74%). Among these, males were more numerous (n=285, 56%) than females (n=225, 44%). The numbers differed significantly from an equal sex ratio (χ^2=6.64, df=1, P<0.01). Birds seen during November–December (n=358), showed a less pronounced and not significant difference between the proportions of the two sexes (54% males vs. 46% females, χ^2=1.75, df=1, p>0.05). In contrast, among late winter observations (February–March) significantly more males (n=59, 61%) than females (n=38, 39%) were observed (χ^2=4.12, df=1, p<0.05).

Geographical distribution

The geographical distribution of Blackcaps reported during different months is shown in Fig. 2. Observations made during November were widespread and occurred in most parts of Sweden. Some concentrations were found in the southwestern part of Sweden and around 60°N, i.e. in areas of the country with a relatively dense human population. In December, observations in the northernmost part of the country decreased, while observations made south of 61°N were still evenly distributed. During the period January–March, observations in northern Sweden were rare while observations in southern Sweden remained relatively common.

In northern Sweden, the number of observed Blackcaps decreased by 98 % from November to March (Fig. 3). The decrease was very rapid during the first part of the winter. The small number of Blackcaps remaining during the latter part of the winter decreased only moderately from January to March. In southern Sweden, the number of observed Blackcaps decreased by 69% from November to March (Fig. 3), the decrease being more gradual than in the north. For the country as a whole, the number of observations decreased by 72% for males and 81% for females from November to March.

In 12 cases, Blackcaps were found dead during the winter. Six of these were found in the northernmost part of Sweden. Some of the dead birds were found in connection with periods of cold weather and much

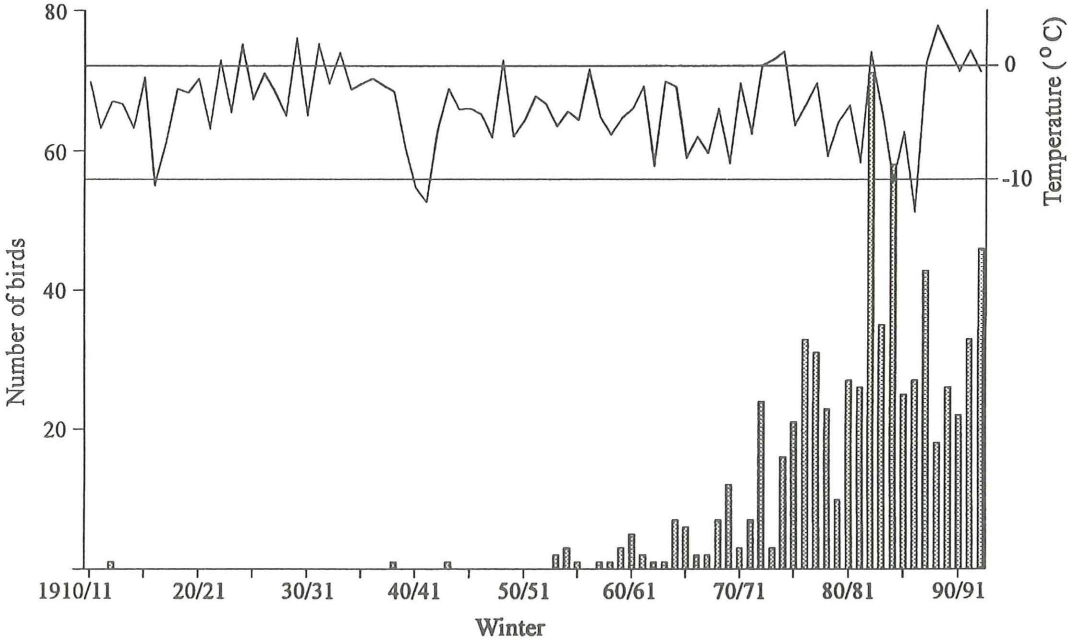


Fig. 1. Annual number of Blackcaps observed in Sweden during winter (November–March) from the period 1910 to 1993. The curve shows the mean temperature during January at Örebro (data from SMHI).

Antalet vinterobservationer av svarthätta i Sverige under perioden 1910–1993. Kurvan visar medeltemperaturen under januari i Örebro (data från SMHI).

snow, and one bird was found dying during snowfall when the temperature was –19°C. In another case, not included in the 12 cases above, a stationary Blackcap disappeared during a snowstorm.

Behaviour and food

In 234 cases (34%) Blackcaps were reported from the same place for more than one day. Several birds were observed during a longer period of time, and 19 individuals stayed more than three months at the same site. About 13% of the Blackcaps were seen at bird-tables. The foodchoice of Blackcaps at bird-tables varied; the most common food items eaten being apples, tallow and bread. Other kinds of food eaten include coconut fat, bananas, pears, raisins, hemp seed, sunflower seeds, cheese, potatoes, butter and liver paste. In some cases the observer mentioned that the Blackcap was aggressive to other birds.

Some Blackcaps were also seen eating berries remaining on trees and bushes, such as berries of Rowan *Sorbus aucuparia*, White beam *S. intermedia*, Wild Cotoneaster *Cotoneaster integerrimus*, Dogwood *Cornus sanguinea*, Wild Asparagus *Asparagus officinalis*, Bryony *Bryonia alba* and Red Currant *Ribes rubrum*.

Discussion

This is the first detailed account of the winter occurrence of Blackcaps in Sweden. Earlier knowledge of winter occurrence in Sweden is only fragmentary. There are, however, some notes in old handbooks. Nilsson (1858) mentions late autumn Blackcaps eating berries and Kolthoff (1898) provides information about a December report from Uppsala. According to the latest edition of the check-list of Swedish birds, winter observations are made almost every winter in south and central Sweden, sometimes also in the northern part (SOF 1990). Our survey shows that winter observations of Blackcaps have been reported regularly in Sweden during the last 30 years and that the geographical distribution includes most of the country.

Many of the observed Blackcaps stayed for a period of time, and some were even seen during almost the whole winter period. If we assume that Blackcaps observed during November stay in Sweden during the following months and that the chance

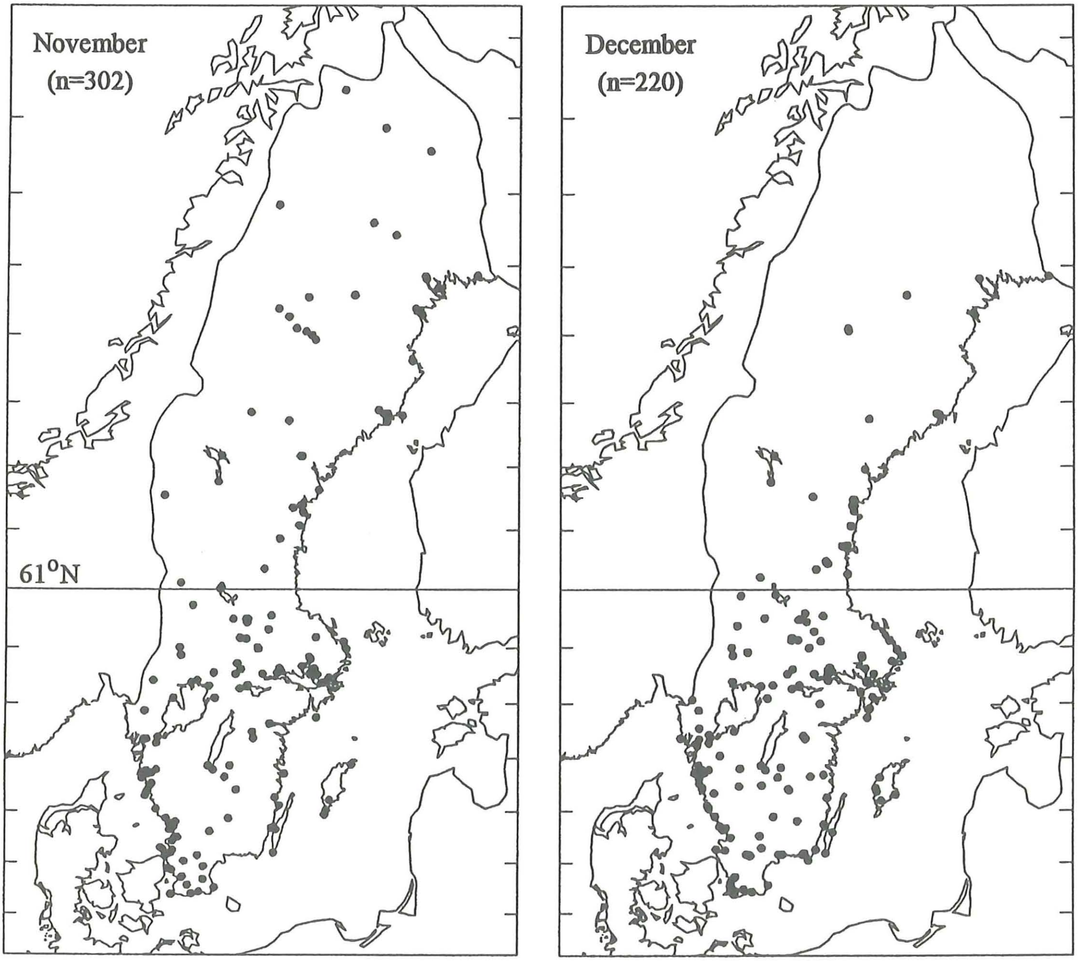
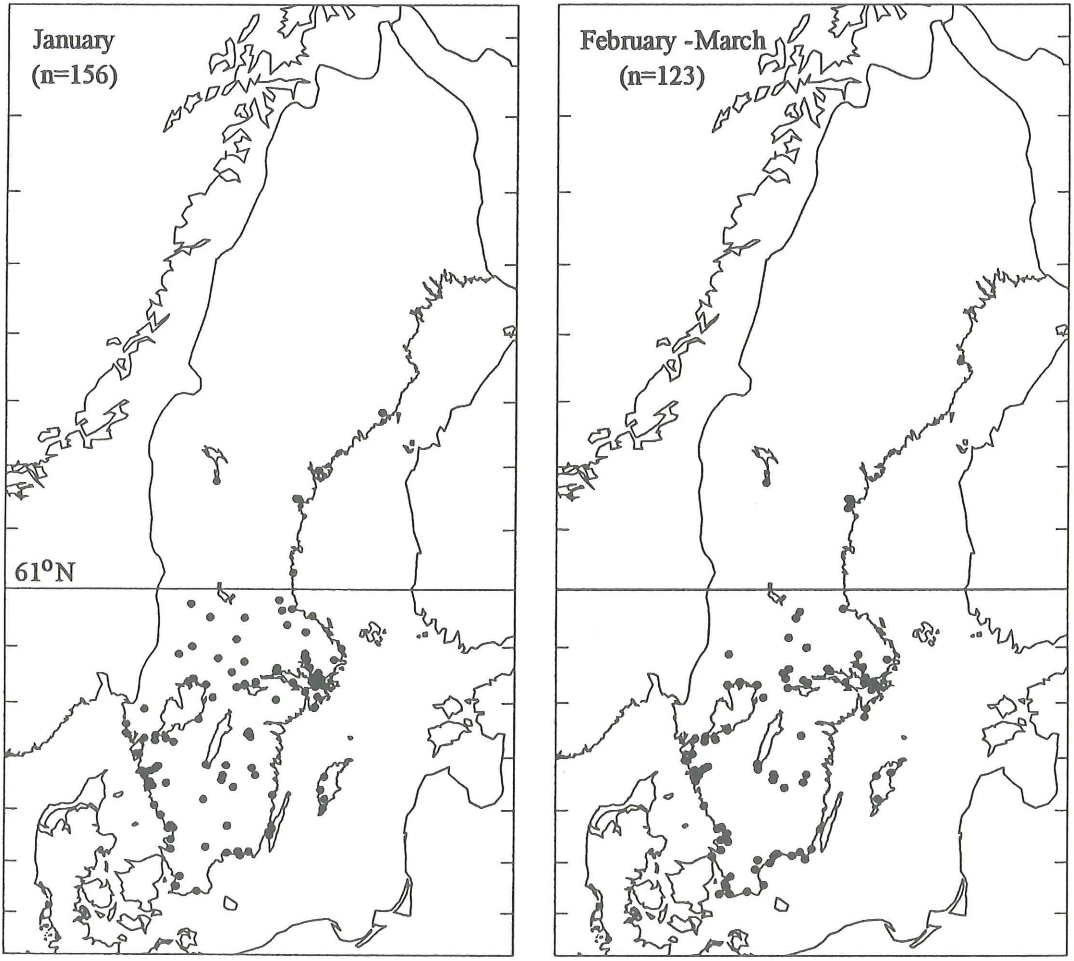


Fig. 2. Geographical distribution of Blackcaps observed in Sweden during different periods of the winter. Each dot represents in some cases more than one individual.

of receiving reports is equal during the course of the winter, the decrease in the number of observed Blackcaps from November–March is a measure of mortality. The large decrease found in northern Sweden indicates a very low winter survival there. In contrast, the decrease in southern Sweden indicates that about one out of three Blackcaps survive in this area. However, a mortality of about 70% during a period of four months is high, especially as first-year mortality in a Continental population of Blackcaps has been estimated at 68% (Bairlein 1978). It is, however, possible that some part of the decrease is not a result of mortality. Even though we have no such information, some winter movements might occur. Observations from southern Europe indicate that winter nomadism occurs (cf. Debussche & Isenmann 1984, Berthold & Schlenker 1991). Individual movements of up to 500 km have been observed in Britain during winter (Leach 1981). It is also possible that some individuals that stay for a long time at one site are reported only when they first appear. This would result in a bias towards a lower number of late winter reports.

In Sweden, a winter predominance of males was found. The same was noted in Britain and Ireland (Leach 1981), but not in Belgium where the sex ratio was equal (Fouarge 1980). Leach gives no explanation of this other than the fact that females of many migrating birds winter, on the average, further south than the males. In North America, a similar distribu-



Geografisk fördelning av svarhättor observerade i Sverige under olika perioder av vintern. Punkterna kan i vissa fall representera mer än en individ.

tion has been found in the Dark-eyed Junco *Junco hyemalis*, and it has been suggested that climate in combination with inter-sexual competition produce this distribution (Ketterson 1976, Ketterson & Nolan 1979). The larger decrease during the winter in observations of females compared to males in the Blackcap, may however indicate that females suffer a higher mortality during winter and also to some extent explain the observed unequal sex ratio.

Several observations show that Blackcaps eat remaining berries, but since this food-source diminishes during the course of the winter, it might in Sweden be most important during early winter. The habit to feed at bird-tables during the winter seems to be common in Sweden, as in Britain and Ireland (Leach 1981). Several observations show that individuals can utilize bird-tables successfully during longer periods of cold weather (Holm 1968, Pärt 1978, Roos pers. comm.). The great flexibility in the food choice and their aggressive behaviour towards other birds are also consistent with results found in Britain and Ireland and facilitate the use of bird-tables.

A number of surveys of wintering Blackcaps have been conducted in Britain and Ireland (Leach 1981), demonstrating a large increase in the number of wintering birds during the 1960s and 1970s. The same pattern was found in Belgium where the numbers of wintering Blackcaps started to increase in about 1960 and continued to increase until the

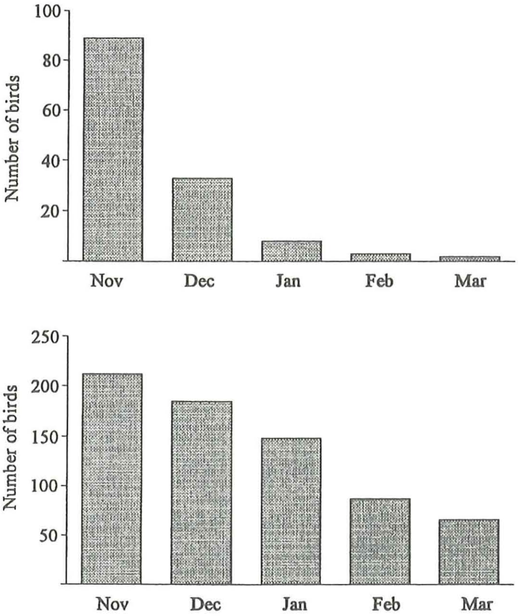


Fig. 3 Monthly distribution of Blackcap observations in northern (above 61°N) and southern (below 61°N) Sweden. Individuals observed for longer periods are included for each month in which they were observed.

Observationer av svarthätta i norra (norr om 61°N) och södra delen av Sverige fördelade på månad. Individer observerade under längre perioder är inkluderade i de månader som de observerats.

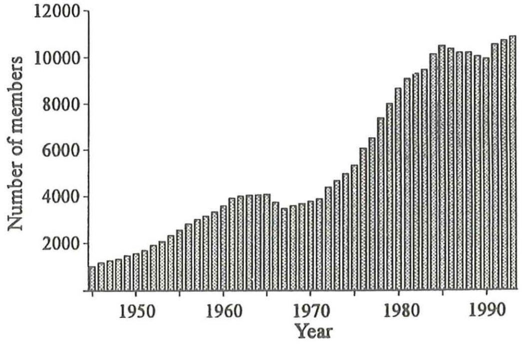


Fig. 4. Annual number of members in the Swedish Ornithological Society during the period 1945–1993.

Antal medlemmar i Sveriges Ornitologiska förening under perioden 1945–1993.

winter of 1977/78, when the study ceased (Fouarge 1980).

We found a corresponding trend in Sweden with an increase in the number of reported observations from the early 1960s to the early 1980s (Fig. 1). For an interpretation of this increase we think that at least four possibilities have to be considered:

1. The observed increase may be the result of a new migratory trait in continental Blackcaps, moving north for the winter. This has been suggested for the birds wintering in Britain. Langslow (1979) showed that Blackcaps wintering in Britain belonged to continental populations. It is supposed that this migratory trait has evolved during recent decades, through increased winter survival at bird-tables, shorter and earlier migration, as well as earlier breeding compared with the traditional migratory pattern (Berthold & Terrill 1988, Terrill & Berthold 1990, Berthold et al. 1992). Ringing recoveries demonstrate that there is also a northward movement of Blackcaps from continental Europe into Scandinavia during the autumn (September–October), and as much as 9% of autumn movements in southern Scandinavia were directed northward (Fransson & Stolt 1993). So far, the only clear evidence of the origin of wintering Blackcaps in Sweden is one bird ringed in Belgium in October 1993 and found dying at Jönköping, southern Sweden on 20 December 1993 (W. Roggeman, pers. comm.).
2. Another possibility is that some Blackcaps spent the winter in Sweden in earlier years too, and that the observed increase is mainly a result of an increased number of birdwatchers and an increased readiness to report winter observations during recent decades. In favour of this interpretation is the fact that the number of members in the Swedish Ornithological Society has increased rapidly during the last 20 years (Fig. 4). This, together with a successful organisation of regional ornithological societies during recent decades, has certainly contributed to a much more efficient faunistical documentation.
3. A third possibility is that the observed increase is a result of a general increase in Blackcap populations, with a small but constant proportion of birds wintering at northern latitudes. In favour of this interpretation it can be argued that the results of a number of bird censuses indicate that a general increase actually has taken place in some of the European Blackcap populations during the last 30 years (Leach 1981, Svensson 1993).
4. The winter temperature probably affects the number of birds seen during winter, but we do not find any evidence that this alone can explain the increasing number of birds seen. It is interesting that recent mild winters coincide with medium,

but slowly increasing, numbers of Blackcaps. One possibility is that the extremely cold winter of 1986/87 had a negative effect on the number of wintering Blackcaps during a sequence of years. In several studies it has been shown that the direction and length of migration in the Blackcap has a heritable component (Berthold 1988, Helbig 1991, Berthold et al. 1992). With this in mind, it seems likely that it will take some years for the number of wintering Blackcaps to recover if the genotype has been strongly decimated during an extremely hard winter.

With the available information it is not possible to identify any single cause for the observed increase in wintering Blackcaps in Sweden. It might well be a combination of different causes. However, we find it reasonable to believe that the number of Blackcaps in Sweden during winter has actually increased during the last 30 years. This would be in accordance with what has been observed in Belgium and in Great Britain (Fouarge 1980, Leach 1981). However, as also pointed out by Leach (1981), the magnitude of the increase might be affected by the increasing number of observers. Information is still lacking on whether local birds from the breeding population also are involved, or if all wintering Blackcaps in Sweden have a continental origin.

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Sammanfattning

Vinterförekomsten av svarthätta Sylvia atricapilla *(L.) i Sverige*

Svarthättor från kontinenten har i ökad omfattning funnits övervintra i England (se Berthold & Schlenker 1991) och nyligen har även en nordligt riktad höstflyttning mot Skandinavien påvisats (Fransson & Stolt 1993). Mot denna bakgrund beslöt vi att samla all information om artens vinteruppträdande i landet för att analysera följande frågor: Hur spridd och regelbunden är vinterförekomsten i Sverige? Ökar antalet övervintrande fåglar? I vilken utsträckning överlever fåglarna vintern?

Material och metoder

Uppgifter om vinterobservationer från november till mars insamlades på två sätt, dels genomsöktes tillgänglig litteratur (bl a lokala fågeltidskrifter), dels erhölls material från SOFs samtliga regionala rapportkommitteer. I vår studie har vi skilt på norra och södra Sverige och då dragit gränsen vid 61°N (Fig. 2). För att ge en uppfattning om vintervädret olika år har vi ur SMHIs officiella publikationer sammanställt medeltemperaturen i Örebro i januari för åren 1911–1993.

Resultat

Vår sammanställning resulterade i 688 vinterobservationer, varav endast tre är från perioden före 1950 (Fig. 1). Sedan vintern 1957/58 har förekomsten varit årlig. Det största antalet observationer inföll vintern 1982/83 då 71 svarthättor rapporterades. Den kallaste januarimånaden sedan 1911 inföll vintern 1986/87 (Fig. 1). Därefter följde sex milda vintrar med ett lägre och endast långsamt ökande antal rapporterade svarthättor.

För 510 fåglar finns kön noterat. Under förvintern, november–december, fanns ingen signifikant skillnad i könskvot men under eftervintern, januari–mars, var skillnaden signifikant med 61% hannar och 39% honor ($\chi^2=4,12$, df=1, $p<0,05$).

Under november månad är fynden geografiskt ganska jämnt fördelade över hela landet (Fig. 2). I december minskar fynden i landets nordligaste delar. Under januari–mars är fynden i norra Sverige få medan förekomsten i södra Sverige förblir ganska jämnt fördelad.

Minskningen av antalet observationer under vinterns lopp skiljer sig dels mellan norra och södra Sverige och dels mellan könen. I norra Sverige är minskningen från november till mars 98% medan den i södra Sverige är 69%. För hela landet minskar antalet observerade svarthättor med 72% för hannar och med 81% för honor.

I 234 (34%) fall sågs svarthättor stanna i mer än en dag och i 19 fall blev fåglarna kvar i mer än tre månader. Svarthättor sågs äta bär av rönn, oxel, kornell, oxbär, sparris och hundrova. Av svarthättorna sågs 13 % vid fågelbord där den vanligaste födan var äpple, talg och bröd, men svarthättorna har också iakttagits äta kokos, banan, päron, russin, hampfrö, solrosfrö, ost, potatis, smör och leverpastej. Flera observatörer uppger att svarthättor varit aggresiva mot andra fåglar vid fågelbordet.

Diskussion

I vårt material ökar antalet övervintrande svarthättor starkt under 1960- och 1970-talen. En samtidig stark ökning har tidigare rapporterats från de Brittiska öarna, Irland och Belgien (Leach 1981, Fourage 1980). Det finns flera möjliga förklaringar till den kraftiga ökningen av rapporter från Sverige. Vi vet att en del svarthättor under hösten flyttar norrut från Centraleuropa till Skandinavien. Detta kan vara ett nytt flyttningsbeteende i likhet med vad som rapporterats för de svarthättor som övervintrar i England (se Berthold & Terrill 1988, Terrill & Berthold 1990, Berthold et al. 1992). De svarthättor som ses i Sverige under vintern skulle därför kunna ha sitt ursprung på kontinenten. Det hittills enda säkra belägget för svarthättornas ursprung är ett vinterfynd i Sverige av en i Belgien ringmärkt svarthätta. Denna fågel märktes i oktober och hittades döende 20 december samma år i Jönköping. En annan förklaring, som ligger nära till hands, är att den starka ökningen av rapporter helt enkelt beror på att den ornitologiska rapporteringsverksamheten byggts ut och ökat kraftigt under samma tid. En tredje förklaring kan vara att beteendet funnits även förut hos en liten andel av svarthättorna och att ökningen är ett resultat av en allmän ökning av antalet svarthättor. Svarthättan har under senare tid också ökat i antal i såväl svenska som västeuropeiska populationer (Leach 1981, Svensson 1993). Det ökade antalet rapporter om övervintrande svarthättor kan mycket väl vara ett resultat av en kombination av olika förklaringar. Vi finner det dock sannolikt att antalet övervintrande svarthättor i Sverige verkligen ökat under de senaste 30 åren. Om några av dessa svarthättor också är svenska häckfåglar eller om de alla kommer hit söderifrån under hösten återstår att visa.

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The distribution of breeding Merlins *Falco columbarius* in relation to food and nest sites

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Abstract

This study deals with nest site selection and with the importance of food and nest sites as determinants of breeding density of Merlins *Falco columbarius*. Merlins preferred Hooded Crow *Corvus corone cornix* nests less than 2 years old, which had not been used previously by Merlins. Artificial nests meeting these requirements were provided in a study area where the number of suitable nests for Merlins was low. Food abundance (number of passerines) was estimated in this area and in a control area where up to 15 Merlin pairs could breed. The number of breeding Merlin pairs did not increase in the nest provision area in relation to the number of nests provided. One possible reason was that the accessability of prey was limited by snow, which was much more abundant in the nest provision area than in the control area. Therefore, we suggest that the density of breeding Merlins in this area was mainly determined by food particularly during the mating period.

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Introduction

The distribution of breeding birds is associated with the abundance of resources necessary for breeding such as food and nest sites (Lack 1968). For instance, food availability may limit the density of breeding raptors such as Kestrels *Falco tinnunculus* and Sparrowhawks *Accipiter nisus* (Newton 1979, 1986, Newton & Marquiss 1986, Village 1990, Korpimäki & Norrdahl 1991). Moreover, the availability of nest sites has been suggested as one factor limiting the density of breeding Kestrels (Village 1983, 1990) and other raptors (Newton 1979). In the case of the Merlin *Falco columbarius*, increasing availability of suitable nest sites is thought to have caused breeding population expansion in some areas (Oliphant & Haug 1985, James 1988, Warkentin & James 1988, Sodhi et al. 1992).

There are few experimental studies on the relationship between nest site availability and the distribution of breeding raptors, probably because it is difficult to manipulate the availability of nest sites. However, some species such as Kestrels and Merlins accept artificial nests for breeding (Hamerstrom et al. 1973, Newton 1979, Village 1983, Rebecca & Payne 1991). These species should, therefore, be well suited for determining the relative importance of nest site availability and food abundance, respectively, in influencing breeding numbers.

Merlins are adapted mainly to open habitats with few and small stands of trees (Oliphant 1974, Wiklund 1977, Newton et al. 1978, 1984, Bibby 1986, James 1988, Warkentin & James 1988, Sieg & Becker 1990). Like other falcons, Merlins do not build a nest. Rather, Merlins may accept various types of nest sites and breed in old nests of corvids and Rough-legged Buzzards *Buteo lagopus* on cliff-ledges and, in some areas, on the ground (for example Newton et al. 1978, Wiklund 1986, Meek 1988, Warkentin & James 1988, Sieg & Becker 1990). This may be one reason that provision of artificial nests has increased the number of breeding pairs in areas where natural nests are rare (Rebecca & Payne 1991).

In some parts of the Scandinavian mountain region, Merlins have bred with fairly stable numbers for more than a decade (Wiklund 1986, unpublished data). There they are found in small Birch *Betula pubescens ssp. tortuosa* forests near lakes and rivers. In such an area, we studied nest site selection by

Merlins and the distribution of breeding pairs in relation to the availability of nests and food. We increased the number of nest sites by erecting artificial nests in an experimental area where few natural nests were available. Before 1987, no more than one breeding Merlin pair were recorded each year in this area. Thus, if nest site shortage reduced the number of breeding Merlins in this area, we expected that provision of suitable nest sites should increase the number of breeding pairs (see also Rebecca & Payne 1991). Food abundance was estimated from point counts of passerines in this area and in a control area where many Merlin pairs regularly bred.

Study area and methods

Data on nest site selection were collected among Merlins breeding in Padjelanta and Stora Sjöfallet national parks, N Sweden, during 1977–1992. We mapped nests of breeding Merlins and Hooded Crows *Corvus corone cornix*, and recorded nest site selection of Merlins in the following breeding season. The Hooded Crow nests were classed according to four age categories: the nest was made in the same year as the Merlins used it, 1 year old, 2 years old and 3 or more years old. The maximum height of trees and height of the nest above ground were measured with an accuracy of 0.5 m using a Suuntometer, provided by the Forestry Department in Jokkmokk. We used the proportion of the tree above the nest as an approximation of overstory cover.

Manipulation of nest site abundance

The experimental area and the control area were on each side of the valley of Vuojatätno (67° 60' N, 17° 35' E, direction NNE–SSW), approximately 12 km long and 5 km wide, with a large river in the valley bottom. The valley is surrounded, in two directions, by steep mountains, and in the other directions by one large lake, Akkajaure, 10 km×80 km, and one smaller lake, Kutjaure. The habitat includes small birch forests and open land such as alpine meadows, Crowberry *Empetrum nigrum* heaths and Dwarf-birch *Betula nana* heaths, marshes and tundra. Important prey items for Merlins, such as Meadow Pipits *Anthus pratensis* and Wheatears *Oenanthe oenanthe* are encountered mainly on meadows and heaths (Wiklund 1986).

The distribution of breeding Merlins in this valley is irregular; many more pairs breed on one side of the valley, the control area (facing to the NW), than on the other side (facing to the SE), where no more than one pair has nested each year (see below). Because the distribution of breeding Hooded Crows in these areas is similar to that of the Merlins, potential nest sites for Merlins are produced continually in and near the control area. In the experiental area, there were only three Rough-legged Buzzard nests that could be used by Merlins attempting to breed during 1988–1991.

In early April 1991, about two weeks before the Merlins arrive, we erected 23 artificial nests in the experimental area. These nests were of Hooded Crow type as described by Rebecca and Payne (1991). Each nest was placed in a birch-tree at about 2/3 of its maximum height (see below) and firmly tied to the tree using wire. The distance between two neighbouring nests was approximately 1 km.

Before the 1992 breeding season in March, the artifical nests were repaired and changed slightly. A nest-cup was made of matted wool and filled with a thick layer of coarse sand allowing the birds to scrape a shallow hollow. It should be noted that we were not allowed to test the artificial nests in the control area due to National Parks regulations.

Estimating food abundance

Six routes, each approximately 6 km long, were used for censuses of passerines. Three routes traversed each of the experimental (routes: 4, 5 and 6) and the control (routes: 1, 2 and 3) areas. On each side of the valley, one route (1 and 6) was high on the slope near the tree border, another was 100–200 m from the river at the valley bottom (3 and 4), and the third between the other two. The routes went through habitats representing hunting as well as nesting areas for Merlins. In 1991, censuses were made from 2 to 7 June. This year the Merlins commenced laying, on average, on 29 May. Thus, some Merlin pairs were still laying when passerine abundance was estimated. In 1992, censuses were made from 6 to 10 May, that is, in the pre-laying period.

The censuses were made as point counts; the observers (CGW, Nigel Harding, Yngve Ryd) stopped after 15 min and recorded all birds during a 3 min period. After each point count, snow depth was measured, and snow cover was classified within a square, 50×50 m, according to: 0=no snow, 1=1–25% of the ground covered, 2=26–50% of the ground covered, 3=51–75% of the ground covered, 4=76–100% of the ground covered. Censuses were made twice per route by walking (1991) and skiing (1992).

We separately examined the abundance of Meadow Pipits and Wheatears because these birds are, by numbers, the most important prey items of Merlins during the nestling period (Wiklund 1986). Other passerines included in the study were: Yellow Wagtail *Motacilla flava*, Redstart *Phoenicurus phoenicurus*, Bluethroat *Luscinia svecica*, Redwing *Turdus iliacus*, Fieldfare *T. pilaris*, Chaffinch *Fringilla coelebs*, Brambling *F. montifringilla*, Redpoll *Carduelis flammea*, Reed Bunting *Emberiza schoeniclus*, Snow Bunting *Plectrophenax nivalis* and Lapland Bunting *Calcarius lapponicus*.

We used ANOVA and Scheffe's F-test to examine any differences in numbers of birds between routes as well as between the experimental and control areas. Since we could predict the relationship between bird abundance and snow from other studies (Svensson 1986, Kostrzewa & Kostrzewa 1991), we used one-tailed tests in this analysis. Other statistical tests follow Siegel (1956) and SAS (1988). Means are given ±one standard deviation.

Table 1. Nest site selection by breeding Merlins. The number of Merlin pairs occupying nests of various origin and age are presented. Age 0 indicates that the nest was built in the same year as the Merlin pair bred, and 3+ that the nest was three years old or older. Cliff-ledge nest and nests on the ground were not aged.

Boplatsval hos stenfalk. Antalet häckande stenfalkspar i bon av olika ursprung, och ålder på bo byggda av kråka och fjällvråk. En nolla betyder att boet byggdes samma år som stenfalkarna häckade i det, och 3+ att boet var minst 3 år gammalt. Bon på klipphyllor och på marken åldersbestämdes ej.

Nest site *Boplats*	Age *Ålder*				Total
	0	1	2	3+	
Hooded Crow *kråka*	20	60	26	28	134
Rough-legged Buzzard *fjällvråk*	–	–	–	8	8
Cliff-ledge *klipphylla*	–	–	–	–	5
Ground *marken*	–	–	–	–	7

Results

Nest site selection

Over the study period, 149 nest sites were categorized according to type and age. There was a clear preference for breeding in nests of Hooded Crows. Thus, 134 (90%) Merlin nesting attempts were in nests made by Hooded Crows and only 8 (5%) were in nests made by Rough-legged Buzzards, including 3 on cliffs (Table 1). The numbers of Merlin pairs breeding on cliffs and on the ground were 5 and 7, respectively (Table 1).

In this area, most Hooded Crow pairs finished nest-building in late April, when the Merlin mating season begin. Therefore, most potential nest sites for Merlins attempting to breed were at least a year old. About 79% of the Merlins occupied a nest less than three years old. Each year some Hooded Crow pairs abandoned their nests, sometimes before the nest was completed, so the mud-cup or the inner nest-lining was missing. Twenty Merlin attempts were in nests built in the same year (Table 1). A significantly larger proportion of the pairs bred in one year old nests than in nests of other age categories (Table 1, $\chi^2_{(3)}=28.98$, $P<0.001$). Only 4 nests had previously been used by Merlins.

The nests made by Hooded Crows were in birch-trees, whose maximum height was, on average, 8.0±2.3 m (N=23), range 5.5–12.5 m. The height above ground of these nests ranged between 3.0 and 8.5 m and was, on average, 5.4±1.6 m. There was a positive correlation between maximum height of the trees and height of the nests ($r=0.87$, $N=23$, $P<0.0001$, Pearson). The overstory cover varied greatly and ranged from 19.0% to 50.0% (mean=32.5±10.0%). However, overstory cover was correlated neither with maximum height of the trees ($r=0.14$, $N=23$, $P>0.50$, Pearson) nor with height of the nest ($r=-0.36$, $N=23$, $P>0.09$, Pearson).

Availability of nests in breeding territories

There is evidence that intra-sexual contests among males occur mainly near the nest and rarely away from it (Wiklund & Village 1992). Moreover, in the case of the Merlin there is a large overlap in hunting ranges of neighbouring Merlins (Sodhi 1993a). Thus, it seems likely that intra-sexual contests for breeding territories concern nest sites and the area near the nesting site.

During the mating period, the Merlin male shows a nest to the female. The presentation is preceded by a display-flight, the V-flight, and after alighting on the nest he walks around in it, scratches and calls, the *tic-call* (Sodhi et al. 1993). If there are several old Hooded Crow nests near each other, he may present more than one nest to the female. We recorded more than 10 instances where females scraped in at least two old Hooded Crow nests before laying started. This behaviour of the female may be associated with

Table 2. The number of Merlin pairs breeding in territories of different quality as determined by the number of old Hooded Crow nests in each territory. The number of territories of each category is shown within parenthesis.

Antalet stenfalkspar som häckade i territorier med olika antal tillgängliga kråkbon. Antalet tillgängliga territorier av olika kvalitet anges inom parentes.

Year *År*	Number of potential nest sites *Antalet potentiella boplatser*		
	1	2	>2
1985	1 (1)	2 (4)	12 (17)
1986	0 (1)	0 (1)	8 (14)
1987	0 (1)	3 (4)	9 (13)
1988	1 (2)	1 (2)	17 (22)
1989	0 (0)	4 (5)	17 (22)

Table 3. The number of Merlin territories in the control area and in the experimental area during 1988–1992. The experimental area was provided with 23 artificial nests of Hooded Crow type in 1991 and 1992.

Antalet stenfalksrevir i experimentområdet och i kontrollområdet under 1988–1992. Försöksområdet försågs med 23 konstgjorda kråkbon under 1991 och 1992.

Year *År*	Number of breeding territories *Antalet häckningsrevir*	
	Control area	Experimental area
1988	12	0
1989	15	0
1990	13	0
1991	10	2
1992	12	1

her requirement of a safe nesting site. For instance, two females switched nest site possibly because they were disturbed on the day before laying commenced (see also Wiklund 1990). Hence, a territory with more than one Hooded Crow nest may be more attractive than a territory with only one nest.

We classed 119 potential nesting territories according to the number of crow nests available. The territories appeared similar in many other respects for example the nest(s) were near the edge of a small Birch forest that was surrounded by open land. Most territories (82%) contained more than two nests while territories with only one nest were rare (4%) (Table 2).

Territories with one old Hooded Crow nest were occupied by Merlins on two out of 5 occasions (Table 2), that is, a rate of occupancy of 40%. The percentage of territories with two nests that was occupied by Merlins was 62.5%, and breeding was confirmed in 64.3% of the territories with more than 2 nests. There was no significant difference in rate of occupancy between the three categories of territories (pooled data, F=0.80, P>0.35, ANOVA).

Occupancy of territories in the experimental and control areas

During 1988–1992, the number of territorial Merlin pairs in the control area varied between 10 and 15 (Table 3). Thus, there might have been some unoccupied territories in this area during the two years when artificial nests were provided in the study area. In 1991, Merlins occupied two territories in the experimental area. One Merlin pair consisting of two first-time breeders, a 2 year old male and a 1 year old female, bred in a Rough-legged Buzzard nest about 600 m away from an artifical nest. This female commenced laying about two weeks later than the earliest Merlin female in the control area did, so the possibility that she reared a replacement brood could not be excluded. In the other territory, a male was observed near an artificial nest during at least 10 days, although breeding could not be confirmed. The male that bred in the experimental area in 1991 also bred in 1992 with a yearling female in the same territory as was used in 1991. A Hooded Crow nest made in the same year was then used by the Merlins. This breeding attempt failed due to predation.

Food abundance

In early June 1991, on average 3.3±1.5 (N=41) passerines per point count were recorded in the control area. There were no significant differences in passerine abundance between the transect routes of this area (P>0.05, mean difference: routes 1 vs 2= 0.31, F= 0.06, routes 1 vs 3=–1.07, F= 0.81, routes 2 vs 3=–1.38, F=1.29). Similarly, no significant differences in passerine abundance were detected between transect routes of the experimental area (P>0.05, mean difference: routes 4 vs 5=–0.62, F= 0.31, routes 4 vs 6=–0.51, F= 0.23, routes 5 vs 6= 0.11, F= 0.01). In this area, mean number of passerines was 2.3±1.4 (N= 52). The abundance of passerines was significantly higher in the control area (F= 9.65, P<0.01, ANOVA). One apparent difference

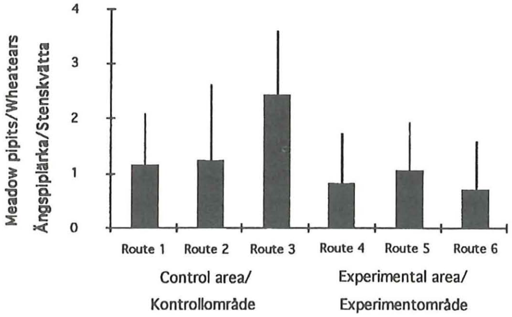

Fig. 1. The number of Meadow Pipits/Wheatears in each line transect route (±SD) in the experimental area and in the control area, respectively.

Medelantalet ängspiplärkor och stenskvättor (±standardavvikelse) längs varje taxeringsrutt i experimentområdet och i kontrollområdet.

was that, on the valley bottom (routes 3 vs 4), there were more passerines in the control area than in the experimental area (mean difference: 2.13, F=3.41, P<0.05, ANOVA).

We separately examined the numbers of Meadow Pipits and Wheatears in each area because they are important prey for breeding Merlins. On average 1.6±1.3 (N=41) Meadow Pipits and Wheatears per point count was recorded in the control area (Fig. 1). The numbers of Meadow Pipits and Wheatears did not differ significantly between the transect routes of this area (Fig. 1, P>0.05, mean difference: routes 1 vs 2=–0.09, F=0.01, routes 1 vs 3=–1.29, F=2.26, routes 2 vs 3=–1.20, F=1.89). The number of Meadow Pipits/Wheatears was significantly higher in the control area (F=11.64, P<0.01, ANOVA). Moreover, Meadow Pipits and Wheatears were more abundant in the valley bottom route (3) of the control area than in any of the routes in the experimental area (Fig. 1, P<0.05, mean difference: routes 3 vs 4=1.62, F=3.81, routes 3 vs 5=1.36, F=2.72, routes 3 vs 6=1.73, F=4.81). In the experimental area, mean number of Meadow Pipits/Wheatears was 0.8±0.9, N=52, (Fig. 1). There were no differences in abundance of Meadow Pipits/Wheatears between the transect routes (P>0.05, mean difference: routes 4 vs 5=–0.25, F=0.10, routes 4 vs 6=0.11, F=0.02, routes 5 vs 6=0.36, F=0.23).

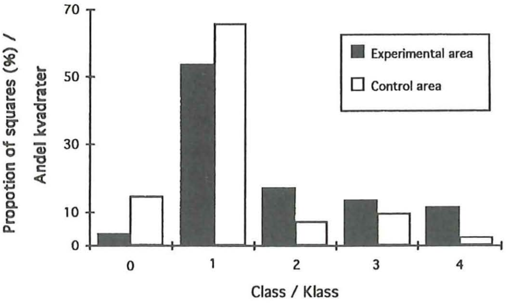

Fig. 2. The proportion of ground covered by snow in the experimental area and in the control area as shown by the frequencies of 50 x 50 m squares of various classes. We classed snow cover of each square by estimating the proportion of the square that was covered by snow, as follows: Class 0=0 %, Class 1=1–25%, Class 2=26–50 %, Class 2=51–75 %, Class 4=76–100 %.

Snötäckets utbredning i experimentområdet och kontrollområdet. Procenten 50 x 50 m. kvadrater av olika snötäckningsgrad: Klass 0=0 % av ytan snötäckt, Klass 1=1–25 %, Klass 2=26–50 %, Klass 3=51–75 %, Klass 4=76–100 %.

In early May 1992, we recorded only 20 and 19 passerines during line transects in the experimental and control areas, respectively. Snow Buntings and Redpolls accounted for 75% of the observations in each area. During this period, we regularly recorded small flocks of Snow Buntings of about 5 individuals on snow-free patches in and near the control area. Some larger flocks of 20 (N=1) and 50 (N=3) individuals were recorded on the largest patches. The range in size of these patches was 5–1000 m^2, on average 110±190 m^2 (N=36). In the experimental area, there were only a few snow-free patches, and they were less than 5 m^2 in size.

Snow and passerine abundance

The proportion of ground covered by snow in early June was higher in the experimental area than in the

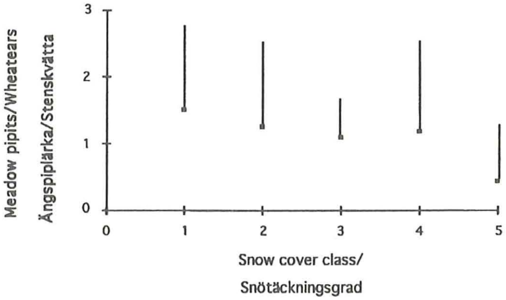

Fig. 3. The number of Meadow Pipits/Wheatears ±SD) in relation to the proportion of ground covered by snow as indicated by snow cover classes (see text and Fig. 2). The proportion of ground covered by snow increased from class 0 to class 4.

Medelantalet ängspiplärkor och stenskvättor (±standardavvikelse) i relation till snötäckets utbredning (se text och Fig. 2). Snötäckets utbredning ökar från klass 0 till klass 4.

control area (Fig. 2, $P<0.05$, ANOVA). Similarly, snow depth was greater in the experimental area (131.4±256.6 mm, $N=52$) compared with the control area, 45.6±133.7 mm, $N=41$, ($P<0.05$, ANOVA). There was a strong correlation between the proportion of ground covered by snow and snow depth ($r_s= 0.82$, $N= 93$, $P<0.01$). Hence, there was much more snow in the experimental area than in the control area.

The number of Meadow Pipits/Wheatears was negatively correlated with snow cover (Fig. 3, $r_s=-0.17$, $N=93$, $P=0.05$), suggesting an inverse relationship between snow and passerine abundance. The total number of passerines was not significantly correlated with snow cover ($r_s=-0.11$, $N=93$, $P=0.13$).

Discussion

Newton (1991) summarized studies of various raptor populations and concluded that in habitats where nest sites are available in excess, breeding density is limited by food supply. The main finding of our study was that Merlins used old Hooded Crow nests for breeding, and that food rather than the availability of nest sites limited the density of breeding Merlins.

Nest site selection

The Merlins mainly used old Hooded Crow nests for breeding (Table 1). There were few pairs that bred on the ground, presumably because such nests often fail due to predation (Newton et al. 1978, Wiklund 1986). Hooded Crow nests were much more common than nests of Rough-legged Buzzards. For instance, approximately thirty Hooded Crow nests were available for five Merlin pairs that bred each year in a birch forest of about 8.0×0.4 km some 20 km away from the nest provision area. The number of Rough-legged Buzzard nests available for Merlins was also reduced because several Rough-legged Buzzards claimed nests each year. The number of nests available in the territory seemed not to affect the Merlins' choice of breeding territories.

One feature of Hooded Crow nests was that they were well concealed compared with those of Rough-legged Buzzards. Nests of the Rough-legged Buzzard were larger and often in the top of the trees and therefore easy for predators to detect. The choice of concealed nests by Merlins is common (Warkentin & James 1988, Sieg & Becker 1990) and probably an adaptation to reduce predation by avian predators.

Merlins showed a strong preference for Hooded Crow nests less than two years old. In these nests, the nest-cup was still intact, although the inner nest-lining and sometimes the mud-cup were missing. However, Merlins rarely used a nest that had been used previously by breeding Merlins. One reason could be that breeding destroyed the nest-cup, so that the nesting base became flat. We recorded some instances of females knocking eggs or chicks out of such nests. In one case, the parents were feeding half grown chicks, two on the ground below the nest and two in it. Another reason could be that, after being used by Merlins in a previous year, a nest might have a high parasite load. Thus, Merlins seemed to select a nest that had not been used by Merlins already, and that provided a shallow hollow for the brood.

In this area, Merlins have been studied since the early seventies (Wiklund 1986, this study). During this study period, we have encountered many Merlin pairs breeding in poor nests. Some examples are (see also above): the mud-cup and a large part of the bottom were missing in one nest (it was possible to look through the nest) leaving only the edge of the nest for the chicks, small and very old Hooded Crow nests with no edge (half the size of a 1 year old nest) consisting of a filled mud-cup and sticks attached to the bottom of the mud-cup. In contrast, our artificial nests were similar in size to fresh Hooded Crow nests, with a strong edge and a shallow hollow. Therefore, we believe that the artificial nests increased the availability of suitable nests in the experimental area, as similar nests did in another area (Rebecca & Payne 1991).

Fidelity to breeding territories is low in Merlins. For instance, average distances moved between successive breeding seasons are among males 1.9±2.0 km, and among females 4.8±6.7 km (Wiklund unpublished data). Moreover, we recorded Merlins in the experimental area in early May. Therefore, we believe that the experimental nests provided an opportunity for Merlins attempting to breed unless some other resource was in short supply. The number of Merlin territories did not increase as a function of the number of nests provided, however. Only a few Merlins established territories in the experimental area. Thus, in terms of proportion available nests for breeding, nest sites seemed not to limit the density of breeding Merlins in this area (see also Warkentin & James 1988).

During the nest provision period, there was a slightly lower density of breeding Merlins in the control area than the maximum recorded for the area. Therefore, breeding territories were probably available in the control area. This created a problem because birds mainly move from poor to rich areas (review in Newton 1992). Thus, more territories could have been occupied in the experimental area, if the breeding densities in the control area had been higher in the years concerned.

Food abundance

Merlins may prefer to nest close to areas with high food abundance (Sieg & Becker 1990) because that would reduce the time spent for hunting and, consequently, the foraging effort particularly for males. The time males spend flying depends on hunting ranges (Sodhi 1993b), which is related to prey abundance (Sodhi 1993a). Moreover, short duration of foraging bouts would allow the male to allocate more time to be near the nest, where the female spends most of her time in the mating period (Newton 1979, Wiklund 1990). This is important because she may not expel other males but accept extra-pair copulations (Sodhi 1991, Wiklund & Village 1992), which could reduce the male's reproductive success.

Newton (1992) reviewed territoriality in birds and pointed out that, in removal experiments, replacements of birds occurred in rich areas but rarely or not in poor areas. Moreover, removed birds in rich areas were often replaced while poor sites remained vacant. During the mating period, we recorded Merlin males hunting Snow Buntings that fed on snow-free patches in and near the control area. Up to mid-May, this was the only passerine that was abundant in large numbers in the mountain region. Hunting Merlins were not encountered in the experimental area, where snow-free patches were small and less common. If food abundance already in the mating period is a que for selection of breeding territories by Merlins, that would also explain the distribution of breeding Merlins in our study area.

The difference in number of Merlin territories between the two areas did not correspond to the difference in passerine abundance in the Merlins' laying period. It is therefore doubtful that food abundance during this period was the most important determinant of the distribution of breeding Merlin pairs.

Breeding of Hooded Crows was rarely recorded in the experimental area. In June and July in N Sweden, Hooded Crows often feed on eggs and nestlings of other birds. Similarly, nestlings as well as newly fledged chicks of passerines form a comparatively large part of the food that Merlin chicks receive (Enemar & Hård 1980). If our passerine counts reflect the difference in number of breeding passerines between the areas, more passerines would have bred in the control area. However, that difference is not large enough to explain why breeding Merlins and Hooded Crows were almost absent from the experimental area.

There is evidence that spacing of breeding raptors is determined by food abundance, which could be associated with land productivity (Newton & Marquiss 1986, Newton et al. 1986, Village 1990). Our study was performed in a mountain area, where in spring the availability of food is strongly reduced by snow, particularly for birds feeding on the ground. Conceivably, this is one important reason that passerines were encountered mainly in areas with little snow. Hence, like low soil productivity snow may reduce food abundance and, consequently, the breeding density of raptors. For instance, the number of Kestrel territories occupied in any one year is negatively correlated with the days of snow cover in the preceeding winter (Kostrzewa & Kostrzewa 1991). We believe, therefore, that the skewed distribution of Merlin territories in this valley reflects passerine abundance particularly the abundance of Snow Buntings during the mating period of Merlins.

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Sammanfattning

Inverkan av födo- och boplatstillgång för den rumsliga utbredningen av häckande stenfalkar Falco columbarius.

Den här rapporten behandlar stenfalkens boplatsval och faktorer som påverkar tätheten av häckande stenfalkspar. Många studier av fåglar, även rovfåglar, indikerar att tillgången på föda och boplatser påverkar häckningstätheten. Ett problem vid studier av rovfågelspopulationer är emellertid att det är svårt att experimentellt undersöka den relativa betydelsen av en viss resurs. Det är till exempel svårt att manipulera boplatstillgången, då få arter accepterar konstgjorda bon. Stenfalken är dock en av dessa arter.

Under häckningstiden finns stenfalken i öppna habitat, där antalet träd och skogsdungar är få och små. Stenfalkarna bygger inget eget bo utan häckar i gamla bon av kråkfåglar och fjällvråk, eller på klipphyllor. Ibland är boet bara en fördjupning i marken. Stenfalkens val av boplats är alltså mångskiftande och kan vara en förklaring till att individer av arten accepterar konstgjorda bon.

I vårt undersökningsområde har det häckande stenfalksbeståndet varit stabilt under mer än 10 år. Stenfalkarnas häckningsplats finns i regel i små björkdungar och jaktområdet utgörs av de öppna markerna som omger häckningsplatsen. Vi undersökte stenfalkens boplatsval och fördelningen av häckande stenfalkspar i en mindre del av undersökningsområdet.

Metoder

Stenfalkens boplatsval undersöktes i Padjelanta och Stora Sjöfallets nationalparker under åren 1977–1992. På kartor prickade vi in bon av stenfalk och kråka. Nästa häckningssäsong noterades stenfalkens val av bo. Kråkbona delades in i fyra ålderskategorier: boet hade byggts samma år som stenfalkarna använde det, 1 år gammalt bo, 2 år gammalt bo och bon som var 3 år eller äldre. Boträdets höjd och boets höjd över marken mättes med en Suuntometer. Proportionen av trädet som var över boet användes som mått på hur väl kamoflouerat boet var.

Experiment- och kontrollområde för manipulering av boplatstillgången valdes i Vuojatätnos dalgång. Den sydöstra delen av dalgången hyser varje år många häckande par av stenfalk och kråka under det att endast enstaka par av de två arterna häckar på den nordvästra sidan. Experimentområdet förlades till den nordvästra delen av dalgången. I detta område fanns enbart 3 fjällvråksbon som kunde utnyttjas av stenfalkar. Kontrollområdet placerades i den sydöstra delen av dalgången. Det första experimentåret, 1991, satte vi upp 23 konstgjorda kråkbon i experimentområdet cirka 2 veckor innan stenfalkarna anlände till trakten. Bona sattes upp i björkar och surrades fast med järntråd. Det andra experimentåret, 1992 reparerade vi bona och försåg dem med en ny bobale gjord av tovad ull som täcktes med grov sand.

Tre taxeringsrutter, var och en 6 km lång, snitslades för kartering av småfåglar i varje område. En rutt gick nära trädgränsen och en i dalbottnen samt den tredje mellan dessa. Rutterna gick igenom både jakt- och boterräng för stenfalk. Under första experimentåret, 1991, taxerade vi småfåglar under stenfalkarnas äggläggningstid, 2–7 juni. Nästa experimentår, 1992, taxerades småfågelförekomsten under stenfalkens parbildningstid, 6–10 maj. Taxeringarna utfördes som punkträkningar; taxeraren stannade efter 15 minuter och noterade alla fåglar under en 3 minuters period. Efter varje punkttaxering mättes snödjupet på platsen och snötäckets utbredning klassifierades i en ruta om 50×50 m. enligt: 0=ingen snö, 1=1–25% av marken snötäckt, 2=26–50% av marken snötäckt, 3=51–75% av marken snötäckt och 4=76–100% av marken snötäckt. Varje rutt taxerades 2 gånger.

Eventuella skillnader i småfågeltillgången mellan rutterna och mellan experiment- och kontrollområde undersöktes med hjälp av variansanalys (ANOVA). Vi gjorde en separat analys av tillgången på ängspiplärka och stenskvätta eftersom dessa arter antalsmässigt dominerar stenfalkens diet under boungetiden.

Resultat

Vi fann att 134 (90%) stenfalkshäckningar skedde i kråkbon och 8 (5%) i fjällvråksbon varav 3 låg på klipphyllor. Övriga häckningar var på klipphylla, 5, och på marken, 7. Cirka 79% av stenfalkarna valde ett kråkbo som var yngre än 3 år. Åldern på de flesta bona var ett år (Tabell 1). Tjugo par häckade i årsbon av kråka.

Boträdens höjd varierade mellan 5.5 och 12.5 m och boets placering över marken varierade mellan 3.0 och 8.5 m. Det var en positiv korrelation mellan trädets höjd och boets höjd över marken. Mellan 19% och 50% av trädet var ovanför boet.

Totalt 119 potentiella stenfalksrevir klassifierades med avseende på antalet kråkbon i reviret. Reviren skiljde sig ej mycket åt i andra avseenden rörande habitatets struktur. Bona fanns nära skogskanten i små björkdungar, som var omgivna av öppen mark. Proportionerna revir med stenfalkar var lika för de 3 revirkategorierna; 1 bo, 2 bon och mer än 2 bon. Antalet bon i reviret påverkade alltså inte stenfalkens val (Tabell 2).

I experimentområdet etablerades 2 stenfalksrevir under 1991. Ett par gick till häckning och 1 hane höll ett revir (med konstgjort bo). Följande år, 1992, häckade den förstnämnda hanen med en ny hona i samma revir som häckningsåret 1991. De två häckningarna skedde i ett fjällvråksbo (1991) och i ett årsbo av kråka (1992).

Småfågeltillgången var lägre i experimentområdet än i kontrollområdet. Detsamma gällde också tillgången på ängspiplärka och stenskvätta (Fig. 1). Det var framför allt i dalgångens botten som antalet ängspiplärka/stenskvätta skiljde sig mellan de två områdena. I maj, 1992, noterades endast ett fåtal tättingar. Snösparven var i särklass vanligast. Den förekom i större antal i och nära kontrollområdet än i experimentområdet.

Tillgången på ängspiplärka/stenskvätta var relaterad till snömängden. Där det var mycket snö var antalet individer litet och tvärtom. Det var mer snö i experimentområdet än i kontrollområdet.

Diskussion

I en översikt av olika rovfågelspopulationer kom Newton (1992) till slutsatsen att tätheten av häckande individer begränsas av födotillgången i områden med överskott på boplatser. Vår studie visar att stenfalkarna i regel väljer att häcka i gamla kråkbon och att det troligen är födotillgången som begränsar antalet häckande par.

Det var en betydligt större förekomst av kråkbon än fjällvråksbon. I en närbelägen dalgång fanns det cirka 30 kråkbon för de 5 stenfalkspar som varje år häckade i dalgången. Antalet tillgängliga fjällvråksbon reducerades också av att ett antal fjällvråkar hävdade revir varje år. En orsak till att antalet markbon var så litet är att sådana bon ofta plundras.

Stenfalkarna visade en klar preferens för kråkbon som var mindre än 2 år gamla. Utmärkande drag för dessa bon är att det finns en fördjupning, en boskål, i boet även om kråkornas byggnation har avslutats innan den inre delen av bobalen och emellanåt även boskålsformen av lera har färdigställts. Stenfalkarna häckade ytterst sällan i bon som vid ett tidigare tillfälle hade utnyttjats av stenfalk. En orsak kan vara att efter en stenfalkshäckning försvinner boskålen och boets översida blir platt. Vid häckningar i sådana bon har honor emellanåt knuffat ägg eller ungar ur boet. Exempelvis matade ett stenfalkspar 2 ungar i boet och 2 ungar nedanför boet. Ett annan orsak är att sådana bon kan innehålla en stor mängd parasiter.

Under de senaste 20 årens studier av stenfalk har vi vid flera tillfällen funnit stenfalkar som har häckat i bon av mycket dålig kvalité. Bon som i princip har saknat botten eller gamla slitna kråkbon som har varit hälften så stora som nya bon. Våra konstgjorda bon var av samma storlek som nya kråkbon och försedda med en boskål och en förstärkt kant. Därför tror vi att de konstgjorda bona utgjorde ett realistiskt alternativ i experimentområdet, där det saknades riktiga kråkbon. Vi noterade också stenfalkar i detta område under den tid då reviretablering sker. Antalet nyetableringar av stenfalk var emellertid så litet att det knappast kan ha varit boplatsbrist som begränsade antalet häckande par.

Stenfalkar häckar ofta nära områden med hög bytestillgång. Detta reducerar jakttiden, vilket minskar i synnerhet hanens ansträngning att skaffa föda. Korta jakttider under parningstiden är viktiga också ur en annan synvinkel. Under cirka två veckor före äggläggningen tillbringar honan merparten av tiden vid boet och hanen förser henne med all mat hon behöver. Det är vid den här tidpunkten som äggen befruktas och om hanen inte vaktar henne emot konkurrerande hanar kan faderskapet riskeras. Honorna accepterar att para sig även med främmande hanar.

Under parbildningstiden såg vi stenfalkshanar som jagade snösparvar på barfläckarna både i och i närheten av kontrollområdet. I experimentområdet var barfläckarna små och sällsynta. Snösparven är den enda vanliga tättingen i området fram till senare hälften av maj. Om födotillgången under parbildningstiden är viktig för stenfalkens val av häckningsterritorier detta förklara den skeva fördelningen av stenfalkar i Vuojatätnos dalgång.

Skillnaderna i småfågeltätheten mellan experiment- och kontrollområde under stenfalkarnas läggningstid var för små för att förklara den stora skillnaden i antalet besatta revir. På samma vis förhåller det sig med skillnaden i antalet häckande småfåglar, om vi antager att våra punkttaxeringar under stenfalkarnas läggningstid också var ett mått på antalet häckande småfåglar.

Det finns samband mellan den häckande tätheten av rovfåglar och bytestillgången och produktiviteten i ett område, mätt som sambandet mellan jordmån och växtlighet. I vårt undersökningsområde reducerades födotillgången i april och maj av snö. I synnerhet för de småfåglar som söker föda på marken. Därför är förhållandet mellan snö och småfågelförekomsten i vårt område jämförbart med förhållandet mellan produktivitet och småfågelförekomst i snöfria områden. Småfågelförekomsten är liten i områden med omfattande snötäcke och vice versa. En konsekvens är naturligtvis att småfågelpredatorernas antal också kan påverkas av snötäckets utbredning. Tornfalken ännu ett exempel på en predator som påverkas av att bytestillgången reduceras av snö. Studier av arten har visat att antalet besatta territorier är omvänt relaterat till antalet dagar med snötäcke. Det är inte bytesvalet i sig som är av störst intresse (tornfalken lever främst av smågnagare) utan det faktum att snö kan påverka bytestillgången för falkarna och därigenom också påverka antalet besatta revir.

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Marine birds drowning in fishing nets in the Gulf of Gdańsk (southern Baltic): numbers, species composition, age and sex structure

LECH STEMPNIEWICZ

Abstract

During 8 seasons (1972–1976 and 1986–1990) 1 254 marine birds of 24 species, drowned in fishing nets in the Gulf of Gdańsk, were collected and studied. As a rule, the most numerous bird species in the Gulf constituted the most common by-catch. The exceptions are the Goldeneye *Bucephala clangula*, Tufted Duck *Aythya fuligula* and Coot *Fulica atra*, the numbers drowned being incommensurably low compared with those observed in the Gulf. The reverse is the case in the Eider *Somateria mollissima*. The percentage share of the Long-tailed Ducks *Clangula hyemalis* and Eiders in by-catches increased in general and that of the Velvet *Melanitta fusca* and Common Scoters *Melanitta nigra* decreased during successive years of the study. The number of birds drowned in nets in different months roughly reflects the seasonal changes in their numbers in the Gulf. Adult birds, particularly males, predominated among the Long-tailed Ducks (68% and 47% respectively) and Velvet Scoters (65% and 46% respectively). The opposite was the case among the Common Scoters and Eiders, where immature birds constituted as much as 71% and 67% respectively. With the passage of the season, these proportions changed in a species specific way. Adult birds became entangled in fishing nets less frequently than expected, considering their percentage share in the wintering population. It is estimated that about 17 500 birds (10–20% of the number observed in the area) die annually in nets. These include Long-tailed Ducks (about 8 400), Velvet Scoters (about 4 000), Scaups *Aythya marila* (about 1 300), Common Scoters and Eiders (each about 1 000).

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Introduction

Marine birds, fish and fishermen concentrate in the same food-abundant regions of the sea for trophic reasons. This convergence in time and space have to lead to conflicts. Large numbers of birds, mainly diving birds (auks, penguins, shearwaters, gannets, divers, grebes, sawbills, diving ducks) drown each year in fishing nets (bottom set and floating gill nets, cod and lobster traps, etc.) in all seas of the world. Scavengers (gulls, petrels) feeding on fish, birds and mammals entangled on the surface, also often die in nets. Incidental catches in fishing nets, together with oil pollution, are considered to be the main anthropogenic factors in marine bird mortality (Ashmole 1971, Bourne 1976, 1977, Cobb 1976, King et al. 1979, Nettleship et al. 1984, Stempniewicz 1991, Harrison & Robins 1992).

The problem occurs during the breeding season (especially in the vicinity of large colonies of seabirds) as well as in the moulting and wintering areas. This has been reported from both Pacific (Ainley et al. 1981, Carter & Sealy 1984) and Atlantic regions (Tull et al. 1972, Piatt et al. 1984, Olden et al. 1985, Piatt & Nettleship 1987). Also in Polish coastal waters it has been noted that birds may drown in fishing nets (Szczepski 1948, Kowalski & Manikowski 1982, Kieś & Tomek 1990). The Gulf of Gdańsk is such a risky region for waterbirds, since the fishing is intensive and large numbers of waterbirds concentrate here during winter, autumn and spring (Górski & Strawiński 1986, Meissner 1989, 1992).

This paper presents data on number, species composition, age and sex structure of diving birds drowned in fishing nets set in the Gulf of Gdańsk during eight wintering seasons, 1972–1976 and 1986–1990. The spatial and temporal (within a season) variability of catches is also described. The results are discussed and compared with data obtained during field observations. On that basis the mortality of diving birds in fishing nets in the Gulf of Gdańsk is estimated.

Material and methods

Birds entangled and drowned in nets were collected with the co-operation of fishermen from two fishing ports (Orłowo – 6 motor boats, and Sopot – 9 motor boats registered). The ports were visited and birds collected 1–3 times a week over 8 seasons (November–May) in 1972–1976 and 1986–1990. During two seasons (1973/74 and 1987/88) drowned birds were regularly stored by fishermen (in their opinion, 65–75% of the total number drowned) and then collected. In the remaining seasons birds were stored irregularly so the proportion of the drowned birds that was collected is not known. Data from these seasons were not taken into account when estimating total number of bird catches in the Gulf. Birds were thoroughly examined and dissected in the laboratory, determining species, age (2 categories: immature and adult) and sex of each individual.

The study area (i.e. fishing grounds) covers shallow (2–10 m) coastal waters from Orłowo to Jantar (including Vistula Mouth), and deeper waters (up to 80 m) in the central part of the Gulf (Fig. 1). In this area both benthic species (Bivalves, Gastropods, Polychaetes, Crustaceans) and fishes are very abundant. The most important fish species netted here are Cod *Gadus morhua*, flatfish (*Platessa platessa, Platichthys flesus*), Herring *Clupea harengus*, Trout *Salmo trutta*, and Perch *Perca fluviatilis*. Also Eel *Anguilla anguilla* and Eelpont *Zoarces viviparus* constitute an important catch but they are trapped, and not netted.

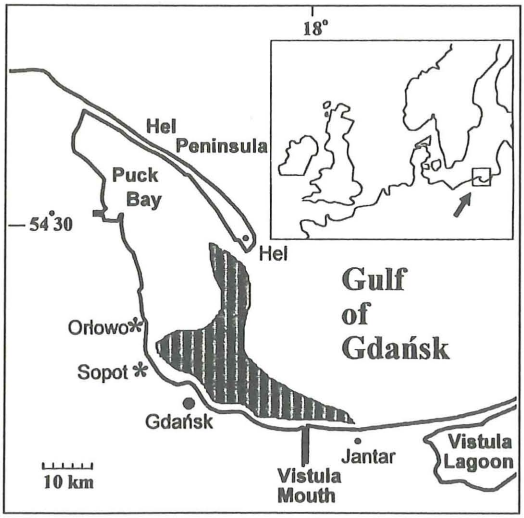

Fig. 1. Area of the Gulf of Gdańsk, Southern Baltic (asterisks indicate the fishing ports, Orłowo and Sopot, where net catches were collected; shading indicates fishing grounds).

Karta över Gdanskbukten i södra Östersjön. Asterisker visar fiskehamnarna där fåglar som drunknat i fisknät insamlats. Skuggning markerar fiskeområden.

Cod is caught in bottom-set gill nets (40×2.5 m, mesh-size 55 mm) at depths from about 10 m (September, October) to 80 m (usually 20–30 m) in the winter months. There are no permanent cod fishing grounds in the Gulf. Flatfish nets (40×1.5 m, mesh-size 60–70 mm) are set anywhere on bottoms in shallow water (2.5–8 m deep). Nets used for trout are of two types. Bottom-set nets (35×2.5 m, mesh-size 65 mm) are put in shallow (2–3 m deep) river mouths, and floating nets (1.5×2–3 m, mesh-size 80 mm) are set only out of the ship routes (mainly in Puck Bay, i.e. out of the study area). Herring nets (2 sizes: 25×6 m, and 50×2.5 m, mesh-size 24–26 mm) are set floating 1–2 m below the water surface at depth not exceeding 10 m. The main herring fishing grounds are situated in the region of Vistula Mouth, spreading eastward to Jantar and westward to Gdańsk (Fig. 1).

The nets are checked usually after one, and sometimes after more days, depending on weather conditions. The crew of one boat uses about 80 cod nets (40 rolled and 40 set during one control), 30–40 nets for flatfish and 20–25 herring nets. The number of salmon nets per boat is very variable depending on specialization of the particular crew. Some of them use as much as 100 nets and others do not use them at all.

Nets are set all year around but the main fishing season (November–April) coincides with the wintering season of diving birds in the Gulf of Gdańsk. Flatfish constitutes the most important catch in October and November, and the second most important in December, April and May. Cod predominates in net catches during the winter months (December–March) and in April. Herring is caught in greatest quantities in May and also much in October/November and March/April. In general, the catch of fish of the majority of species decreased during the study period except for flatfish and Perch. However, detailed data are not available.

Total catches of birds during one season were based on material collected in two fishing ports

Table 1. Number (%), age and sex structure of waterbirds drowned in nets in the Gulf of Gdańsk (ad - adult; im - immature; m - males; f - females

Antal, ålders- och könsfördelning av sjöfåglar drunknade i fisknät i Gdanskbukten (ad - adult, im. - ung, m - hane, f - hona)

Species	Total	%	ad m	ad f	im m	im f
Clangula hyemalis	606	48.3	286	124	75	106
Melanitta fusca	289	23.0	132	56	48	48
Aythya marila	96	7.7	17	36	31	9
Melanitta nigra	78	6.2	9	9	28	28
Somateria mollissima	69	5.5	13	9	25	21
Podiceps cristatus	28	2.2	9	11	2	2
Aythya fuligula	19	1.5	11	3		1
Fulica atra	12	1.0		1		1
Uria aalge	10	0.8	2		6	
Cepphus grylle	9	0.7	3	3	2	
Mergus serrator	8	0.6	2		2	1
Podiceps grisegena	5	0.4		2		
Gavia stellata	5	0.4		1	1	
Alca torda	5	0.4			1	4
Gavia artica	3	0.2	1			
Bucephala clangula	3	0.2	1			2
Podiceps auritus	2	0.2		1		
Somateria spectabilis	1	0.1				1
Mergus albellus	1	0.1	1			
Mergus merganser	1	0.1	1			
Gavia immer	1	0.1	1			
Gavia adamsi	1	0.1				1
Phalacrocorax carbo	1	0.1	1			
Alle alle	1	0.1				1
Total number	1254	100.0	489	257	222	225
%	100		39.0	20.5	17.7	17.9

Note: Age and/or sex of some birds has not been noted. *Ålder och/eller kön har inte registrerats för vissa fåglar*

during two seasons (1973/74 and 1987/88) and extrapolated from calculated catch per registered motor boat per season to total fishing effort in the Gulf. Rowing boats (46 registered in the Gulf, usually assisting but also fishing) were not included in the calculations. Information concerning the number of boats registered was obtained from the Maritime Office in Gdynia.

Results and discussion

Species composition

Altogether, 1 254 birds of 24 species were examined. Represented by 8 species, diving ducks were most frequently entangled in nets, being followed by auks and divers (4 species each), grebes and sawbills (3 species each). The Long-tailed Duck *Clangula hyemalis* was the most numerous species (606 birds – 48.3%), followed by the Velvet Scoter *Melanitta fusca* (289 birds – 23.0%). Birds of other species did not exceed 10%, the majority constituting less than 1% of the material. Also, some rare species (*Somateria spectabilis, Gavia immer, G. adamsi, Alle alle*), observed sporadically on the Polish Baltic coast, were found during the study (Table 1).

The species composition of birds drowned in nets in different fishing grounds did not differ much, despite significant differences in their distribution in the Gulf. The Long-tailed Duck was the first and the Velvet Scoter the second most frequent prey entangled in nets set in the Vistula Mouth (48.3% and 23.0%, respectively, this study), in Puck Bay (41.0% and 21.9%, respectively, Kieś & Tomek 1990) and in the central part of the Polish Baltic coast, in the Dziwnów area (53.0% and 26.8% respectively, Kowalski & Manikowski 1982). There seem to exist differences concerning bird species drowning in nets in smaller numbers (<10% of the total share), since auks (*Uria aalge, Alca torda*) constitute a common by-catch (25%) in Puck Bay (Kieś & Tomek 1990), where they concentrate during the winter period (Meissner 1989).

The number of birds drowned in nets roughly reflects their proportions in the Gulf. However, exceptions are Goldeneye *Bucephala clangula*, Tufted Duck *Aythya fuligula* and Coot *Fulica atra*, since they winter in large numbers (Górski & Strawiński 1986, Strawiński 1990, Meissner & Klawikowska 1993, Michno et al. 1993), but are rarely found in the nets (Table 1). Kowalski & Manikowski (1982) and Kieś & Tomek (1990) also did not report these species in by-catches from other localities, probably because these species may forage away from the main fishing grounds. Covered areas (ports, piers, breakwaters, etc.) and very shallow waters often occupied by these species are usually free of the fishing nets.

The opposite is the case with the Eider *Somateria mollissima*, which winters in the Gulf in small numbers (Górski & Strawiński 1986, Strawiński 1990, Meissner & Sikora 1993) and yet is frequently found drowned in nets. The reasons for this are not clear, although a likely explanation is that the distribution of the Eider is limited to coastal waters overlapping with fishing grounds. For example, in the opinion of fishermen, Eiders concentrate in areas with an abundance of Herring and become entangled mainly in herring gill nets. This is supported by an analysis of stomach contents (Stempniewicz, unpubl.). Also the Velvet and Common Scoters drown in nets more frequently than would be expected considering their relatively low numbers in the Gulf (Meissner 1993, Stempniewicz 1986).

During successive seasons different numbers of birds were collected (Table 2). The percentage share of the five most numerous ducks in by-catches changed in successive seasons. The Long-tailed Duck was the commonest prey during the whole study period, with the exception of 1987/88, when more Scaups were caught. However, the Scaups generally occurred only sporadically, and such erratic changes in numbers are characteristic for this species, at least in the Gulf of Gdańsk (Michno et al. 1993). During the years of study, the proportion of Long-tailed Ducks generally increased. By contrast, the second most numerous species, the Velvet Scoter, showed a continuous decrease in share over successive years. Also the proportion of Common Scoter tended to decline, while the number of Eiders obviously increased, during the consecutive seasons (Table 2). It is difficult to explain these trends. Unfortunately, it is not possible to relate these figures to changes in the number of seabirds wintering in the Gulf of Gdańsk during the study period because of the lack of such data in the 1970s. However, existing data for the 1980s do not show any consistent trends (Meissner, unpubl.).

For five of the most common species drowned, it was possible to show how abundance varied during the wintering season. Long-tailed Ducks showed their first peak in December and a second peak in

Table 2. Collected waterbirds of the five most numerous species drowned in fishing nets in the Gulf of Gdańsk .

Insamlade i fisknät drunknade individer av de fem vanligaste övervintrande sjöfågelarterna i Gdanskbukten.

Species		72/3	73/4	74/5	75/6	86/7	87/8	88/9	89/90	Total
Long-tailed Duck	N	37	217	36	19	80	80	77	60	606
Clangula hyemalis	%	42.5	42.5	45.0	70.4	68.4	35.1	68.1	65.9	48.3
Velvet Scoter	N	28	203	16	4	8	21	5	4	289
Melanitta fusca	%	32.2	39.7	20.0	14.8	6.8	9.2	4.4	4.4	23.0
Scaup	N	1	0	0	0	0	93	2	0	96
Aythya marila	%	1.1	0.0	0.0	0.0	0.0	40.8	1.8	0.0	7.7
Common Scoter	N	4	52	14	0	5	0	2	1	78
Melanitta nigra	%	4.6	10.2	17.5	0.0	4.3	0.0	1.8	1.1	6.2
Eider	N	1	8	3	2	10	8	13	24	69
Somateria mollissima	%	1.1	1.6	3.7	7.4	8.5	3.5	11.5	26.4	5.5
All 24 species in total	N	87	511	80	27	117	228	113	91	1254
% of total number	%	6.9	40.7	6.4	2.1	9.3	18.2	9.0	7.3	100.0

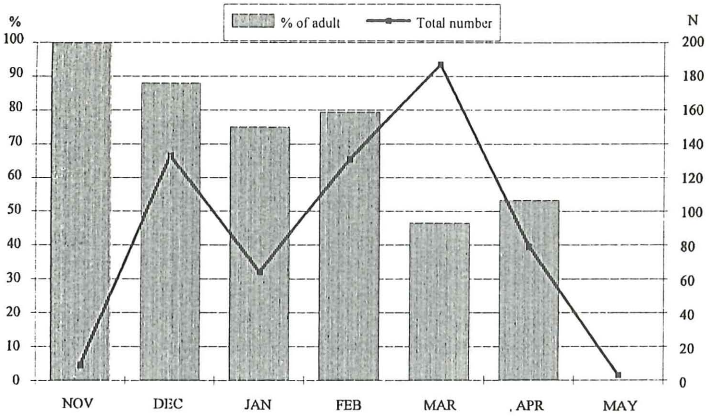

Fig. 2. Number of Long-tailed Ducks (N) and proportion (%) of adult birds in the material collected during particular months of the whole period of study. Percentage not shown for May because of small sample size.

Månatlig fördelning av antal alfåglar som drunknat i fisknät (heldragen linje; N) och andel adulta individer (staplar; %) i Gdanskbukten. Procentstapel för maj utelämnad på grund av litet stickprov.

February and March (Fig. 2, Table 3). This confirms the views of a 2-peak temporal distribution of the Long-tailed Ducks in the Baltic wintering grounds (Mathiasson 1970, Górski & Strawiński 1986, StrawiÒski 1990, Meissner & Maracewicz 1993). The Velvet Scoter, on the other hand, showed only one peak in February (Fig. 3, Table 4). This pattern resembles that observed in the Gulf of Gdańsk (Górski & Strawiński 1986, Strawiński 1990, Meissner 1993).

Scaups were collected almost exclusively in March (98%), while Common Scoters were numerous in by-catches in November (20%) and in February and March (25% and 27%, respectively). A very similar two-peak temporal distribution of the wintering Common Scoters was observed in the Gulf (Manikowski 1968, Meissner 1993). Eiders displayed two peaks, the first one in December (42%) and the second one in March (28%). The first Eiders were found in nets in November and the last in April. Field observations in the Gulf offer a similar picture, but the peaks are slightly shifted in time (January and February/March) (Meissner & Sikora 1993). This may be related with local and inter-seasonal differences of Eider wintering phenology in the Gulf.

Age and sex proportions

In the catch of the Long-tailed Duck, adults predominated (68%) and among them the males (Table 3). During the successive months of the wintering season the share of adults gradually dropped from 100% in November to about 50% in March and April (only 3 individuals were picked up in May). These proportions were mainly due to the share of males, being almost 90% at the beginning and only about one third towards the end of the season. The change in the share of females was not as distinct as the season passed. Young Long-tailed Ducks drowned with

Table 3. Number (%) of Long-tailed Ducks drowned in different months during the whole period of study.

Månatlig fördelning av fisknätsdrunknade alfåglar av olika kön och ålder i Gdanskbukten.

Month	Total		Adult (%)		Immature (%)	
	number	(%)	males	females	males	females
Nov	9	(1.5)	88.9	11.1	0.0	0.0
Dec	133	(21.9)	63.9	24.1	5.3	6.0
Jan	64	(10.6)	46.9	28.1	6.3	3.1
Feb	131	(21.6)	42.2	25.2	6.1	14.5
Mar	187	(30.9)	32.6	13.9	17.1	34.2
Apr	79	(13.0)	35.4	17.7	30.4	16.5
May	3	(0.5)	100.0	0.0	0.0	0.0
Sum (%)	606	(100)	286 (47.2)	124 (20.5)	75 (12.4)	106 (17.5)

Note: Age and/or sex of some birds has not been noted. *Ålder och/eller kön har inte registerats för vissa fåglar.*

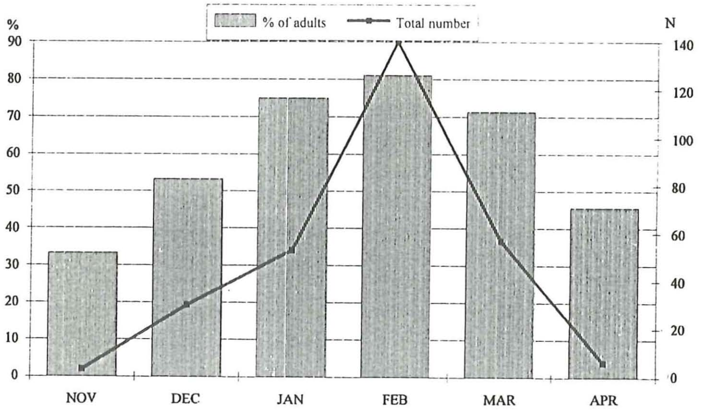

Fig. 3. Number of Velvet Scoters (N) and proportion (%) of adult birds in the material collected during particular months of the whole period of study.

Månatlig fördelning av antal svärtor som drunknat i fisknät (heldragen linje; N) och andel adulta individer (staplar; %) i Gdanskbukten.

increasing frequency in the consecutive months (Fig. 2, Table 3).

The age-sex structure of the Velvet Scoter was similar. Almost two thirds of the total were adults, 46% being males (Table 4). The changes in age-sex groups in consecutive months were less distinct in the Velvet Scoters than in the Long-tailed Duck. Adult Velvet Scoters tended to show lower proportions at the beginning and end of the season, with the maximum (81%) in January (Fig. 3, Table 4).

In Scaups the proportions of adults and immatures, females and males were fairly even, with a slight predominance of adults. As already mentioned, the Scaups appeared only once in large numbers (in March 1988), hence the analysis of age and sex structure refers only to that period. Females were the most common sex among the adults, while males were more common among immatures (Table 1).

Among the Common Scoters and Eiders young birds predominated (71% and 67%), with an equal proportion of the sexes within both age groups (Table 1). In both species the share of immature birds tended to increase in the consecutive months of the season (Table 5).

A comparison of the age-sex structure of birds drowned in fishing nets with that observed during field counts in the Gulf is only partially possible. In the field it is usually possible to distinguish only two "age-sex" groups, i.e. adult males and the rest (adult females plus juveniles), hence the incomplete data (Nilsson 1970). The material collected in the present study, on the other hand, provides detailed information on the subject, at least for the most numerous species, thus constituting a valuable supplement to field studies. However, we lack enough information about possible differences between age groups and sexes concerning their vulnerability to fishing nets and the ensuing winter losses. Hence only adult males can be analysed.

Field counts of all Long-tailed Ducks in the Gulf

Table 4. Number (%) of Velvet Scoters drowned in different months during the whole period of study.

Månatlig fördelning av fisknätsdrunknade svärtor av olika kön och ålder i Gdanskbukten.

Month	Total		Adult (%)		Immature (%)	
	number	(%)	males	females	males	females
Nov	3	(1.0)	33.3	0.0	33.3	0.0
Dec	30	(10.4)	50.5	3.3	16.7	20.0
Jan	53	(18.3)	56.5	24.5	11.3	7.5
Feb	140	(48.4)	50.7	20.7	12.1	15.7
Mar	57	(19.7)	26.3	19.3	29.8	24.6
Apr	6	(2.1)	0.0	33.3	33.3	33.3
Sum (%)	289	(100)	132 (45.7)	56 (19.4)	48 (16.6)	48 (16.6)

Note: Age and/or sex of some birds has not been noted. *Ålder och/eller kön har inte registerats för vissa fåglar.*

Table 5. Number of Common Scoters and Eiders and proportion of immatures drowned in different months during the whole period of study.

Antal i fisknät drunknade sjöorrar och ejdrar, samt andel ungfåglar under olika månader.

	Common Scoter		Eider	
Month	Total	% immatures	Total	% immatures
Nov–Dec	23	47.8	33	63.6
Jan–Feb	28	71.4	14	64.3
Mar–Apr	27	92.6	22	77.3

in the winter months (December–February) show that adult males constitute from 60% (in sheltered bays) to 85% (in open areas, e.g. the region of Hel and the Vistula Estuary, from where the birds caught in nets originated (Fig. 1, Meissner & Maracewicz 1993). This should be compared to the distinctly lower estimate based on drowned birds, fluctuating from 54% in February to 64% in December (Table 3). This difference suggests that adult males avoid fishing nets.

The same conclusion is obtained for the Velvet Scoter when comparing the share of adult males present in the Gulf (about 70%; Meissner 1993) with their share among those drowned in nets (about 50%; Table 4), and also for the remaining species analysed. It is possible that a greater proportion of juveniles than of adult males are used for consumption. This would overestimate the share of adult males in the material collected and strengthen the suggestion that adult males learn to avoid nets.

Table 6. Estimated number of diving birds drowned in nets in the Gulf of Gdańsk during one season.

Uppskattat antal fåglar som drunknat i fisknät i Gdanskbukten under en säsong.

	1973/74	1987/88	Total
No. collected in 2 ports * *Antal insamlade i 2 hamnar* *	511	288	799
No. drowned (2 ports) *Antal drunknade (2 hamnar)*	730	411	1141
No. of registered motor boats (2 ports) *Antal registrerade motorbåtar (2 hamnar)*	9	6	15
Mean no. drowned per boat *Medeltal drunknade per båt*	81	68	76
Total no. of motor boats registered *Totala antalet registrerade motorbåtar*			
whole Polish part of the Gulf *hela polska delen av bukten*			230
west of Vistula mouth ** *väster om Vistulas mynning* **			82
Total no. of birds drowned *Totala antalet drunknade fåglar*			
whole *hela*			17 480
western part *västra delen*			13 832

* Estimated at 70 % of those drowned.
Uppskattat till 70 % av antalet drunknade.

** The birds wintering in this area are censused regularly.
Fåglarna som övervintrar i detta område räknas regelbundet.

Mortality of marine birds in fishing nets

Data obtained in the 1973/74 and 1987/88 seasons, when material was collected most regularly, calling at the fishing berth 2–3 times per week throughout the whole season, were taken as the basis for calculations. In the opinion of the fishermen, during these two seasons, 65–75% of all the birds caught in the nets were collected. After an appropriate correction (assuming that 70% of netted birds were collected), the number of drowned birds per boat was estimated at 76. The number of birds caught in the nets by all the boats registered in the Gulf (230) could then be calculated (Table 6). The result was that about 17 500 diving birds die in the nets in the Polish part of the Gulf of Gdańsk during one season. Of this total, about 13 800 birds are lost in nets in the western part of the Gulf (to the west of the Vistula Estuary) for which numbers of wintering birds are available. These 13 800 birds constitute about 15% of the maximum number of birds noted here during the counts.

Table 7 gives estimates of the numbers lost in nets during a single season. Their percentage share in the material available was taken as the basis. The results obtained have been compared with the estimated numbers of the particular species in the western part of the Gulf. This comparison suggests that birds caught in nets in the western part of the Gulf constitute about 10–20% of the peak numbers recorded in field counts in the area.

An exception is the Eider where the estimated number of individuals lost in the nets annually exceeds the maximum number of birds noted during

Table 7. Estimated number of drowned birds among the five most common diving ducks in the Gulf of Gdańsk during one winter season.

Uppskattat antal fåglar av de fem vanligaste dykänderna som drunknat i nät under en vinter i Gdanskbukten.

Species *Art*	% share whole* *% andel hela**	No. drowned	western** *Antal drunknade västra***	Est. winter peak no.*** *Uppsk. högsta vinterantal****		% drowned of peak no. *% drunknade av högsta antal*
Clangula hyemalis	48.3	8443	6681	30–40000	MM	16.7–22.3
Melanitta fusca	23.0	4020	3181	14800	M	21.5
Aythya marila	7.7	1346	1065	10000	Mi	10.6
Melanitta nigra	6.2	1084	858	4200	M	20.4
Somateria mollissima	5.5	961	761	500	MS	152.2
Other species *Andra arter*	9.3	1626	1286			

* Whole Polish part of the Gulf of Gdańsk. *Hela polska delen av Gdanskbukten*

** Western part of the Gulf (west of Vistula mouth). *Västra delen av bukten (väster om Vistulas mynning)*

*** References *Referenser*: MM – Meissner & Maracewicz (1993), M – Meissner (1993), Mi – Michno et al. (1993), MS – Meissner & Sikora (1993)

the counts. Either the estimated number of this species in the Gulf is too low, or the share of birds in transit substantially increases the overall number of Eiders staying in the region. This is backed by the fact that the largest winter concentration of this species in the Western Palearctic (about one million birds) is relatively near by (on the Danish coast; Laursen 1989). Because of the same reason, it is possible that the estimates of mortality rate of the other common species also are too high.

Despite all the reservations below, the estimated number of birds lost in fishing nets in the Gulf of Gdańsk, based on material collected over 8 years, does not seem overestimated. Kieś & Tomek (1990) give a much higher figure – 250 birds caught in nets per season and boat, and the total number of birds lost in fishing nets in one port alone (Kuźnica, 15 boats) as 3 750. Kowalski & Manikowski (1982) counted 581 birds drowned in one season in fishing nets from Dziwnów. Given a maximum number of three boats fishing with ground nets we have no less than 194 birds per boat. The basis for calculation in the present paper is much lower, 76 birds/boat/season. In fact, the average number of birds caught in nets by the active crew of one boat, was higher. In the 1973/74 and 1987/88 seasons, 1 141 birds were caught in nets set by 8 regularly working boats from Orłowo and Sopot, i.e. 143 birds/boat/season (Table 6). The maximum by-catch brought to the port after one net control by fishermen from Sopot on 20–22 February 1974 amounted to 97 birds, of these 50 Long-tailed Ducks, 32 Velvet Scoters, 10 Common Scoters, three Crested Grebes, one Red-necked Grebe *Podiceps griseigena* and one Red-breasted Merganser *Mergus serrator*. Durinck et al. (1993) reports that 340 Velvet and Common Scoters were caught in one night in 120 fishing nets set on Danish coastal waters near Hanstholm, North Sea.

Estimating mortality of marine birds in fishing nets in the Gulf of Gdańsk during the whole post-breeding period is associated with several problems. First, the number of birds drowned in nets is only an estimate of the actual number. This is because not all drowned birds are reported. Some are utilized as food for foxes and minks or even humans. Furthermore, fishing effort (number of nets/days per season), related with fishing profitability as well as weather conditions (storm and ice-bound periods), considerably influence the by-catch size.

Types of nets used and areas of their setting also strongly affect the numbers of killed birds. Most dangerous for diving birds are nets of mesh-size exceeding 35 mm, set in shallow water (up to 20 m) in some food-attractive regions (e.g. river mouths, banks, etc.). In the nets set at depth exceeding 30 m (max. 65 m) only single Long-tailed Ducks and Common Guillemots were found. Bottom diving birds are most threaten by nets set loose (not strained; e.g. flatfish nets) or loosen by storms. A majority of birds collected (although detailed data are lacking) drowned in nets used for flatfish, cod and salmon. Herring nets are relatively safe because of fine mesh-size, unless set loose in very shallow water. The number of drowned birds usually increased after a storm since birds concentrated closer to shore, the nets came loose and water transparency dropped (making the nets difficult to perceive).

A fundamental difficulty in the quantitative assessment of the mortality of marine birds in fishing nets is also the lack of data on the total number of birds in the Gulf during the whole post-breeding season. Long-term counts by the Waterbird Research Group "Kuling" (Gdańsk University's Department of Vertebrate Ecology and Zoology) suggest that the total number of individuals, appearing for short periods in the waters of the Gulf, substantially exceeds maximum numbers noted during counts. Not knowing the proportion of the transit to stationary fraction it is impossible to estimate the global number of birds of particular species in the Gulf of Gdańsk during the season.

It is for these reasons that any attempt at estimating the mortality of birds in fishing nets in the Gulf can only be of an approximate character. This naturally refers to maximum numbers of particular species of birds observed in the Gulf. The more mobile the species, i.e. the more individuals there are which belong to the transit fraction, the lower is the true mortality of birds lost in fishing nets.

Irrespective of the accuracy of the results, there is no doubt that fishing activities (especially set-nets) in the Gulf of Gdańsk result in substantial losses among the diving birds wintering here in large numbers. In recent years this has been a much stronger anthropogenic mortality factor than oil pollution.

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Sammanfattning

Drunknade sjöfåglar i fisknät i Gdanskbukten: antal, artsammansättning, köns- och åldersfördelning.

Denna undersökning analyserar antal, artsammansättning, köns- och åldersfördelning av sjöfåglar drunknade i fisknät i Gdanskbukten under vintermånaderna 1972–1976 och 1986–1990. Totalt undersöktes 1254 fåglar av 24 arter. Av dessa arter var 11 dykänder, 4 lommar, 4 alkor, samt 3 doppingar. De två i särklass vanligast fångade arterna var alfågel (48,3%) och svärta (23,0%), därefter följde bergand (7,7%), sjöorre (6,2%), ejder (5,5%), skäggdopping (2,2%) och vigg (1,5%). Övriga arters andel understeg 1 % av totala fångsten. Generellt tycks artsammansättningen av drunknade fåglar återspegla sammansättningen övervintrande sjöfåglar. Undantagen är knipa, vigg och sothöna, som samtliga fångades i mindre antal än förväntat, samt ejder som fångades i större antal än förväntat. Orsakerna till dessa avvikelser kan troligen förklaras av artskillnader i överlapp mellan huvudsakliga födosöksområden och intensivt utnyttjade fiskeområden. Flera arter uppvisar stora mellanårsskillnader i antal, varav några arter uppvisade långtidstrender. Sålunda ökade andelen fångade alfåglar (från 42% 1972–1974 till 65% 1989/90), medan andelen svärtor minskat drastiskt (från 35% 1972–1974 till 4% 1989/90). Ålders- och könsfördelning av drunknade fåglar varierade kraftigt mellan arter och mellan månader inom arter. Adulter var vanligast hos alfågel (68%) och svärta (65%), medan juveniler dominerade bland ejdrar (71%) och sjöorrar (67%). Hanar var dominerande kön hos både alfågel och svärta, men andelen adulta hanar som drunknade i fisknät var dock lägre än observerat i den övervintrande populationen alfåglar och svärtor. En trolig orsak till denna skillnad är att gamla individer är skickligare på att undvika fisknät. Totalt uppskattas att 17 500 sjöfåglar drunknar årligen i fisknät i Gdanskbukten, vilket motsvarar ca 10-20% av den övervintrande populationen inom området. Sålunda uppskattas 8400 alfåglar, 4000 svärtor, 1300 bergänder, 1000 ejdrar och 1000 sjöorrar gå drunkningsdöden till mötes i fisknät. Även om dessa uppskattningar är något osäkra råder det inget som helst tvivel om att fiskenäringen orsakar stora förluster av sjöfåglar i Gdanskbukten. För tillfället är dessa förluster mycket större än de som orsakas av olja.

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Bivråkens *Pernis apivorus* överlevnad och beståndsutveckling i Sverige

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Abstract

The survival rate of the Honey Buzzard *Pernis apivorus* was estimated using recovery data from 140 ringed nestlings that later were found dead or shot. The annual survival rate was 48.8% in the first year, 85.8% in the second year and 86.0% thereafter. By only including a subset of 53 Honey Buzzards found dead, the survival was 58.1% in the first year, 85.5% in the second year and 91.7% thereafter. For a stable population and under the assumption that Honey Buzzards breed for the first time when two years old, the reproduction must be 0.67 young/pair and year. Without hunting, however, a reproductive rate of 0.34 young per pair is enough for keeping a stable population. With knowledge of reproduction and survival rates, the stability of the population can be estimated. In Uppland, central Sweden, the reproductive rate was 0.60 fledged young per established pair in 1986-91. However, figures from counts of migrating Honey Buzzards at Falsterbo indicate a lower reproductive rate – possibly around 0.30 fledged young/pair –and this is probably a more representative reproduction value for the total Swedish population. A reproductive rate around 0.3 young/pair and year is close to the estimated value for a stable population without hunting.

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Inledning

Den svenska bivråkspopulationen uppskattades till ca 8000 par i början av 1980-talet (Nilsson 1981). Arten var dock troligen vanligare under 1960- och speciellt 1950-talet, då mycket höga sträcksummor noterades vid Falsterbo (Ulfstrand 1958). Vid de standardiserade räkningarna i Falsterbo konstaterades en minskning i antalet sydflyttande bivråkar under perioden 1973–1992 (Roos 1991a och Roos muntl.), vilket torde ha återspeglat ett minskande bestånd i Sverige. Bivråkens minskande trend har varit en bidragande orsak till att arten numera är rödlistad i Sverige (Ahlén & Tjernberg 1992). Vår kunskap om artens grundläggande biologi är emellertid fortfarande bristfällig.

I denna rapport presenteras skattningar av bivråkens överlevnad baserade på återfynd av ringmärkta boungar. Dessutom har prognoser om beståndsutvecklingen gjorts utifrån några valda värden på häckningsframgång. De skattade överlevnadstalen diskuteras också i relation till antalet sydflyttande bivråkar räknade vid Falsterbo.

Material och metoder

Fram till och med 1992 hade Ringmärkningscentralen erhållit meddelanden om 140 återfynd av i Sverige pull.- och juv.-märkta bivråkar (138 ungar märkta i boet samt två juv. märkta i september), och där återfyndskoden för dessa fåglar indikerade att de skjutits eller att fågelkroppen hittats (= funnen död). Koderna för funna individer säger inget om hur länge fågeln kan ha legat död innan fyndet gjordes, men med den normalt snabba förruttnelseprocessen som sker i naturen så försvinner döda djurkroppar vanligtvis inom några veckor (se t.ex. Pain 1991). Vi har vidare antagit att alla bivråksungar kläckts fram 1 juli (vid en undersökning i Uppland 1986-91 var mediandatum för 1:a äggets kläckning 6 juli, som tidigast 24 juni och som senast 22 juli; Tjernberg opublicerat). De återfunna fåglarna kan således åldersbestämmas med en säkerhet på cirka ±20 dagar.

Överlevnaden har beräknats enligt North & Morgan (1979). Modellen utgår från att överlevnaden är åldersspecifik de första två åren, men konstant för individer äldre än två år. Flera undersökningar styr-

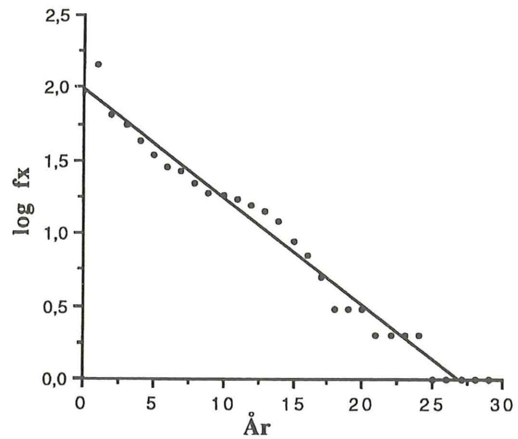

Fig. 1. Överlevnadskurva för bivråkar ringmärkta i Sverige som boungar, grundat på återfynd av 140 döda fåglar (skjutna eller döda på annat sätt). Linjens ekvation är y=2,0069–0,075779x; R=0,98511.

Survival of Swedish Honey Buzzards based on recoveries of 140 dead birds (shot or found dead).

Tabell 1. Överlevnad för bivråkar, grundat på återfynd av skjutna fåglar eller fåglar funna döda (n = 140).

Survival of Honey Buzzards, based on recoveries of shot birds or birds found dead (n = 140).

fx Antal levande ex. *Number of live birds*	log fx	Början av år *At the beginning of year*
140	2,14612804	1
65	1,81291336	2
55	1,74036269	3
44	1,64345268	4
35	1,54406804	5
28	1,44715803	6
27	1,43136376	7
22	1,34242268	8
19	1,27875360	9
18	1,25527251	10
17	1,23044892	11
16	1,20411998	12
14	1,14612804	13
12	1,07918125	14
9	0,95424251	15
7	0,84509804	16
5	0,69897000	17
3	0,47712125	18
3	0,47712125	19
3	0,47712125	20
2	0,30103000	21
2	0,30103000	22
2	0,30103000	23
2	0,30103000	24
1	0	25
1	0	26
1	0	27
1	0	28
0		29

ker detta överlevnadsmönster hos långlivade fåglar, eventuellt med undantag för mycket gamla individer (t.ex. Lack 1946, Henny & Wight 1969, Fordham & Cormack 1970, Clutton-Brock 1988, Newton 1989). Med hjälp av de skattade överlevnadsvärdena har vi räknat fram förväntad ungproduktion vid stabil populationsstorlek samt förväntad populationsförändring med observerad ungproduktion, enligt metoder redovisade av Henny m.fl. (1970).

Ungfågelproduktionen har skattats dels med hjälp av data från bostudier i Uppland 1986–1991 (Tjernberg, in prep.), dels utifrån resultaten av sträckfågelstudier i Falsterbo höstarna 1977–1986 (Søgård & Østerby 1989) samt 1986–1992 (Kjellén 1993). Våra resultat har även jämförts med data från de standardiserade sträckfågelräkningarna vid Falsterbo 1973–1992 (Roos 1991b och Roos muntl.). Vid de uppländska bostudierna har termen "lyckad häckning" avsett att minst en unge blivit flygg med en ålder av cirka 55 dygn.

Resultat

Hos bivråken är den beräknade överlevnaden det första året 48,8% (SE ± 4,3%), det andra året 85,8% (SE ± 4,2%) och de följande åren 86,0% (SE ± 1,3%) (Tabell 1 och Fig. 1). Dessa siffror grundar sig på 140 ringmärkningsfynd, av totalt cirka 1560 ringmärkta boungar, gjorda under nästan 70 års tid. Det äldsta återfyndet är en bivråk som märktes 1922 och det senaste en fågel märkt 1985. Den äldsta svenska bivråken blev drygt 28 år gammal och en bivråk märkt i Tyskland blev närmare 29 år (Staav 1989). Dessa tillhör de högsta åldrar som uppmätts bland vilda fåglar.

Av de 140 återfunna bivråkarna var 87 skjutna och 53 funna döda (sannolikt död på annat sätt än skjuten). Överlevnadstiden för dessa två grupper av bivråkar är signifikant skilda (medelvärde 932 resp. 1677 dagar, t=2,30, P=0,023). Andelen skjutna bivråkar har, av återfyndsrapporterna att döma, blivit färre under de senaste årtiondena. Mellan 1922–1969 angavs 76 ha blivit skjutna och 32 funna döda, medan motsvarande siffror för perioden 1970–1990

Tabell 2. Överlevnad för bivråkar, grundat på återfynd av bivråkar som hittats döda (n = 53).

Survival of Honey Buzzards, based on recoveries of birds found dead (n = 53).

fx Antal levande ex. *Number of live birds*	log fx	Början av år *At the beginning of year*
53	1,72427587	1
28	1,44715803	2
23	1,36172784	3
21	1,32221929	4
16	1,20411998	5
13	1,11394335	6
13	1,11394335	7
13	1,11394335	8
12	1,07918125	9
11	1,04139269	10
10	1.00000000	11
10	1,00000000	12
9	0,95424251	13
9	0,95424251	14
7	0,84509804	15
5	0,69897000	16
4	0,60205999	17
3	0,47712125	18
3	0,47712125	19
3	0,47712125	20
2	0,30103000	21
2	0,30103000	22
2	0,30103000	23
2	0,30103000	24
1	0	25
1	0	26
1	0	27
1	0	28
0		29

var 11 resp. 21 (χ^2=13,99, df = 1, P<0,001). Andelen dödade bivråkar genom jakt har möjligen fortsatt att minska även under den senare 21-årsperioden; 43,5% rapporterades skjutna mellan 1970–1979 (n=23) och 11,1% mellan 1980–1990 (n=9). En skattning av överlevnaden (± SE), baserad på de 53 vråkarna som hittats döda, visar att 58,1% (± 6,8%) överlevde det första året, medan överlevnaden det andra året var 85,1% (±6,3%) och de följande åren 91,7% (±1,0%) (Tabell 2 och Fig. 2).

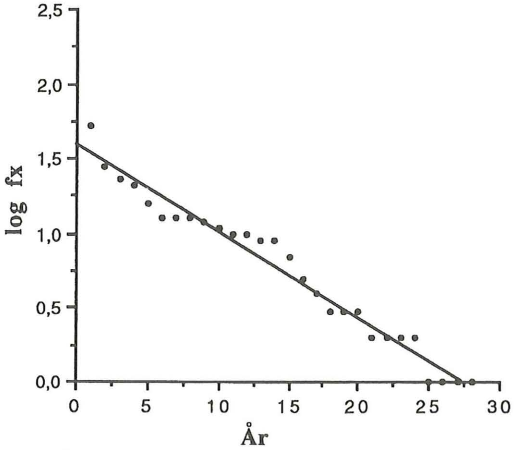

Fig. 2. Överlevnadskurva för bivråkar ringmärkta i Sverige som boungar, grundat på återfynd av 53 döda fåglar (skjutna fåglar ej inkluderade). Linjens ekvation är y = 1.5845 – 0.056059x; R = 0.97843.

Survival of Swedish Honey Buzzards based on recoveries of 53 birds found dead (shot birds excluded).

Det råder osäkerhet om vid vilken ålder bivråken häckar första gången, men vi antar här att detta normalt sker vid slutet av dess andra levnadsår (d. v. s. under tredje kalenderåret). I det svenska materialet omfattande 140 återfunna bivråkar finns endast två fynd gjorda i Europa av bivråkar i sitt andra kalenderår, medan det finns tio fynd i Europa av bivråkar i sitt tredje kalenderår (Anon. 1992, se även Münch 1955, Gamauf 1984 och Forsman 1984). Med förutsättningarna 48,8% överlevnad första året, 85,8% andra och 86,0% de övriga åren, samt att första häckningen sker vid två års ålder, blir den nödvändiga produktiviteten, uträknad enligt den metod som angetts av Henny m.fl. (1970), 0,67 ungar per par och år. Om vi antar att bivråkarna inte avsiktligt dödas (d.v.s. skjuts) blir den nödvändiga produktiviteten för att upprätthålla en stabil population endast 0,34 ungar per par och år.

Med kännedom om överlevnadstal och ungproduktion kan stabiliteten hos populationer studeras (Henny m.fl. 1970). Av totalt 99 häckningsförsök i Uppland, fördelade mellan minst 47 olika par över sex år, lyckades i genomsnitt endast 35%, och i 36% av fallen (n=99) lade de studerade paren överhuvud taget inga ägg. I medeltal producerades 0,60 flygga ungar per etablerat par och år. Med denna årliga ungproduktion och med 48,8% överlevnad första året, 85,8% andra året och 86,0% de övriga åren blir populationstillväxten sannolikt negativ, –1,5% per år (med 95% konfidensintervall –5,9 till +3,3%, se Tabell 3). Om vi antar samma häckningsframgång, men att bivråkarna inte dödas genom jakt, d.v.s. överlevnaden är 58,1% första året, 85,1% andra året

Tab. 3. Överlevnad, nödvändig produktion vid stabil population samt populationstrend för bivråk i Sverige. Beräkningarna grundas på återfynd av ringmärkta boungar i Sverige samt på reproduktionsstudier i Uppland och flyttfågelsräkningar i Falsterbo.

Survival, essential reproduction at stable population and population trend for Honey Buzzards. The calculations are based on recoveries of ringed nestlings in Sweden, estimates of reproductive success in Uppland, and counts of migrating birds at Falsterbo.

	överlevnad 1:a året	överlevnad 2:a året	överlevnad adulter	nödvändig prod./år vid stabil pop.	pop. trend per år vid repr. 0,60 juv./par & år	pop. trend per år vid repr. 0,23 juv./par & år
	survival 1st year	*survival 2nd year*	*survival adults*	*essential repr./year at stable pop.*	*population trend per year with repr. of 0.60 juv./pair and year*	*population trend per year with repr. of 0.23 juv./pair and year*
	(%)	(%)	(%)	(juv./par)	(%)	(%)
Med jakt *With hunting*	48,8	85,8	86,0	0,67	–1,5	–9,2
95% konf. intervall	40,2–57,4	77,4–94,2	83,4–88.6	0,42–1,13	–5,2–+3,3	
Utan jakt *Without hunting*	58.1	85,1	91,7	0,34	+6,5	–2,6
95% konf. intervall	44,5–71,7	72,5–97,7	89,7–93,7	0,18–0,64	–0,6–+12,4	

och 91,7% övriga år, skulle populationen däremot öka med 6,5% årligen (Tabell 3).

Vid sträckfågelstudier i Falsterbo noterades en ungfågelandel på 10,9% under perioden 1977–86 (Søgård & Østerby 1989) och 13% under perioden 1986–92 (Kjellén 1993). Totalt för 16-årsperioden 1977–92 var andelen juvenila fåglar 10,2% (1986 års ungfågelandel enbart inkluderad från Kjelléns material), vilket svarar mot en genomsnittlig reproduktion på 0,23 juv. per par och år. De högre värdena för perioderna 1977–86 och 1986–92 jämfört med hela perioden 1977–92, beror på att den höga ungfågelandelen 1986 inkluderats i båda perioderna 1977–86 och 1986–92. Med en årlig reproduktion runt 0,23 flygga juv. per par och år skulle beståndet minska oavsett om det förekom jakt eller ej (–9.2% resp. –2.6% årlig minskning; se Tabell 3). Emellertid omkommer en okänd andel av ungfåglarna under flyttningen från boplatserna till Falsterbo. Den högre dödligheten det första jämfört med det andra levnadsåret är ca 37% med jakt och 27% utan jakt. En relativt stor del av dödligheten under det första levnadsåret sker troligen under de inledande veckorna av sydflyttningen. Om vi gissar att 20% av de flygga ungfåglarna omkommer innan de når södra Sverige, motsvarar Falsterbomaterialet en årlig reproduktion av 0,29 flygga juv. per par och år.

De standardiserade räkningarna vid Falsterbo visade på en signifikant minskande trend av utsträckande bivråkar för 20-årsperioden 1973–1992 (Fig. 3, $r^2=0,399$, $P=0,003$). Om detta överensstämmer med den verkliga minskningstakten för den svenska bivråkspopulationen blir den cirka 3,8% årligen för nämnda tidsperiod. Utesluts 1974 års höga sträcksiffra (11 000 ex) från Falsterbomaterialet erhålles fortfarande en klar signifikant minskning ($r^2 = 0,33$,

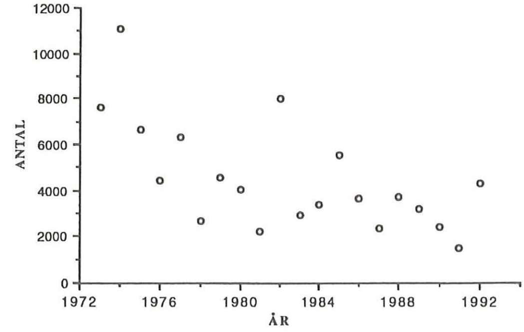

Fig. 3. Antalet utsträckande bivråkar vid standardiserade räkningar utförda vid Falsterbo 1973-92 (enligt Roos 1991b samt Roos muntl.).

Number of south-migrating Honey Buzzards at standardized counts at Falsterbo 1973–92.

P=0,01; cirka 3,1% årlig minskning 1973–1992). Fig. 3 visar dock att den huvudsakliga minskningen i antalet utsträckande bivråkar vid Falsterbo skedde under perioden 1973–81. En möjlig tolkning av Fig. 3 är därför att bivråkspopulationen har stabiliserat sig på en lägre nivå under senare tid. Om vi väljer det korrigerade värdet på den årliga ungfågelsandelen vid Falsterbo, cirka 0,3 ungar per par och år, som ett representativt mått på genomsnittlig årlig reproduktion för den svenska stammen 1977–92, så kan konstateras att detta hypotetiska värde ligger nära den reproduktion som krävs för en stabil population utan jakt enligt våra överlevnadsberäkningar (0,34 juv. per par och år).

Diskussion

Den sexåriga studien i Uppland visade att bivråkarna producerade 0,60 flygga ungar per etablerat par och år (Tjernberg, opublicerat material). Jørgensen (1989), som redovisade data från 103 bon, angav att häckningsframgången i Danmark var 55%. Antalet flygga ungar var enligt samma undersökning 0,9 per påbörjad häckning och år, men denna studie hade uteslutit etablerade par som ej lade ägg. Om "ägglösa" par utesluts från det svenska materialet blir därför de svenska och de danska reproduktionsvärdena synnerligen lika. I en sjuårig studie i Tyskland (1979–1985) var reproduktionen för 80 häckningsförsök i genomsnitt 0,59 flygga ungar per par och år och i genomsnitt 35% av de studerade paren (n=80) lade inga ägg (Kostrzewa 1987). Även dessa reproduktionsvärden är mycket lika de som konstaterades i Uppland. Undersökningen i Uppland genomfördes i huvudsak i för bivråken optimala habitat (lövskogsrika marker i anslutning till Mälaren), där reproduktionen kan tänkas ligga högre än genomsnittet i Sverige.

De åldersfördelningsstudier som genomförts hos höststräckande bivråkar vid Falsterbo (Søgård & Østerby 1989, Kjellén 1993) indikerar en lägre reproduktion än de ovan redovisade, och återspeglar förmodligen mer korrekt den genomsnittliga reproduktionen för den totala svenska bivråksstammen. Emellertid måste Falsterbosiffrorna kompenseras för en viss dödlighet som sker hos ungfåglarna under flyttningen mellan boet och Falsterbo (se under Resultat). Å andra sidan menar Søgård & Østerby (1989) att ungfåglarna förmodligen är mer ledlinjeberoende än de gamla bivråkarna och är därför troligen överrepresenterade vid Falsterbo.

Bivråken är en långlivad fågel. Typiskt för långlivade fåglar är att de har låg ungfågelproduktion - bivråken är i detta avseende närmast jämförbar med t.ex. kungsörnen *Aquila chrysaetos* (Tjernberg 1983), storlommen *Gavia arctica* (Andersson m.fl. 1980) och tranan *Grus grus* (Bylin 1987). Eftersom långlivade fåglar med låg reproduktionstakt är betydligt känsligare för förföljelse och jakt än kortlivade arter med hög reproduktion, kan förhållandevis små skillnader i jakttryck medföra stora ändringar i stammarnas storlek, speciellt om jakten riktas mot de adulta individerna (Newton 1979). Om jakten på bivråk slår jämnt över alla åldersklasser borde de gamla fåglarna drabbas förhållandevis kraftigt, eftersom sydflyttande svenska bivråkar enligt undersökningen i Uppland till 77% och enligt Falsterbostudierna 1977–1992 till 90% består av adulter (Tjernberg, in prep. resp. Søgård & Østerby 1989, Kjellén 1992), och eftersom det bland vårflyttande bivråkar i stort sett saknas fåglar i andra kalenderåret. Av de 140 återfunna bivråkarna var emellertid överlevnadstiden väsentligt lägre för de skjutna än för de naturligt avlidna (se under Resultat). Detta indikerar att unga bivråkar (fåglar i sitt första kalenderår och möjligen även fåglar i sitt andra och tredje kalenderår) är mer oförsiktiga under flyttningen än gamla vråkar. I detta sammanhang bör påpekas att vårjakten, bl.a. i Medelhavsområdet, sannolikt är allvarligare än höstjakten eftersom nästan samtliga nordflyttande bivråkar är presumptiva häckfåglar.

Det avsiktliga dödandet av bivråkar har, enligt rapporterade fyndomständigheter till Ringmärkningscentralen, minskat betydligt mellan perioderna 1922–1969 och 1970–1990 (70,4% resp. 34,4%). En annan möjlighet är dock att skjutna bivråkar ej rapporteras i samma omfattning som tidigare, eftersom arten numera är fredad i de flesta länder. Om de allt färre rapporterna om skjutna bivråkar i realiteten speglar ett minskat jakttryck borde detta återspeglas i de standardiserade räkningarna vid Falsterbo. Den stabilisering som förefaller ha skett i antalet höstflyttande bivråkar under 1980-talet (Fig. 3) kan vara en indikation på att jakten verkligen har minskat i omfattning.

Resultaten från föreliggande undersökning bygger på 140 återfynd av ringmärkta boungar av bivråk. Materialet är litet vilket innebär stor osäkerhet vid överlevnadsberäkningar (Tabell 3). Den redovisade analysen indikerar dock att jakt på bivråk kan ha betydelse för artens populationsutveckling, samtidigt som mycket tyder på att jakten har minskat i omfattning under de senaste årtiondena (se även Saurola 1985). För att bivråksbeståndet skall hålla sig på en stabil nivå eller möjligen åter öka, bör den utländska jakten dock upphöra helt. I en överskådlig framtid är nämligen jakt av vuxna fåglar ingalunda den enda hotbilden för arten. Förändrad markanvändning inom skogs- och jordbruk kommer sannolikt att leda till försämrad häckningsframgång genom sämre tillgång på bytesdjur. Detta kan på sikt få allvarliga konsekvenser för bivråkens populationsutveckling.

Tack

Tack till personalen på Ringmärkningscentralen i Stockholm för stor vänlighet vid framtagandet av data och till Tomas Pärt och Sven G. Nilsson för synpunkter på en tidigare version av uppsatsen. Medel till statistiska dataprogram har erhållits från Kungl. Vetenskapsakademiens Hierta-Retzius fond och medel till studier av bivråkens reproduktionsframgång från WWF.

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Summary

Survival and population development of the Honey Buzzard Pernis apivorus *in Sweden.*

Up to 1992, 140 Honey Buzzards, ringed as nestlings in Sweden, were reported as found dead or shot. The annual survival rate (±SE) was estimated at 48.8% (±4.3%) in the first year, 85.8% (±4.2%) in the second year and 86.0% (±1.3%) thereafter (Table 1 and Fig. 1; for calculating methods, see North & Morgan 1979).

Out of the 140 recoveries, 87 Honey Buzzards were reported as shot and 53 as found dead. The life span for these two categories of birds were significantly different (mean life span 932 and 1677 days, respectively; t = 2.30, P = 0.023). The number of shot Honey Buzzards seems to have decreased during the study period. Between 1922 and 1969, 70.4% (n=108)

were reported as shot, whereas only 34.4% were reported as shot between 1970 and 1990 (n=32) ($\chi^2=13.99$, df=1, $P\leq0.001$). The survival rate (±SE) of the 53 Honey Buzzards reported as "found dead" (shot birds excluded) were 58.1% (±6.3%) in the first year, 85.1% (±6.3%) in the second year and 91.7% (±1.0%) thereafter (Table 2 and Fig. 2).

Assuming that the Honey Buzzards reproduce from their third calender year (two years old) and have a survival rate of 48.8% in the first year, 85.8% in the second and 86.0% in following years, the necessary reproductive rate for maintaining a stable population should be 0.67 fledged young per pair and year (for calculation methods, see Henny et al. 1970). If we assume that the buzzards are not shot, the necessary reproductive rate for maintaining a stable population is only 0.34 fledged young per pair and year.

When the survival rate and production of young are known, it is possible to estimate the stability of populations (Henny et al. 1970). In Uppland, central Sweden, the reproduction was 0.60 fledged young per pair and year in 1986–91 (99 breeding attempts were studied, including pairs that laid no eggs; Tjernberg, unpubl.). With a reproductive rate of 0.60 and with 48.8% survival in the first year, 85.8% in the second year and 86.0% thereafter, the population probably should decrease (Table 3). If we assume the same reproductive rate, but that the Honey Buzzards are not shot, the population should increase (Table 3). However, the observed reproductive rate in Uppland is probably higher than the average for Sweden. The proportion of young birds among migrating Honey Buzzards at Falsterbo, south Sweden, in the autumns 1977–92 (Søgård & Østerby 1989, Kjellén 1993) indicated a mean reproductive rate of 0.23 fledged young per pair and year. However, some young Honey Buzzards probably die before reaching south Sweden. If we assume that 20% of the fledged birds died before they reached Falsterbo, the yearly reproductive rate should be 0.29 fledged young per pair. This is a value quite close to the necessary reproductive rate for maintaining a stable population, provided that the hunting of the Buzzards is at a low level (see above).

The standardized counts of south-migrating birds at Falsterbo showed a significantly decreasing trend for Honey Buzzard between 1973 and 1992 (Fig. 3, $r^2=0.399$, $P=0.003$). Fig. 3 shows, however, that the main decrease was during 1973–81. A possible interpretation of Fig. 3 could be that the Swedish Honey Buzzard population has stabilized at a lower level during the last decade, and that decreased hunting could be responsible for this. We assume that the corrected value of 0.3 young per pair as derived from south-migrating Honey Buzzards at Falsterbo reflects the mean reproductive rate for the total Swedish Honey Buzzard population during 1977–92. According to our survival estimates (0.34 fledged young per pair and year) this hypothetical value is close to the necessary reproductive rate for a stable population without hunting.

The small sample (140 recovered Honey Buzzards) used in this investigation makes the survival estimates rather uncertain. Despite this, our analyses indicate that hunting of Honey Buzzards probably has a significant and negative effect on the development of the population. Furthermore, the analyses show that hunting probably has decreased during recent decades. For obtaining a stable/increasing population of the Honey Buzzard it is probably important that hunting is totally prevented, especially along the species migrating route across the Mediterranean countries.

Nya böcker *New books*

Redaktör ***Editor:*** **A. Hedenström**

R. Vaughan 1992: **In Search of Arctic Birds.** T & AD Poyser, London. 431 sid. Ill. av G. Brusewitz. Medlemspris i Naturbokhandeln: 306 kr. ISBN 0-85661-071-2.

De polara trakterna hör till de senast upptäckta och minst utforskade områdena på jorden både vad gäller geografiskt och zoologiskt material. Därmed är även fåglarna i dessa trakter dåligt kända och än i dag kan arktisfarare göra nya upptäckter. I *In Search of Arctic Birds* tar Richard Vaughan sig an uppgiften att sammanställa det mesta som rör arktisk ornitologi, dvs vad vi vet om fåglarna som lever i polarnära områden på norra halvklotet. Detta är sannerligen ingen liten uppgift, men författaren lyckas riktigt bra att i 13 kapitel förmedla allt ifrån arktisornitologins historia till hur man numera kan resa till dessa avlägsna områden.

Boken börjar med en allmän översikt av arktiskt klimat, miljö och allmänt om fåglarna som lever där. Ett kapitel behandlar även hur folk som lever i dessa trakter jagade fåglar och deras mytologiska förhållanden till olika arter. Sedan övergår författaren till att i flera kapitel beskriva tidiga arktisfarares vedermödor och deras ornitologiska insamlingsarbete. Man undrar vad som drev dessa pionjärer till dessa ojästvänliga trakter och till deras bedrifter, men man gissar att viss nyfikenhet kopplad till chansen att genom sina upptäckter bli erkända hemma i England utgjorde drivkraften. För många av hjältarna som beskrivs i boken var engelsmän, även om författaren bemödat sig att även framhålla ornitologer från andra länder. Flera skandinaver är ju starkt förknippade med den arktiska ornitologins historia, t ex finlandssvenske A. E. Nordenskiöld som under Vegas färd utmed Sibiriens norra kust gjorde många intressanta fynd och dessutom förmodligen utrotade en hel population skedsnäppor!

Huvudpunkten i boken ligger på utbredning och häckningsfynd av fågelarterna i arktis, men även information om häckningsbiologi och flyttningsvägar presenteras. I tre kapitel behandlas ornitologiska skrifter om regionala fågelfaunor och en fyllig genomgång av studier utförda från den ryska och sibiriska tundran samt från områden mellan Alaska och Spetsbergen. Dessa genomgångar upprepar till viss del vad som redan sagts i tidigare kapitel. Avslutningsvis behandlas "fågelskådarens arktis" och fågelskydd.

Sammanlagt 40 kartor visar de behandlade områdena, men oftast får man tyvärr bläddra åtskilliga sidor för att hitta en i texten refererad karta. Bildmaterialet är ursprungligen av god kvalitet men de svartvita fotografierna har i trycket blivit alldeles för grå. Detta kompenseras emellertid mer än väl av Gunnar Brusewitz' utsökta teckningar.

Sammanfattningsvis är detta en mycket innehållsrik bok, även om dispositionen är något rörig och samma information presenteras ibland på flera ställen. Alla som har det minsta intresset av arktisk ornitologi bör ha den här boken på sin bokhylla.

ANDERS HEDENSTRÖM

Altenburg, W., E. Wymenga & L. Zwarts (eds) 1992. **Ornithological importance of the coastal wetlands of Guinea-Bissau.** WIWO-report nr. 26, Zeist. 166 sid. Pris: Dfl 40 (inkl. frakt).

Allt eftersom kunskapen om fågelskydd har ökat i Västeuropa har man även blivit mer medveten om bristen på kunskap om fåglarna under vinterhalvåret, och då speciellt de som övervintrar i Afrika. Som ett resultat av denna medvetenhet har på senare år flera studier av övervintrande fåglar gjorts i Afrika. Den rescencerade rapporten har kommit till som ett resultat av en Nederländsk expedition till Guinea-Bissau vintern 1986/87. Expeditionens syfte var att kartlägga förekomsten av fåglar som är knutna till kustmiljöerna och hur dessa utnyttjas. För att lättast kunna besöka de mest intressanta platserna i arkepelagerna vid flodmynningarna färdades man med båt som seglades från Nederländerna.

Rapporten är indelad i två delar, en på engelska och en på franska. Den engelska är på 114 sidor och består av fyra uppsatser som redan är publicerade i tidskrifterna *Ardea* och *Lutra*. Dessa uppsatser behandlar i tur och ordning (i) förekomsten och numerär av vadare, (ii) häckningsområden för vadare som övervintrar i Västafrika, (iii) fåglars utnyttjande av mangroveträsken och (iv) förekomsten av delfiner i de kustnära vattnen utanför Guinea-Bissau. Dessutom innehåller den engelska delen en kort introduktion, en uppsats om förekomsten av övervintrande tärnor, en artlista och en sammanfattning med rekommendationer om hur man skall bevara fågellivet i de områden som man har undersökt. I den franska delen av rapporten är endast sammanfattningen av respektive uppsats med. Däremot innehåller artlistan mer detaljerad information om de fåglar man sett.

Rapporten är välskriven och innehåller mycket information, vilket är att vänta om arbetena redan är fackgranskade och publicerade. Här finns grunddata föredömligt lättillgängliga i tabeller vilket är nödvändigt om man i framtiden skall kunna avgöra om det skett några förändringar i populationernas numerärer. Författarna till respektive artikel redovisar också jämförelser med data från andra platser i Afrika och Europa. Detta gäller både tätheten av fåglar och deras biometri. Vid jämförelser mellan lokaler både inom Guinea-Bissau och utanför finner man en en stor variation i tätheter av vadare. För att förklara denna variation har man relaterat tätheterna till typ av substrat och tätheten och typ av föda i dessa. Av de 15 funna vadararterna fann man att sex (Drillsnäppa, Småspov, Kustpipare, Större strandpipare, Roskarl och Storspov) kan mer eller mindre betraktas som specialister på att äta vinkarkrabbor.

För att spåra häckningsområdet för de övervintrande vadarna i Guinea-Bissau har man gjort en analys av de biometriska mått man har tagit i samband med ringmärkning. Här har man gjort en direkt jämförelse med fåglar övervintrande i Mauritanien och kommit fram till att bl a Större strandpipare, Kustpipare och Rödbena som övervintrar i Guinea-Bissau kommer från mer nordliga och östliga häckningsområden. Här finns även redovisat de återfynd som ringmärkningen har gett. Bland de många kontrollerna av redan märkta fåglar fanns t ex en Roskarl som var märkt som pull i Uppland.

Rapporten vänder sig främst till dem som är speciellt intresserade av födosöksekologi och populationers utbredning. För dessa kan rapporten betraktas som en unik dokumentation av de i Guinea-Bissau övervintrande fåglarna. Övriga ornitologer tror jag har lite utbyte av rapporten.

NOËL HOLMGREN

Bird Population Studies. Relevance to conservation and management. Redigerad av C.M. Perrins, J.-D. Lebreton & G. J. M. Hirons. Oxford University Press, Oxford. 683 sid. Först publicerad 1991, paperback-upplaga 1993. Medlemspris i Naturbokhandeln: 387 kr.

Fågelskyddet är ofta starkt beroende av "spektakulära" arter eller händelser med vilkas hjälp det tunga, vardagliga arbetet för att bevara fåglarna och deras miljöer kan åka snålskjuts. En del fåglar blir på detta sätt symobolarter som kan föra en hel sektor av fågelskydd framåt. Ett par exempel i Sverige är vitryggspetten och storken. Vitryggen representerar en hel naturtyp som håller på att försvinna och med den en lång rad mossor, lavar, svampar och insekter. Till vitryggens miljö av äldre skog med rikt inslag av död ved hör också andra fågelarter, som automatiskt gynnas om man kan bevara vitryggen. Storken har på liknande sätt lyfts fram som en symbol för ett äldre, mindre hårdexploaterat jordbrukslandskap, rikt på betade och slåttrade våtmarker. Symbolarterna varierar naturligtvis från plats till plats och även från en tid till en annan. I Nordamerika har nu under flera år "Spotted Owl" (som troligen kommer att döpas till fläckuggla på svenska) varit ett verkligt hett objekt i naturskyddsdebatten. Denna uggla är nära släkt med kattugglan och är obetydligt större. Den nordliga rasen *Strix occidentalis caurina* finns i gammal barrskog längs USA:s västkust och en sydlig ras finns sedan längre söderut, ner i Mexiko. Orsaken till att denna uggla kommit i fokus är att den minskat mycket kraftigt under bara fyra decennier och särskilt under de allra senaste femton åren. Orsaken till minskningen är att man infört klassiskt kalhyggesbruk i skogar som tidigare varit tämligen förskonade från hårdexploatering. Ugglan är helt beroende av vidsträckta bestånd av mogen, åldrig barrskog. Skogsbruket har nu medfört både en radikal föryngring av skogarna och en omfattande uppsplittring av de kvarvarande äldre skogsresterna. I slutet av 1700-talet var nära 70 % av dessa skogar äldre än 200 år, resten var yngre p.g.a. skogsbrand och stormfällning. I dag finns det få sammanhängande äldre skogspartier som är större än ugglans normala spridningsavstånd. Just kampen för att rädda en art av detta slag blir naturligtvis särskilt kontroversiell eftersom det rör sig om så stora ekonomiska värden och så stora arealer som behövs för att man skall säkerställa så många par att det blir ett livskraftigt bestånd. Vi känner igen problemen från vårt skyddsarbete för den vitryggiga hackspetten.

Frågan om hur många par av ugglorna och hur stort område som måste bevaras är den centrala. För att försöka besvara den har man använt olika modeller, dels genetiska, dels demografiska. De genetiska modellerna har inriktat sig på att klarlägga hur många ugglor man måste ha för att undvika skadlig inavel och förlust av genetiska variation. De demografiska modellerna analyserar i stället effekter av beståndstäthet, dödlighet, ungproduktion och spridning.

Russel Lande är författare till kapitlet om fläckugglan. Han är en av de mest framstående auktoriteterna på demografi och dynamik hos små populationer. Han börjar med att kritisera den hittillsvarande forskningen inom bevarandebiologin, som lagt mycket stor vikt vid att förhindra inavel och förlust av genetisk variation. Lande menar att man försummat de mycket viktigare demografiska analyserna. Anledningen till att de senare är viktigare än de förra är att risken för inavel och förlust av genetisk variation uppträder först vi en mycket mindre populationsstorlek än vid vilken risken för utdöende på grund av obalans mellan födelse- och dödstal uppträder. De flesta hotade populationer har alltså passerat den demografiska långt innan de nått den genetiska risknivån.

Det har hänt en del sedan Lande skrev sin uppsats. Bl. a. har man funnit genom mera förfinade analyser, som tar hänsyn till rumsliga förhållanden (biotopens fördelning och fläckugglornas spridningsmöjligheter), täthetsberoende effekter (att föryngringstakten avtar starkt när populationen blir mycket gles) samt slumpartade förändringar i miljön. Hur dessa nyare analyser påverkar handlingsprogrammet för att bevara den nordliga fläckugglan framgår av en uppsats av R. H. Lambersson m.fl. i Conservation Biology 6:505–512 (1992). Den viktigaste slutsatsen är att det finns en nedre antalsgräns, en tröskel, som innebär katastrof för ugglan om den passeras. Ännu är dock kunskapen om artens biologi för dålig för att värdet skall kunna fastställas. Det är också oklart om den strategi man hittills valt, nämligen att försöka skydda spridda områden av gammal skog som vart och ett kan hysa 1–3 par ugglor, är den riktiga. Det kanske i stället är effektivare att skapa ett mindre antal större reservat.

Boken är en bearbetning av ett symposium som hölls i december 1988 vid den biologiska stationen ”Tour du Valat” i Camargue. Med den nu utkomna paperbackversionen blir boken prismässigt mera lättillgänglig. Inklusive en avslutande sammanfattning av Ian Newton omfattar den 30 olika uppsatser. Det är ganska stor blandning på bidragen. Det är dock mest stora fåglar som behandlas, såsom snögås, stork, rapphöna och änder. Ämnesmässigt täcker bidragen både demografiska beskrivningar och analyser av populationer, teoretiska modeller för populationsutveckling och utdöenderisker samt tillämpningar i praktiskt fågelskyddsarbete. Att här sammanfatta alla trettio uppsatserna är inte möjligt, men några smakprov utöver fläckugglan bör ändå nämnas.

Robin McCleery och Christopher Perrins analyserar effekten av predation på bestånd av talgoxe med hjälp av 30 års data. Slutsatsen blir att predation på småfåglar sannolikt inte förmår reducera beståndsstorleken. En del resultat från Bialowieza-skogen i östra Polen, den rest av Europas forna naturliga lövskogstyp, där talgoxen sannolikt utvecklats, tyder dock på att småfåglarna faktiskt mycket väl kan vara utsatta för mycket hög predation och leva i utglesade bestånd. Den låga predation som registreras i så många studier skulle således kunna vara ett resultat av att människan skapat miljöer som avviker starkt i predationstryck.

Franz Bairlein ger en god och koncentrerad sammanfattning av den vita storkens populationsutveckling. Det som styrt nedgången i Västeuropa tycks i mindre grad ha varit dålig ungproduktion utan i stället låg överlevnad (för få återvändande fåglar), såväl bland de juvenila fram till könsmognaden som hos de häckande adulta. Orsaken till denna dåliga överlevnad är enligt Bairlein minskad födotillgång p.g.a. torka och överbetning i Afrika samt modernt jordbruk med insektsbekämpning både i Afrika och Europa. Förbättrade biotoper är nyckeln till storkens framtid, den enda enligt Bairlein, som slutar sin uppsats med stark kritik mot inplanteringarna av stork, som han till och med anser kan vara skadlig för de små återstående vilda beståndens fortlevnad.

Två uppsatser handlar om andjakten i Nordamerika. Dena ena, av James Nichols, handlar om hur andfåglarna påverkas av jakten. Det finns två teorier, den ena säger att jakten är ”kompensatorisk”, den andra att den är ”additiv”. Nichols slutsats är att för gräsanden stödjer de flesta undersökningar den första teorien, att jakten dödar fåglar som ändå skulle dö till nästa häckningssäsong och att därför också de olika jaktregleringarna inte har någon positiv effekt.

När det däremot gäller övriga andarter stödjer forskningen i stället den andra teorin, att jakten lägger en ytterligare dödlighet på den övriga och att därför jaktregleringarna har betydelse för stammens utveckling. Den andra uppsatsen är av Hugh Boyd och handlar om "vetenskap och praktik" i vården av andfågelbestånden. Den klarlägger tydligt hur svårt det är att kombinera vetenskapliga resultat (ofta osäkra och svårtolkade) med politiska mål och praktiska möjligheter (som ofta blir styrande oberoende av forskningsresultaten). De amerikanska erfarenheterna är värdefulla om man vill skapa ett liknande sameuropeiskt program utan att göra om de amerikanska misstagen igen.

SÖREN SVENSSON

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Andra bidrag än uppsatser bör ej överstiga 2000 ord (eller motsvarande om det ingår tabeller och figurer). De skall inte ha någon inledande Abstract men däremot en kort sammanfattning på det andra språket.

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Referenser *References*

I texten *In the text:* Andersson (1985), Bond (1913a, 1913b), Carlsson & Dennis (1956), Eriksson et al (1989), (Andersson 1985), etc.

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