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

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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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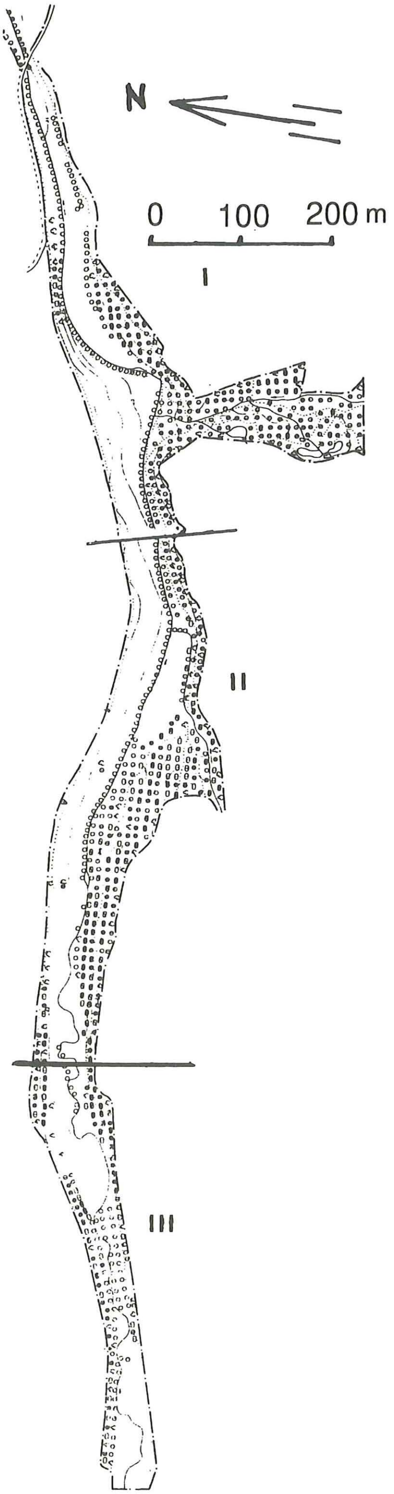
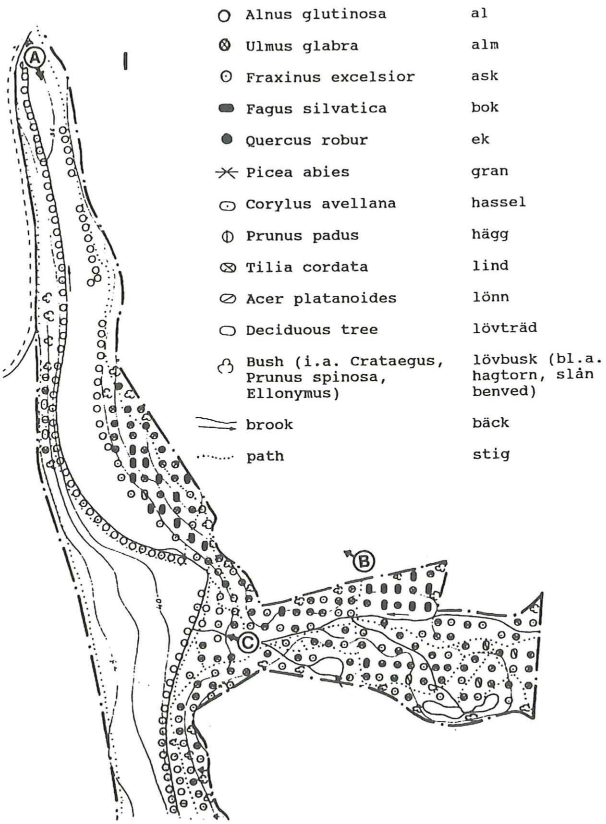




Introduction

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-

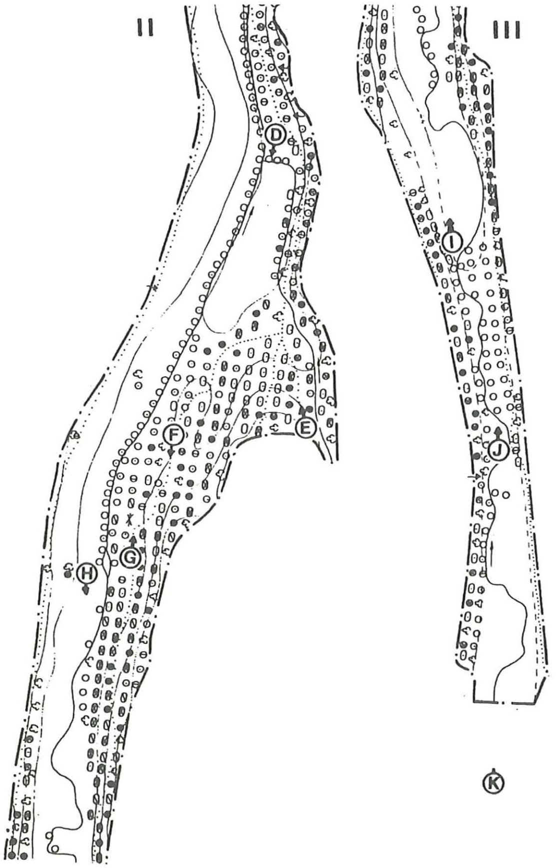


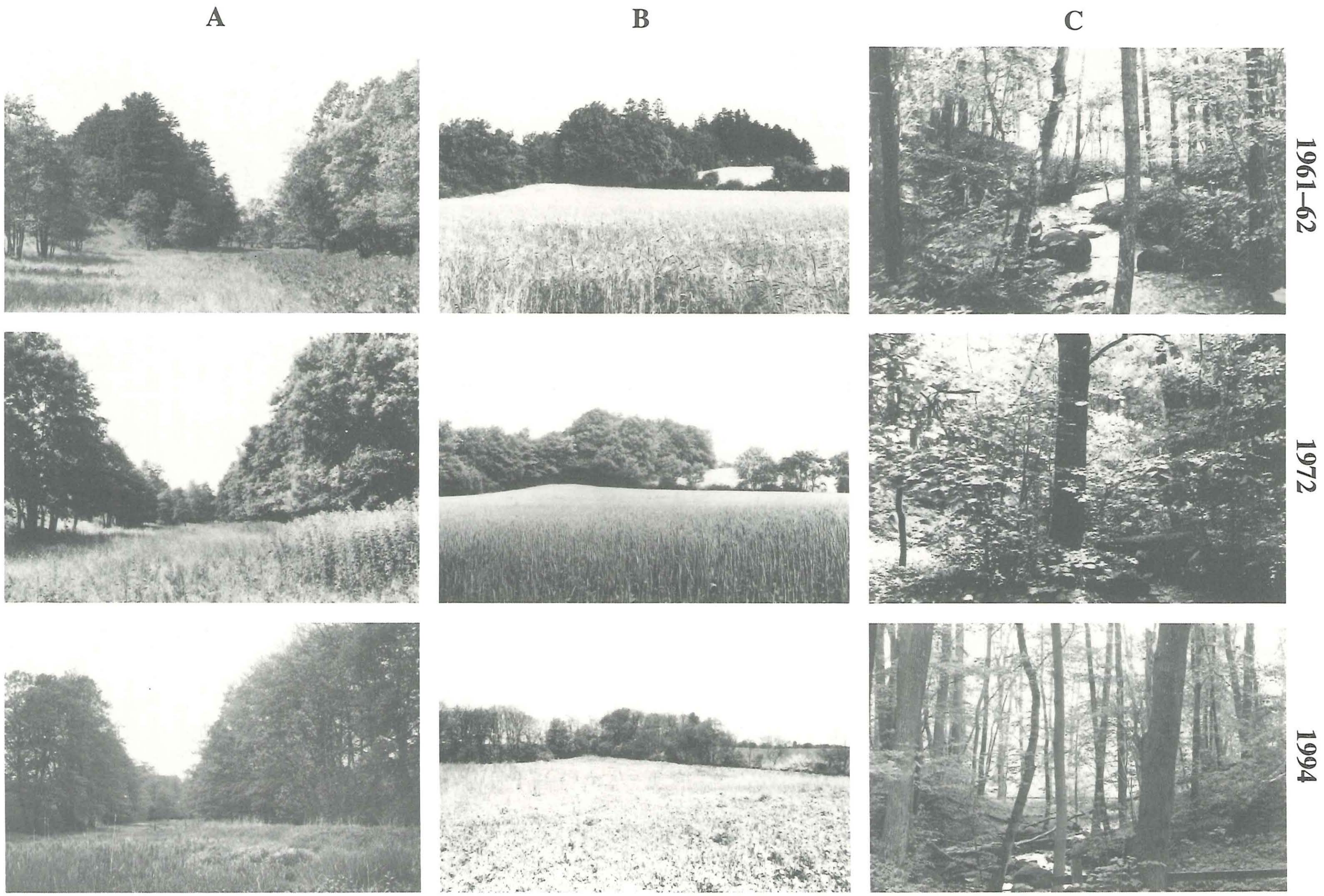
Fig. 1. Map showing the size and shape of Birdsong Valley (=the study plot) and indicating the distribution of wooded and of open, mostly grazed areas. The distribution of the different species of trees and some bush species are denoted by symbols which are seen on the three magnified sections of the 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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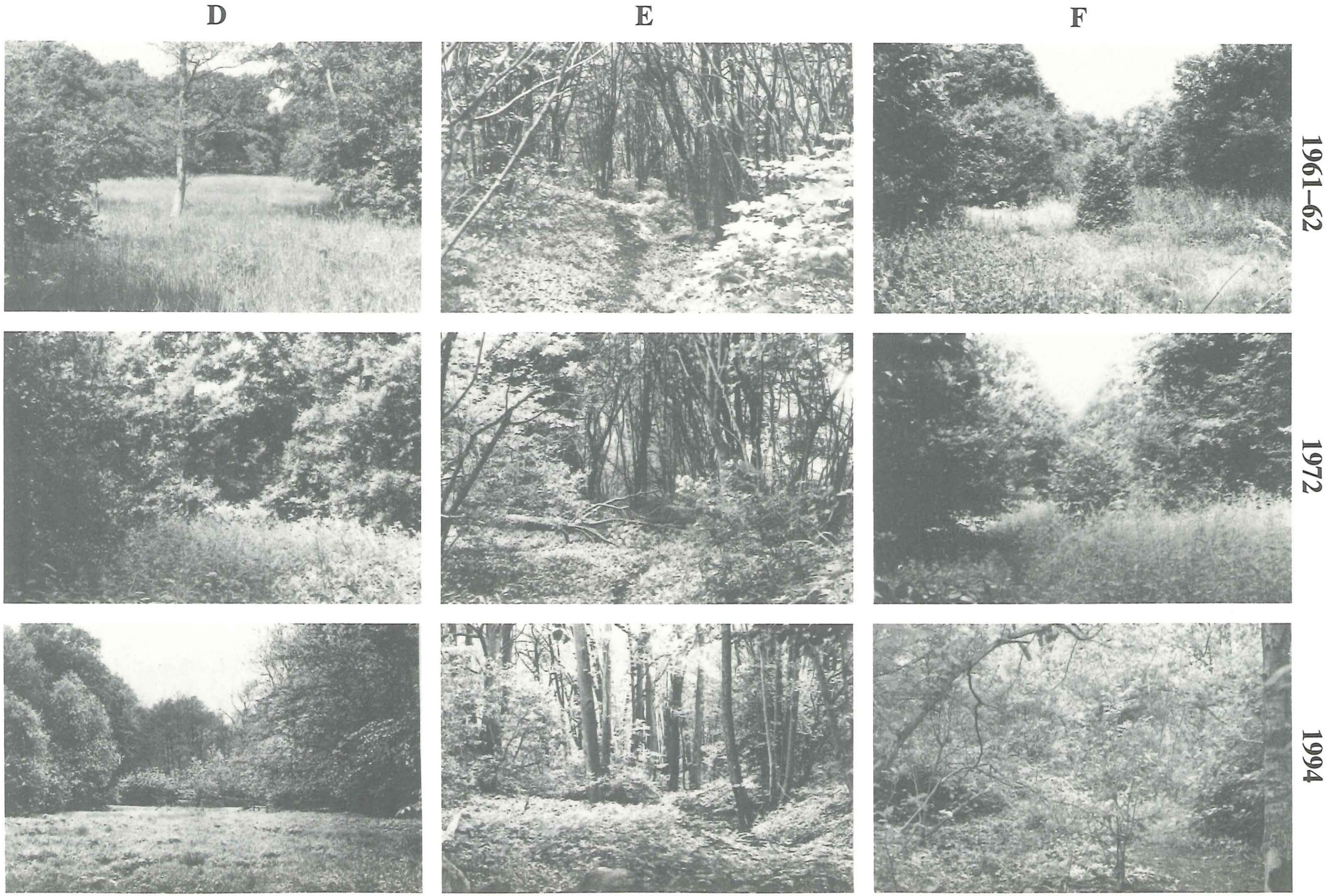

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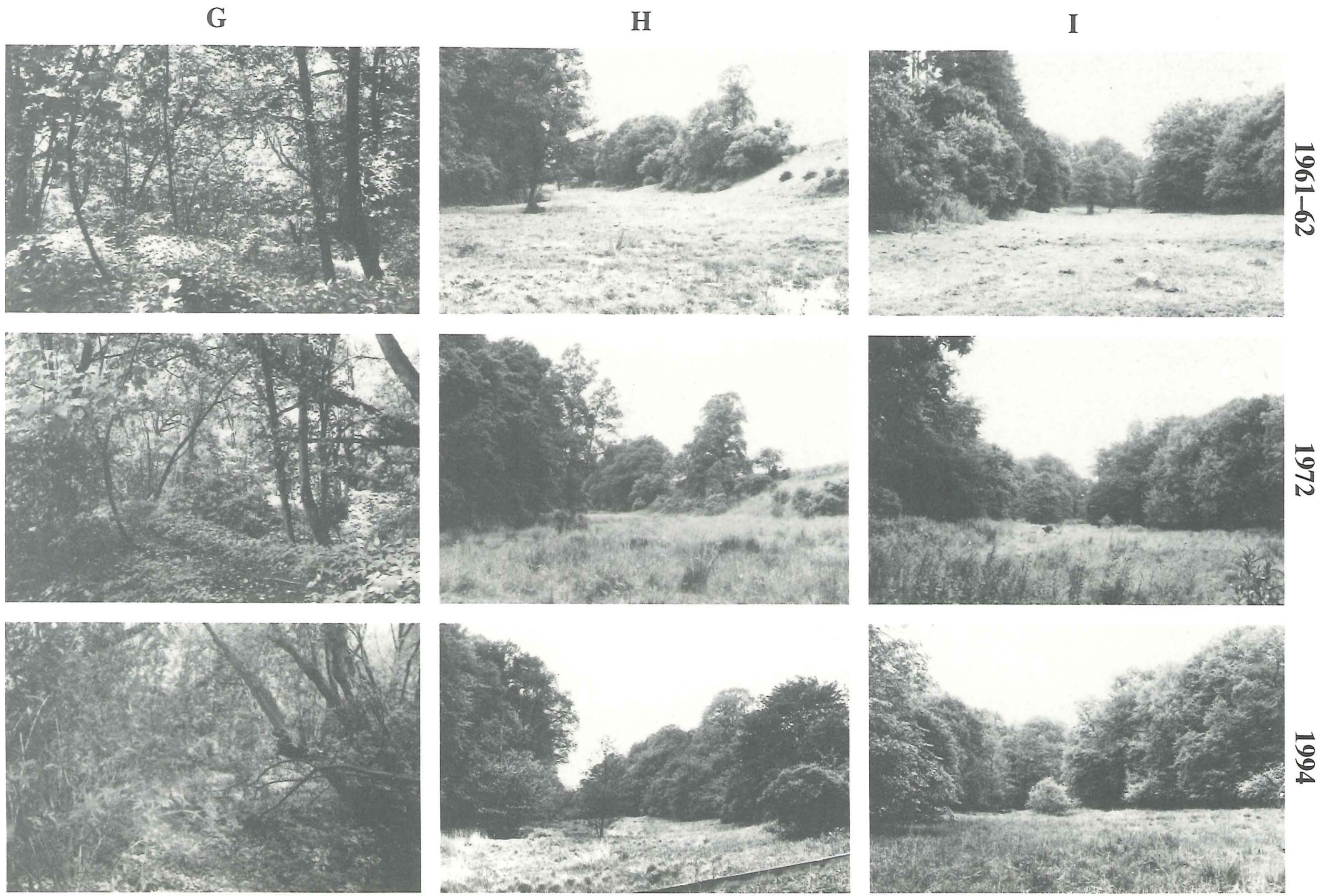

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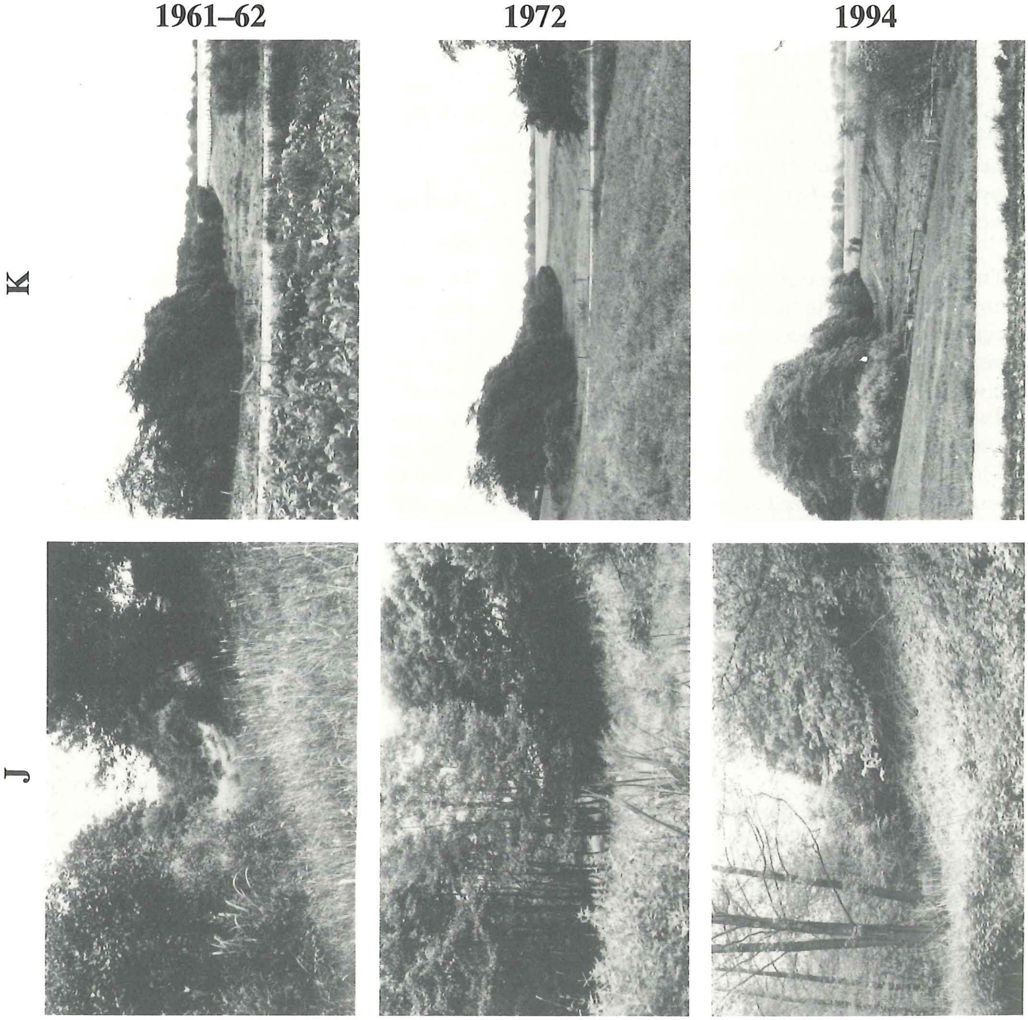


Fig. 2. (Pages 68–71.) Photographs showing 11 views (A to K) of the study plot in 1961/62, 1972, and 1994. The positions and directions of the camera have been the same all three years and are shown in Fig. 1. (The camera on position C was erroneously directed upstream instead of downstream along the 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 1953–1972	116	112	103	112	132	121	110	128	139	121	127	140	162	131	132	111	139	105	113	104
Totals 1973–1992	104	125	145	158	127	112	107	149	132	113	155	113	120	137	120	122	125	138	132	116
Number of	20	17	17	15	18	19	17	18	21	23	19	21	23	18	21	21	22	22	22	23
species *Antal arter*	22	23	23	22	22	20	17	21	19	19	23	19	17	17	21	22	21	22	19	19

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 frândragna.*

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

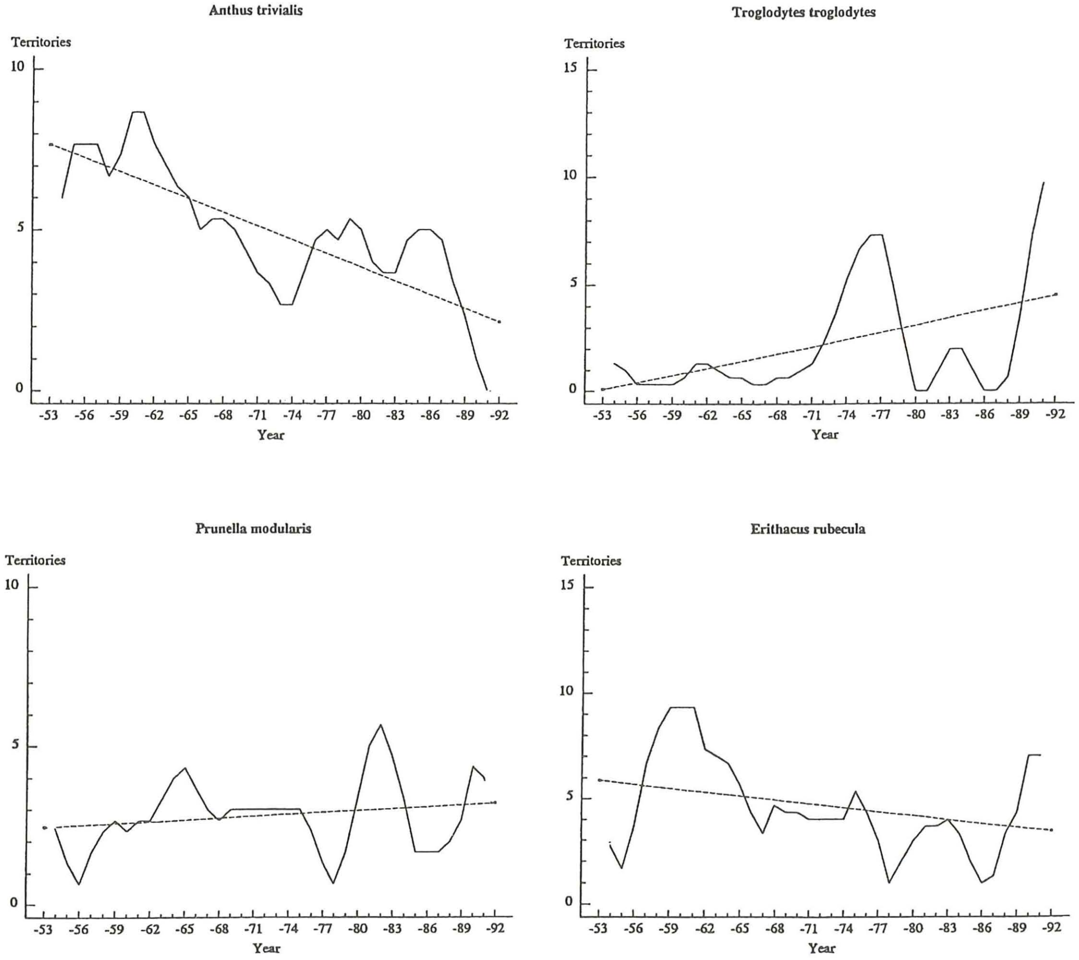


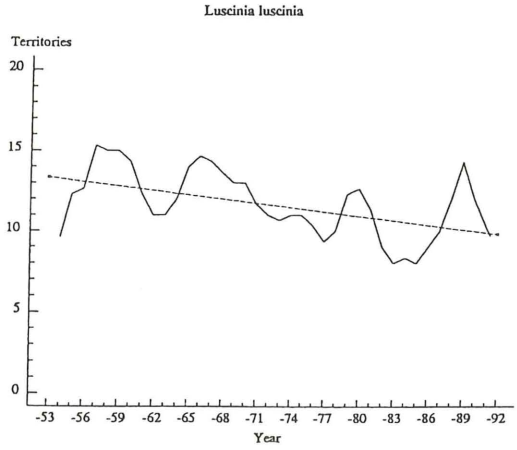
Fig. 3. (Pages 77–80.) The general trends in the fluctuations of the population sizes of the 19 most abundant species in Birdsong Valley, presented as curves based on moving averages of three seasons together with the regression lines of population sizes on time. The slope values (b) together with their 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.*

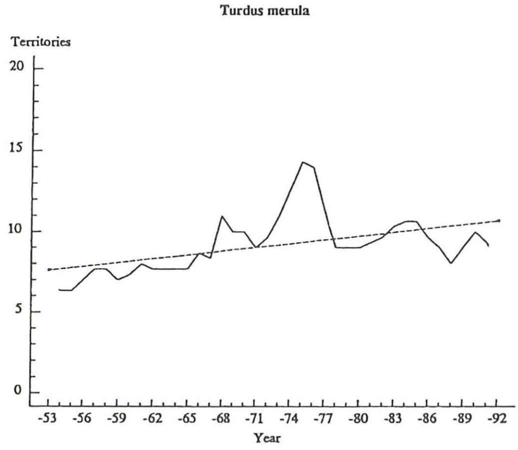
(Sid. 77–80). Diagram som visar den allmänna trenden i beståndsfluktuationerna för de 19 talrikaste arterna i Fågelsångsdalen i form av dels kurvor, som är baserade på s k glidande medelvärden över treårsperioder, dels s.k. regressionslinjer, som pekar ut medelriktningen i beståndsutvecklingen. Arterna 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.

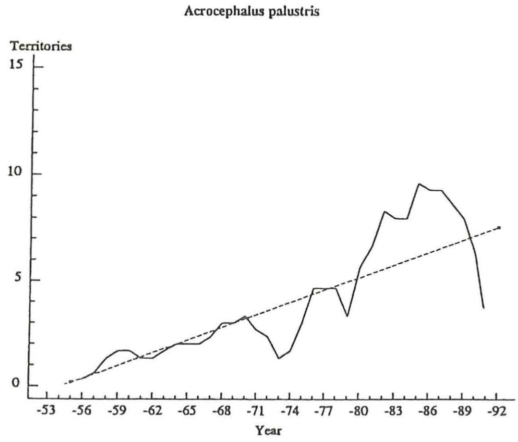
other population and community processes. This might be true even for the sparsely occurring species, as the long sequence of investigated years probably eliminates part of the "noise" caused by random events and occasional errors in the field work. Consequently, the analyses will be centered on the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

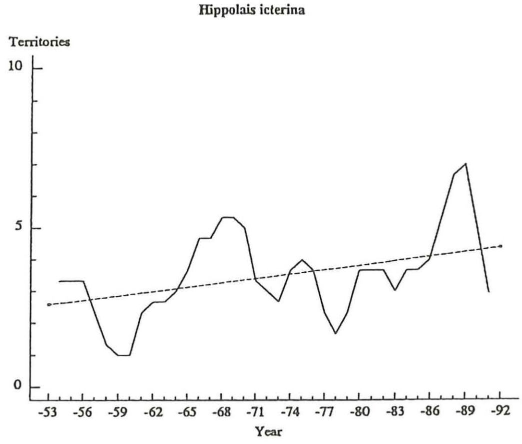
The species populations

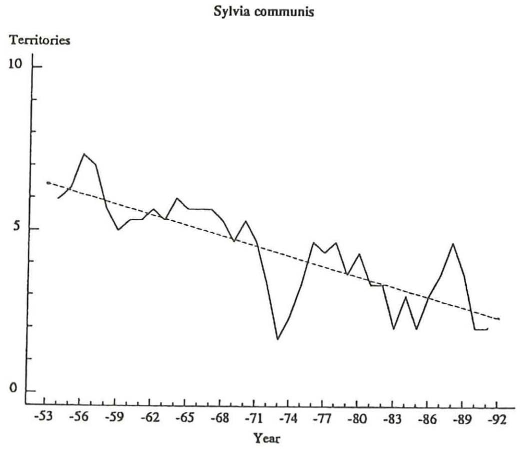
Most of the analyses and discussions below will be restricted to the 19 species with average population sizes surpassing one territory. They are listed in Table 3. Some analyses concern the 24 most abundant species, which means that *Motacilla alba, Turdus philomelos, Sitta europaea, Passer montanus,*

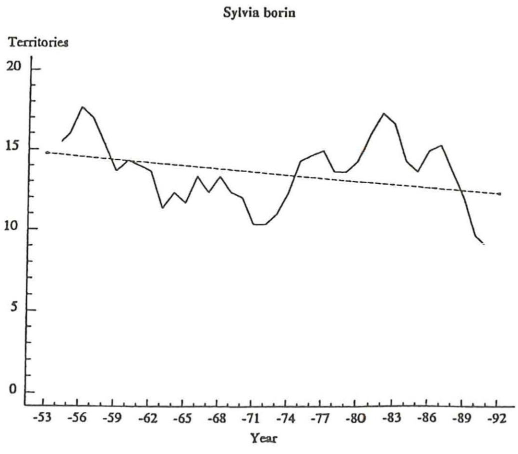




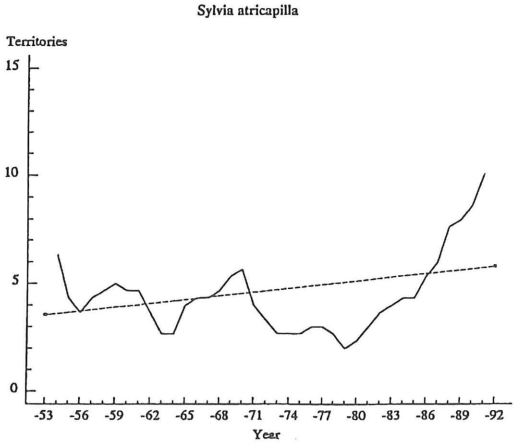


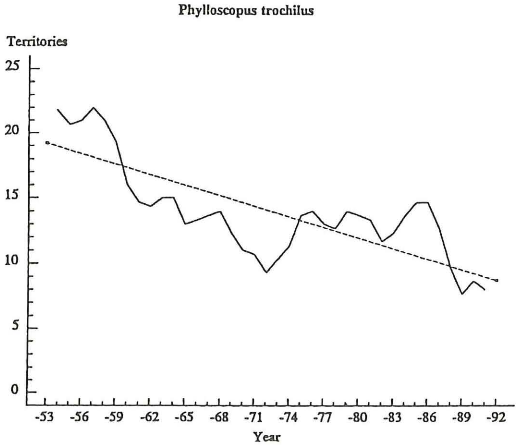


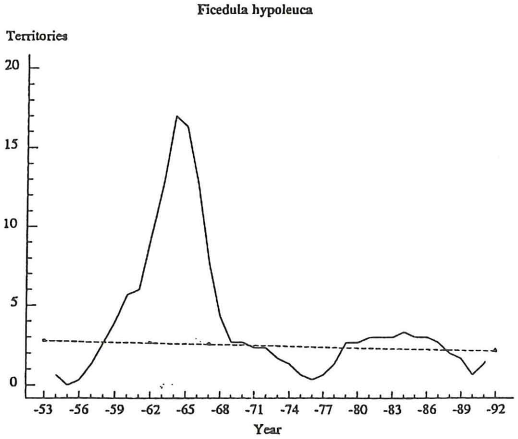


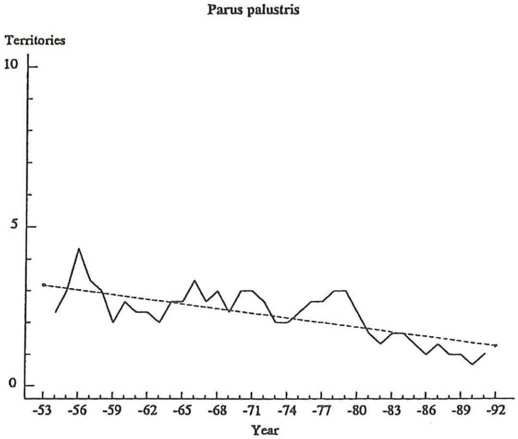


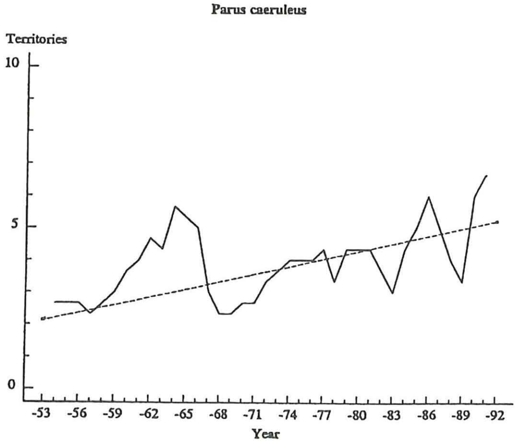
Caption Figuttext p. 77

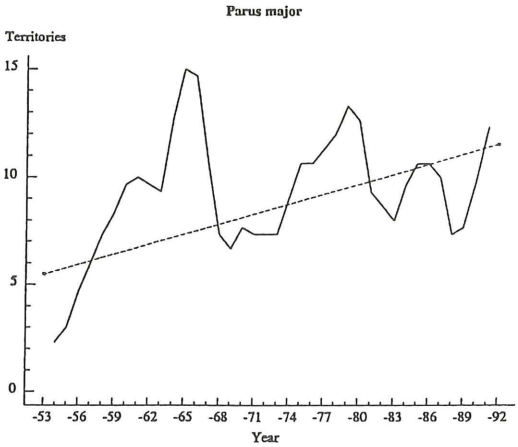

Sylvia atricapilla


Phylloscopus trochilus


Ficedula hypoleuca


Parus palustris


Parus caeruleus


Parus major

Caption Figuttext p. 77

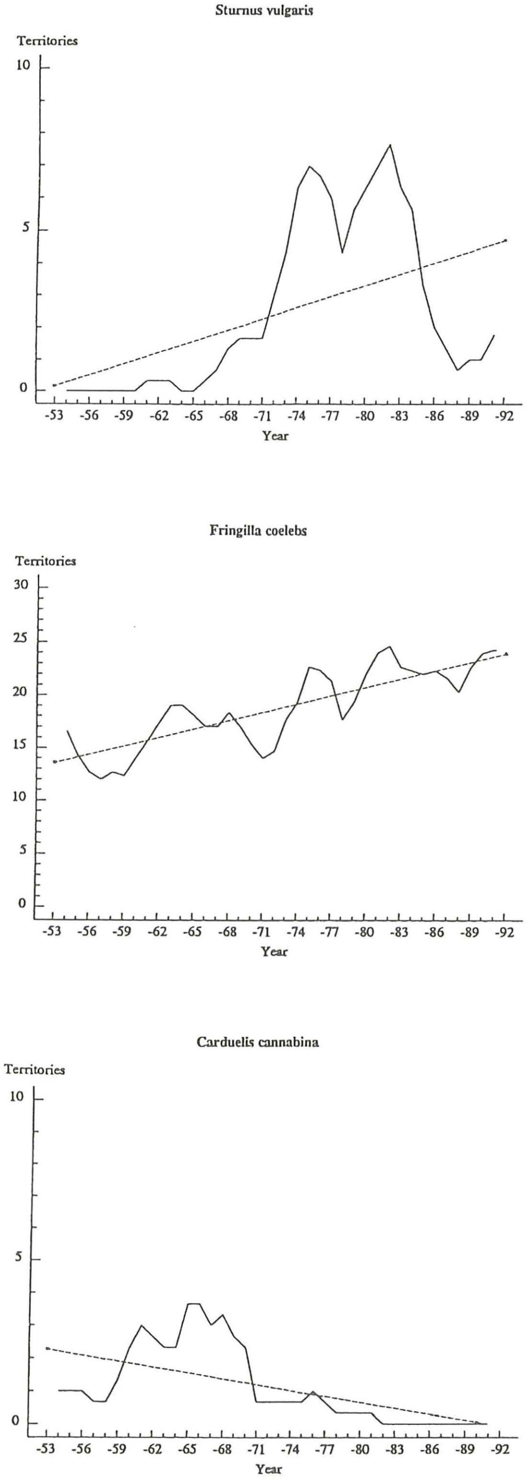
and *Carduelis chloris*, all with average populations of 0.5 to 1.0 territories, have been added to those of Table 3. These 24 species make up 98.5 % of the average community size.

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.

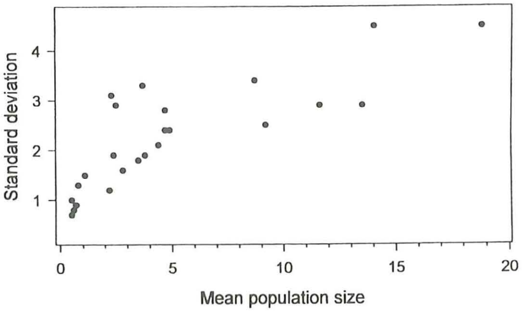

Fig. 4. The correlation between the fluctuations, expressed as the standard deviations (SD), and the mean size of the populations of 24 species in Birdsong Valley. The linear regression of SD on mean population size is $y=1.4+0.17x$, $r=0.81$, $df=22$, $p<0.001$.

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

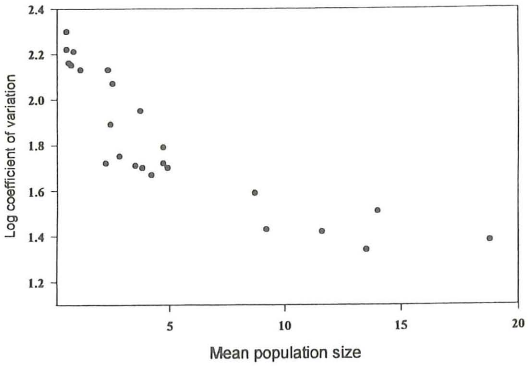

Fig. 5. The correlation between the coefficients of variation (CV) and the mean population size of 24 species in Birdsong Valley. The linear regression of logCV on population size is $y=2.1-0.05x$, $r=-0.85$, $df=22$, $p<0.001$.

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

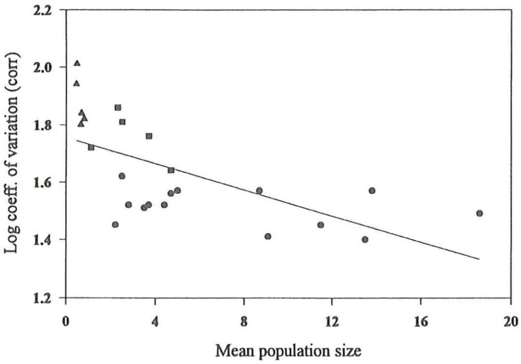

Fig. 6. The correlation between the logarithm of the coefficients of variation, adjusted to a common population size of 10, log CV(corr), and the mean population size of 24 species in Birdsong Valley. The linear regression of log CV(corr) upon mean population size is $y=1.8-0.02x$, $r=-0.41$, $df=22$, $p<0.001$. ● = 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.

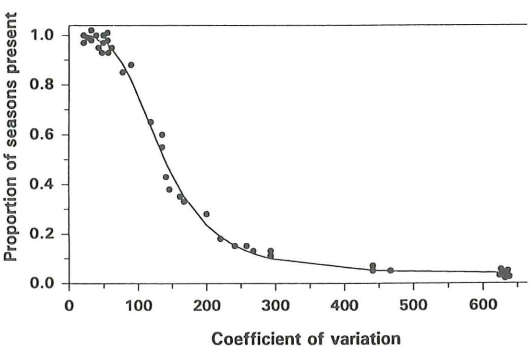

Fig. 7. The relationship between proportion of years present in Birdsong Valley and the coefficient of variation. The logistic equation best fitting the sigmoidal curve is

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

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

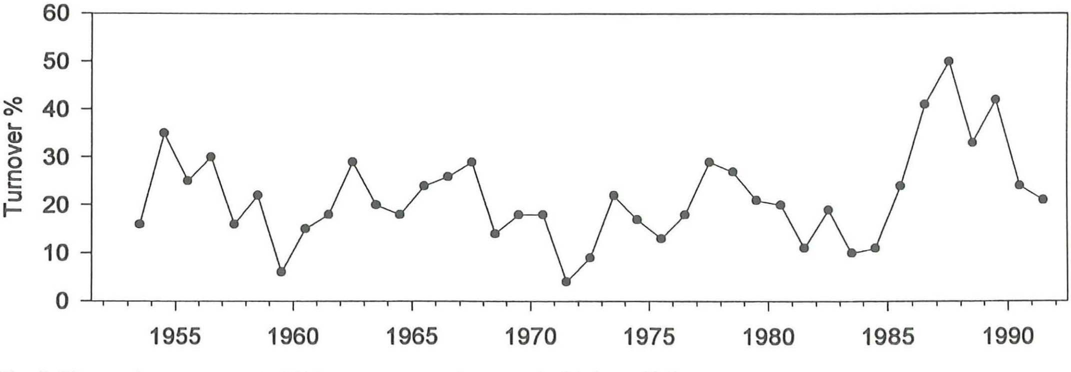

Fig. 8. The species turnover rate (%) between successive years in Birdsong Valley.

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

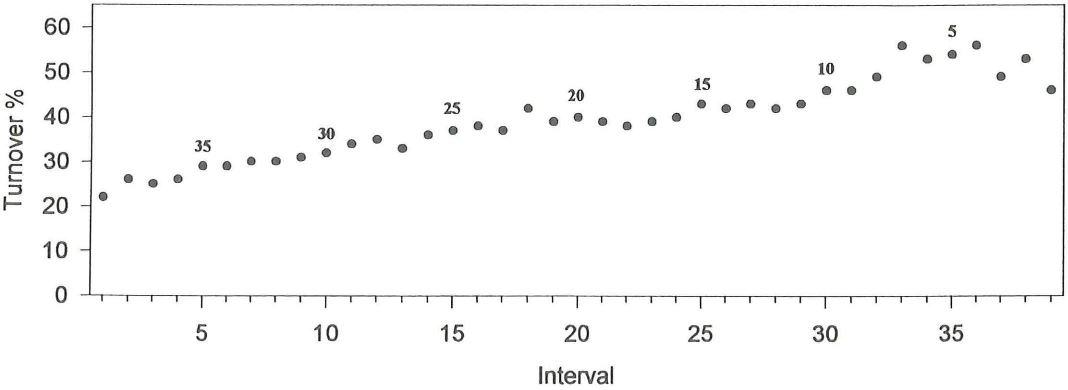

Fig. 9. The relation between the mean species turnover rate (%) and the interval (number of years) between the compared seasons. The figures above every five dots indicate sample size. The linear regression of the turnover percentage upon interval length is $y=24.2+0.75x$, $r=0.96$, $df=37$, $p<<0.001$.

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 $P=(X-X_{min})/(X_{max}-X_{min})$, 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

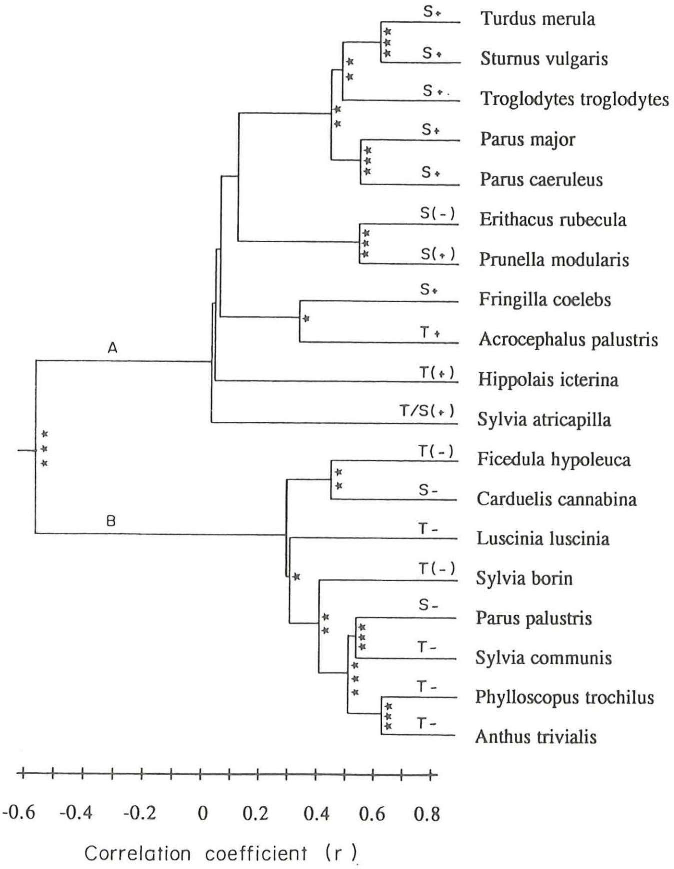

Fig. 10. Dendrogram showing the grouping av the 19 most abundant species according to the degree av similarity, expressed as the correlation coefficients (r), of their density fluctuations in Birdsong Valley 1953–1992. The derivation of the dendrogram (see text) unveils two "fluctuation groups", A and 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 have 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.

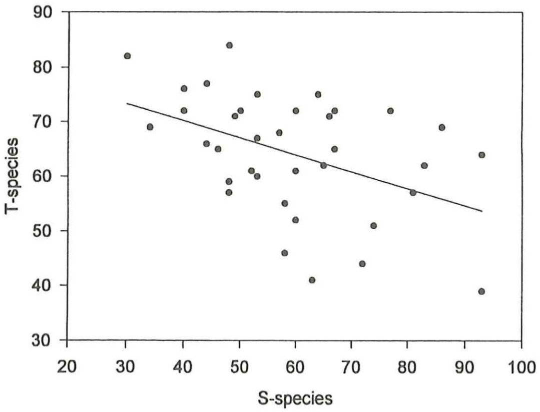

Fig. 11. The correlation between number of mapped tropical migrants (T-species) and residents and short-distance migrants (S-species) during the breeding season in Birdsong Valley. The negative correlation is significant ($y=82.7-0.31x$, $r=-0.45$, $df=34$, $p<0.01$).

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 non-breeding 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

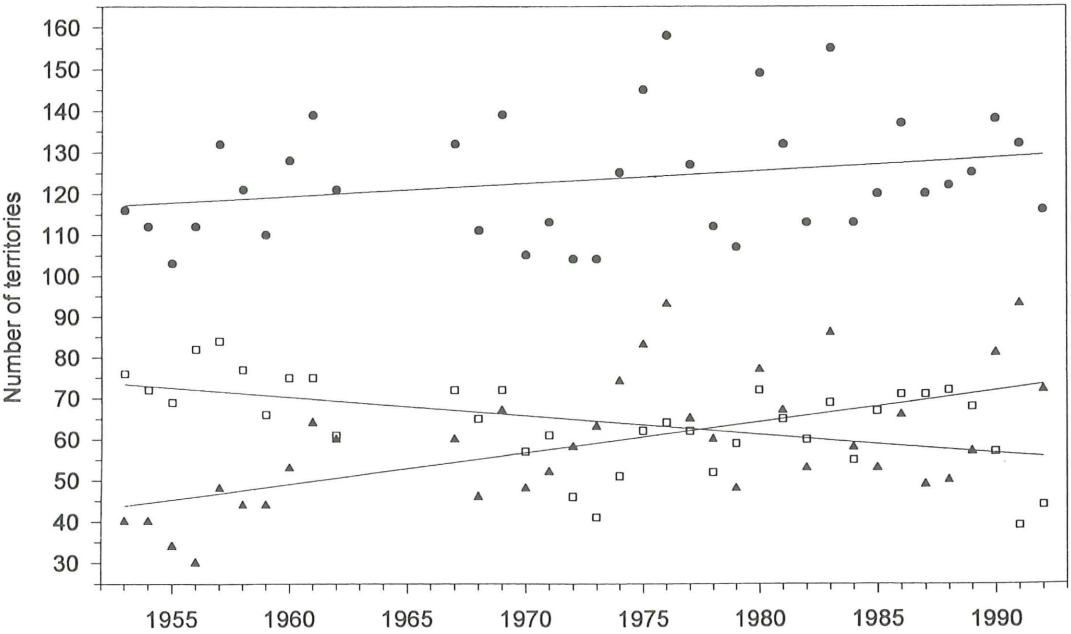

Fig. 12. Diagram showing the successive increase of the residents and the short-distance migrants (▲), and the simultaneous decrease of the tropical migrants (☐) in Birdsong Valley. The total community (●) remains at a relatively constant level. The figures of the four nest-box years are excluded. The 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

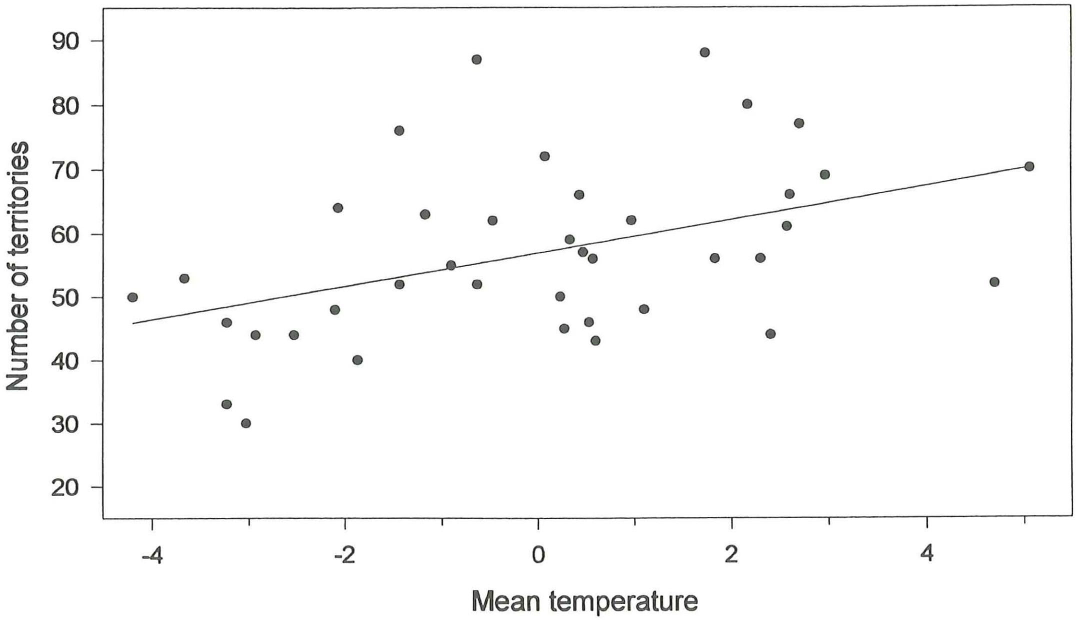

Fig. 13. The number of mapped residents and short-distance migrants (the S-species group) in the breeding season in Birdsong Valley as a function of the mean temperature of the preceding winter (Fig. 14). The correlation is significant ($y=56.9+2.6x$, $r=0.44$, $df=37$, $p<0.01$).

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

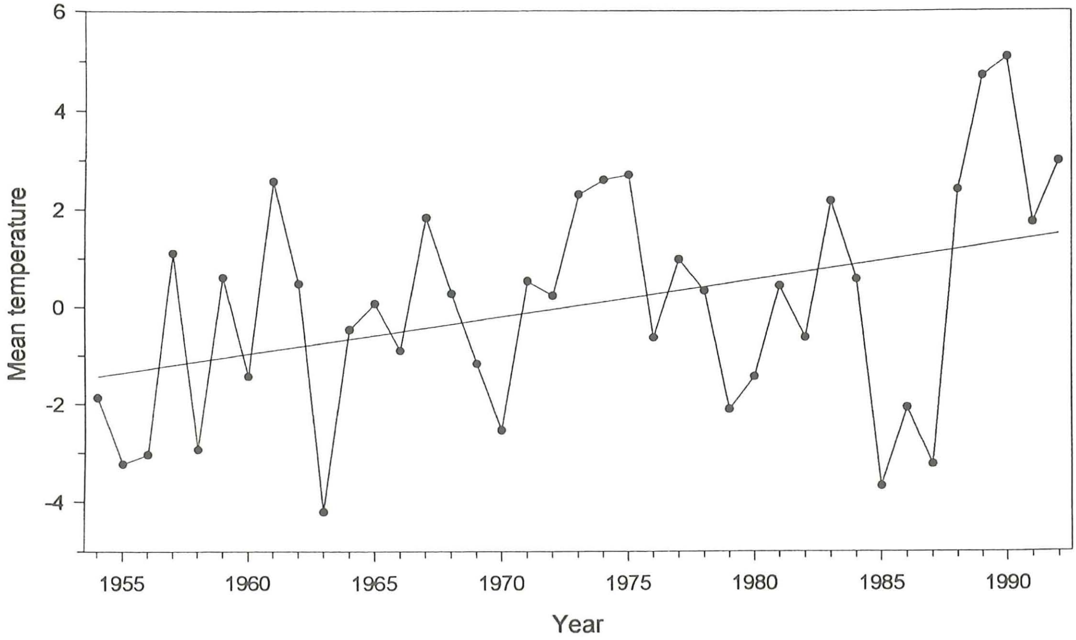

Fig. 14. The variation of the mean temperature of the winter periods, January through March, in the vicinity of Birdsong Valley 1954–1992. The increasing linear regression of the mean temperature upon time is significant ($y=-1.51+0.08x$, $r=0.38$, $df=37$, $p<0.02$).

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 inträngling.

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.