The Garden Warbler *Sylvia borin* as a member of a breeding bird community

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This paper is an attempt to compare different approaches in evaluating the role of a species in its environment. The significance of a dominant Garden Warbler population in a bird community in southern Finland was estimated on the basis of bird numbers, adult biomass, and annual energy consumption and production. The community inhabiting the study area of 30 ha consisted of 50 species and c. 380 pairs. The Garden Warbler was the fourth most abundant species, averaging c. 6 % of the total pair numbers. Its proportion in the total biomass (2.4 %) was relatively small because of the high total density and considerable mean weight (48 g) of the birds in the community. The low annual energy consumption of the Garden Warblers (1.0 % of total) was due to their low biomass (19 g per bird) and the short period spent in the study area. Their biomass production (1.5 % of total) was also rather small. In spite of its great abundance, the species is considered to play a relatively insignificant part in the annual energy flow through the bird community.

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Introduction

The significance of a species in a community, or an entire ecosystem, can be approached on the basis of numbers, biomass, or energy values. The difficulty and information content of these approaches increase in the above order. Because there are many difficulties in estimating energy relations, we usually have to be content with combining data from various sources (Petrusewicz & Macfadyen 1970, Gessaman 1973, Holmes & Sturges 1973, 1975, Grodziński et al. 1975, Wiens & Dyer 1977).

This paper is an attempt to compare different approaches in evaluating the significance of a species in its environment. I will attempt to demonstrate what these approaches, combined with relevant additional data, may tell about the relationships between populations and the organization of the community, and what information is still needed for a more complete picture. The species chosen here, the Garden Warbler *Sylvia borin,* is an open-nesting, mainly insectivorous migratory passerine, which is abundant in a large part of its range in the temperate region. Numbers and adult biomass were used to estimate the significance of a Garden Warbler population (Solonen 1979) in a breeding bird community inhabiting an area covered mainly by luxuriant mixed forest vegetation in southern

Finland. In addition, rough estimates were made of the energy consumption and production of different bird species and various ecological groups of birds. The results of an earlier analysis of the community (Solonen, unpubl.) are also presented.

Material and methods

The study area (30 ha) and general methods have been described by Solonen & Tiainen (1978a). The pair numbers of different species were estimated mainly by the mapping method (Anon. 1970). The biomass values (fresh weight) were calculated chiefly according to the data presented by v. Haartman et al. (1963—72), and their energy equivalents were determined assuming that the average energy content of bird tissue is c. 6.7 kJ (1.6 kcal)/g fresh weight (cf. Varley 1970, Górecki 1975, Pinowski & Myrcha 1977).

In calculating the energy consumption I assumed that the dry weight of the daily intake of a full-grown bird corresponds to 25 % of the fresh weight of the bird, and that a brood consumes as much food during the nestling period as both the parents in the same time (Saurola 1971—73, cf. also Royama 1966, Varley 1970, Kendeigh et al. 1977). The energy content of the food of all the species was roughly estimated to average 23.0 kJ (5.5 kcal)/g dry weight (cf. Kendeigh et al. 1977). The average time spent annually in the study area by each species was estimated from my own observations and data from the literature (v. Haartman et al. 1963—72). Passage migrants and wintering individuals of the breeding species were included in the estimate, occasional and rare visitors were omitted.

In calculating the energy deposited in production, data from the above-mentioned references were used to determine the clutch size and number of clutches for each species. Fifty per cent of the eggs of the open-nesting birds and 70 % of the eggs of the hole-nesting species were assumed to produce fledglings (Nice 1957, Weiner & Głowacinski 1975) because no detailed values for each species were available. The proportion of losses (eggs and nestlings lost, deserted, taken by predators, etc.) during the incubation and nestling period was estimated at 30 % of the energy production, and the proportion of the moult (energy content of new plumage) at roughly 5 % of the production (per pair) (Saurola 1971—73).

Results

The bird community inhabiting the study area of 30 ha in 1971—77 consisted of, on average, 50 ($SD \pm 2$) species and 383 ($SD \pm 25$) pairs (Solonen 1976, Solonen & Tiainen 1978a, b, Tiainen & Solonen 1979). The Garden Warbler was the fourth most abundant species, accounting for 6.0 % of the total number of pairs (Table 1). The biomass of the adults (c. 874 g), however, constituted only 2.4 % of the total biomass (c. 36 600 g), being greater in 12 other species. The estimated gross energy intake of the Garden Warbler population (adults, nestlings, and fledglings) was c. 1900 J (500 cal)/m^2/year; 20 other species consumed more energy. The production of the Garden Warblers, about 30 J (8 cal)/m^2/year, was 1.5 % of the production of the entire bird community.

Table 2 and Fig. 1 present the proportions of the Garden Warbler and various groups of birds in the community in terms of numbers, adult biomasses, annual energy consumption and production. Passerines constituted 81 % of the breeding species in the community. In 1977, 71 % of the species were open-nesting forms, the remainder hole-nesters. Eighty per cent of the pairs belonged to migratory and 20 % to sedentary species. The biomass of the migratory species constituted 66 % of the biomass of the adult terrestrial birds, but the annual consumption and production only 50 % and 59 %, respectively. Their mean weight was 38 g, whereas that of the nonmigratory birds was 78 g. The weight of the adult Garden Warblers averaged 19.0 g (Solonen 1977). The mean weight of all the birds in the community was 48 g (Solonen & Tiainen 1978a, b).

TABLE 1. Average numbers of pairs, adult biomass, annual energy consumption and production of birds breeding in the study area of 30 ha in southern Finland in 1971—77.

Species or group	Numbers pairs ± *SD*	%	Biomass g	%	Consumption kJ/m²/y	%	Production kJ/m²/y	%
Ficedula hypoleuca	71±19	18.5	1846	5.0	3.6	1.9	0.12	5.6
Fringilla coelebs	49± 9	12.8	2058	5.6	7.7	4.0	0.10	4.7
Phylloscopus trochilus	27± 5	7.1	508	1.4	1.4	0.7	0.02	0.9
Sylvia borin	23± 1	6.0	874	2.4	1.9	1.0	0.03	1.5
Parus major	22± 7	5.7	880	2.4	6.9	3.6	0.10	4.7
Sturnus vulgaris	20± 8	5.2	3200	8.7	12.6	6.6	0.17	7.9
Turdus pilaris	17± 3	4.4	3604	9.8	17.1	8.9	0.17	7.9
T. iliacus	12± 4	3.1	1488	4.1	6.0	3.1	0.08	3.7
Corvus monedula	10± 3	2.6	4300	11.8	27.9	14.6	0.23	10.7
Carpodacus erythrinus	10± 3	2.6	460	1.3	0.9	0.5	0.02	0.9
Erithacus rubecula	9± 2	2.3	292	0.8	1.6	0.8	0.02	0.9
Residents (39 species)	113±11	29.5	17090	46.7	104.1	54.3	1.08	50.6
Total 50(±2) species	383±25	100	36600	100	191.7	100	2.14	100

TABLE 2. The contributions of the Garden Warbler and various ecological bird groups in 1977 to the numbers (N_1 = species, N_2 = pairs/30 ha), adult biomasses (B, kJ/m²), annual energy consumption (C, kJ/m²/y) and production (P, kJ/m²/y). *Note:* The percentages are calculated from the values for the entire bird community.

Species or group	N_1	%	N_2	%	B	%	C	%	P	%
Sylvia borin	1	2	20	6	0.02	2	1.76	1	0.03	1
Passerines	42	81	340	95	0.55	65	119.13	58	1.32	59
Non-passerines	10	19	17	5	0.29	35	87.66	42	0.92	41
Open-nesters	37	71	254	71	0.58	69	131.35	64	1.28	57
Hole-nesters	15	29	103	29	0.26	31	75.44	36	0.97	43
Terrestrial										
— migratory species	31	59	280	79	0.47	56	85.81	41	1.00	45
— sedentary species	18	35	72	20	0.25	30	85.64	41	0.69	31
— primary consumers	11	21	89	25	0.22	26	57.72	28	0.50	22
— secondary or higher-level consumers	34	65	252	71	0.38	46	79.34	38	0.94	42
— omnivores	4	8	11	3	0.12	14	34.39	17	0.25	11
Terrestrial total	49	94	352	99	0.72	86	171.45	83	1.69	75
Predators	5	10	12	3	0.14	17	45.81	22	0.29	13
Waterfowl	3	6	5	1	0.12	14	35.34	17	0.55	25
Total (entire community)	52	100	357	100	0.84	100	206.79	100	2.24	100

About 25 % of the terrestrial birds were mainly primary consumers, about 72 % mainly secondary or higher-level consumers, and the remainder more or less omnivorous. Their respective biomass proportions were 30 %, 53 % and 17 %. According to a rough estimate, about 42 % of the annual consumption of the terrestrial species in the study area was derived directly from primary production (mainly in the form of seeds), about 36 % from

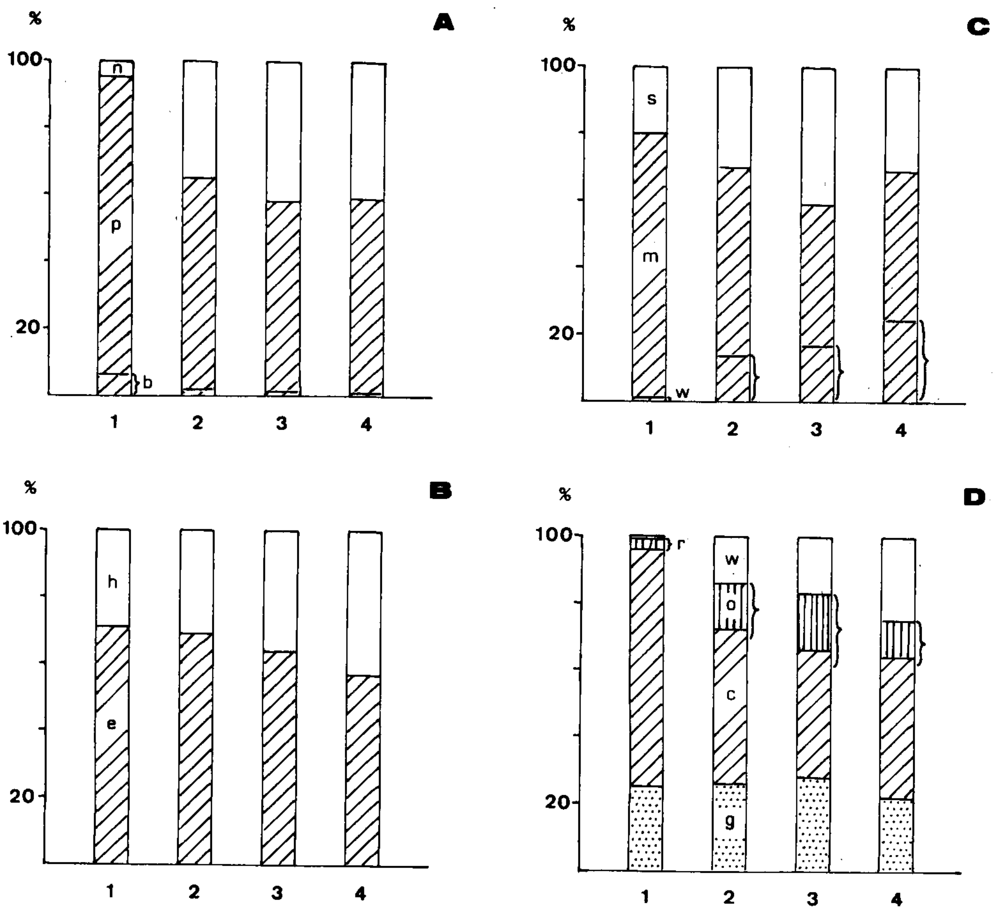

FIG. 1. Contributions of various groups of birds in the community studied in 1977 to pair numbers (1), adult biomasses (2), annual energy consumption (3) and production (4). A) Taxonomic groups: p = passerines, n = non-passerines, b = *Sylvia borin;* B) Nesting groups: e = open-nesters, h = hole-nesters; C) Movement groups: m = migratory species, s = sedentary species; and D) Feeding groups: g = terrestrial primary consumers, c = terrestr. secondary or higher-level consumers, o=terrestr. omnivores, r=predators, w=waterfowl.

soil invertebrates, about 14 % from other invertebrates (mainly insects) and about 8 % from vertebrates.

Avian predators (species preying on birds) contributed 3 % of the individuals in the community, their consumption and production being 22 % and 13 % of the total, respectively. A considerable proportion of the production of the Garden Warbler population studied was consumed by predators, probably primarily by Jackdaws *Corvus monedula* (Solonen 1977, 1979), which accounted for about 11 % and 9 % of the total community consumption and production. An unestimated part of the energy consumed by the breeding populations was obtained outside the study area, especially by some ground-feeding species and predators. About 17 % of the energy consumed by the community was obtained outside the terrestrial ecosystems, from waters, by Anatidae, whose production was about 25 % of that of the entire community.

Discussion

Ecological considerations. In spite of their great abundance (Solonen 1979), the total biomass of the Garden Warblers in the study area was relatively small because of the high total density (c. 1 250 pairs/km^2) and the relatively large mean body weight of the birds in the community. The small energy consumption of the Garden Warblers, about 1 % of the annual consumption of the entire bird community, is due to their low biomass and the short period spent in the study area. On a peak-period basis, however, the proportion would be greater (Weiner & Głowaciński 1975); in June it was about 5 % (Solonen, unpubl.). The energy flow (assimilation) through bird populations is estimated to be 70—75 % of the consumption (e.g. Wiens & Innis 1974, Weiner & Głowaciński 1975).

Garden Warblers are migratory, as are the majority (80 %) of the birds breeding in the area. These birds, and passage migrants of the breeding species, are mostly seen only during a period of 3—5 months, from May to September. Some visitors also rest and feed in the area earlier in the spring and later in the autumn, but less than a third of the breeding bird species occur in the area more or less regularly throughout the year. In the breeding area the ratio of the annual production to the consumption is usually considerably lower for nonmigratory than for migratory species. In migratory birds the main part of the production (reproduction) occurs there, but a great part of the annual energy consumption takes place elsewhere (cf. Weiner & Głowaciński 1975). Although their total consumption is relatively small, passerines and small-sized species consume more energy per unit body mass than other birds because of their higher metabolism (Kendeigh et al. 1977).

Final comments. Although useful for numerical comparisons and as a speculative starting-point, numbers, biomasses and simple energy consumption and production values like those calculated here are insufficient for a full understanding of the role of a species. Numbers are fairly easily obtained, but the more dissimilar the organisms that are compared, the less they tell. They and their accuracy are, however, of basic importance in other more detailed approaches. The biomass gives a better basis for comparisons because it takes account of the size of the organisms, but its information content is also rather limited. Energy values, which reflect both the quantity and function of the organisms, offer the best, although the most laborious, comparative approach of those dealt with here. Annual energy consumption is a fairly good measure of the total impact of a population on the food resources of its environment (cf. however Mertens 1972, Grodziński et al. 1977, Wiens & Dyer 1977, Wiens 1977), but it reveals little about the underlying interactions, which may have important effects upon the significance of the species in the community.

Because of the high number of species in the community studied and the many general assumptions made in the calculations, some of the values obtained here may not be very realistic (cf. e.g. Wiens & Dyer 1977). This concerns especially the consumption values and the proportion of the moult included in the production estimates. More accurate calculation methods would be preferable, but these require much more information about the habits and energy budgets of the different species than are yet available. What are especially needed are more detailed examinations of interspecific relationships, predation, competition, resource partitioning, niches, etc. (Lack 1971, MacArthur 1972, Fretwell 1972, Cody 1974, Hespenheide 1975), and, of the interactions of various biotic and abiotic factors, and their effects on the energy budgets of the species (Gessaman 1973, King 1974, Kendeigh et al. 1977).

In comparisons of energy estimates and other values, careful account must be taken of possible variation due to different calculation methods (cf. e.g. Głowaciński & Weiner 1975). Energy values should not be presented without sufficient information about numbers and biomasses, and relevant ecological data (e.g. Table 2). The total density and biomass or mean weight of the birds should always be included.

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Selostus: **Lehtokerttu pesimälintuyhteisön jäsenenä**

Lajin merkitystä yhteisössä voidaan arvioida mm. vertailemalla sen runsautta, biomassaa tai energiankäyttöä vastaaviin tietoihin koko yhteisöstä tai sen muista lajeista. Lukumäärät ovat kaikkien arviointien perustana, mutta sellaisenaan ne kertovat suhteellisen vähän. Biomassoihin sisältyy jo enemmän vertailukelpoista tietoa ja täydellisimmän kuvan antavat tietyt energia-arvot. Kuvaa voidaan vielä syventää yhdistämällä em. tietoihin mahdollisimman paljon ekologista tietoa kohteista.

Eri menetelmiä vertailtiin arvioitaessa eteläsuomalaisen lehtokerttupopulaation merkitystä pesimälintuyhteisössä, jossa pesi n. 50 lajia ja 380 lintuparia/30 ha. Lehtokertun osuus oli n. 6 % kokonaisparimäärästä ja se oli keskimäärin yhteisön neljänneksi runsain lintulaji (taul. 1). Yhteisön lintujen keskipaino oli 48 g, kun taas lehtokertut painoivat keskimäärin 19 g. Ne muodostivat vain n. 2.4 % kaikkien lajien kokonaisbiomassasta. Vastaavasti lehtokertut kuluttivat vain n. 1.0 % ja tuottivat n. 1.5 % pesimäyhteisön vuotuisesta energiankulutuksesta ja tuotannosta. Taulukossa 2 ja kuvassa 1 verrataan lehtokerttua eräisiin yhteisön linturyhmiin lukumäärien, biomassan, energiankulutuksen ja tuotannon suhteen.

Huolimatta yksilörunsaudesta lehtokertun biomassaosuus on suhteellisen vähäinen, mikä johtuu koko lintuyhteisön suuresta tiheydestä ja lajien huomattavasta keskipainosta. Lehtokertun merkitystä kuluttajana pesimäalueella vähentää sen vähäinen biomassa ja muuttolintuluonteesta johtuva pitkäaikainen poissaolo alueelta. Runsautensa perusteella lehtokerttu on tutkitussa lintuyhteisössä tärkeä laji, biomassan mukaan arvioiden vähemmän tärkeä ja energeettisesti sen merkitys näyttää olevan kovin vähäinen. Monenlaiset lintujen ja niiden ympäristön väliset vuorovaikutussuhteet kaipaavat kuitenkin vielä lisävalaistusta.

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