Population dynamics of the Garden Warbler *Sylvia borin* in southern Finland

TAPIO SOLONEN

SOLONEN, T. 1979: *Population dynamics of the Garden Warbler* Sylvia borin *in southern Finland.* — Ornis Fennica 56:3—12.

A population of 21—26 territories was studied in Lammi commune in 1971—78. In an area of 27 ha the density of the birds was about 86 territories/km². In a luxuriant part of the area it averaged 112 t./km²; in a less fertile part, where the annual variations were also larger, the average was only 49 t./km². The percentages of the obviously stationary, ringed birds (*N* 164) recovered in the study area in later years were 25 % for males and 6 % for females. Non-return rates, corrected according to trapping efficiency, were 52 % for males and 82 % for females. The non-return rate was 73 % in the year after ringing but dropped to 33 % for later years.

More than half the nests were successful; failures were due to predation in 29 % of the cases. Some males and a few females participated in a real second clutch. About 71 % of the eggs laid hatched, and 46 % produced a fledgling; 1.2 to 4.9 (mean 3.3) young fledged per female per year. There was a slight positive correlation between numbers of offspring and the population size in the following year. At least in many years the production of young by the population probably did not suffice to compensate the annual mortality. However, it might do so if the adult mortality did not exceed 50 % and the first year mortality 70 %. In practice, it seems that the equilibrium of the Garden Warbler population in the study area is maintained by immigration, the recruitment of mostly one year old but probably also older individuals from other breeding areas.

Tapio Solonen, Lammi Biological Station, SF-16900 Lammi, Finland

Although the Garden Warbler *Sylvia borin* is one of the most abundant bird species in Finnish forests, its population dynamics is comparatively difficult to study. The skulking way of life of the birds makes observation difficult, the search for nests is time-consuming, and the sexing of living birds is not always reliable. In addition, the ageing of adult birds is uncertain.

The present study reports the structure and dynamics of a south Finnish Garden Warbler population studied for eight breeding seasons (1971—78). The results are partly preliminary.

Study area, methods and material

The study area, about 27 ha, is situated in southern Tavastia (61°03'N, 25°03'E), mainly in the area of Lammi Biological Station (Solonen 1976, 1977, Solonen & Tiainen 1978a, b, Tiainen & Solonen 1979). Field studies included direct observations, mist-netting, individual marking of birds, mapping of territories (Enemar 1959, Anon. 1970) and systematic searching for nests.

The numbers ringed during the study were 187 obviously stationary adult birds, 38 other adults and 233 nestlings. The adult birds were marked both with normal aluminium rings and with individual combinations of 2—3 plastic colour-rings, and the nestlings of the different years were marked with normal or coloured anodized aluminium rings. In all, 208 territories and 97 nests with eggs or nestlings of Garden Warblers were recorded.

TABLE 1. Numbers of territories and nestings, and the size of the local Garden Warbler population of Lammi in 1971—78. Late territories are shown in parentheses.[1] Study area 27 ha.

	1971	1972	1973	1974	1975	1976	1977	1978
Territories[2] with nesting								
recorded	2	14 (4)	18 (3)	18 (1)	9	11	13	10
probable	4	7 (2)	5 (5)	6	11 (2)	9	6	8
possible	18	3*	2*(2)	2*	2 (2)	3	2	3 (1)
Total	24	24 (6)	25(10)	26 (1)	22 (4)	23	21	21 (1)
Nestings[2]	24	27	33	25	26	23	21	20
Population size[2]								
males	24	25	24	27	22	23	21	21
females	24	24	23	24	22	23	21	19
Total	48	49	47	51	44	46	42	40

Notes: [1] These are territories used for real second clutches of the male, female or both parents, and for some late first clutches (not obvious replacements). [2] Some males occupied two territories simultaneously and nested in both, some territory-holders were considered to be single males (*), and some males failed to establish a permanent territory. Some birds probably arrived in the study area during the breeding season for a replacement or second clutch.

Results

Population density. The population size was estimated on the basis of recorded territories, nests and marked birds. The number of territories, nestings, and stationary birds are presented in Table 1. Nesting was considered probable if a courting pair, or a bird feeding or giving alarm calls was met in a permanent territory, and possible if only a singing male was recorded. Hence, the group of "possible nestings" may also include some unpaired birds. There were 21—26 more or less clear-cut territories in the study area during the first half of the breeding seasons. Defence of territorial boundaries weakens during the nestling period at the latest, and replacement and second clutches may change the territorial boundaries.

The population density in the study area (27 ha), calculated on the basis of the average number of territories (23) in the 8 study years, was about 86 pairs/km^2. This value is about tenfold the normal densities in the district (7—9 pairs/km^2; O. Järvinen & R. A. Väisänen, unpubl.). Most territories were situated in the luxuriant southern part of the study area, where the density was about 112 pairs/km^2 (Table 2). In the less fertile northern part there was more space between territories, although territory size seemed to be larger than elsewhere. In the first 3 study years (1971—73) the territories were divided rather similarly between these two parts but in 1974—77, when conditions were unfavourable because of cold and rainy days, the density decreased markedly in the less fertile area, whereas in the luxuriant habitat it first increased slightly and then fluctuated between narrow limits.

The edge effect, i.e. the concentra-

TABLE 2. Number and density of the Garden Warbler territories in luxuriant (16 ha) and less fertile (11 ha) parts of the study area in 1971—78.

	Luxuriant part		Less fertile part	
	N	*N*/km²	*N*	*N*/km²
1971	17	106.3	7	63.6
1972	17	106.3	7	63.6
1973	17	106.3	8	72.7
1974	20	125.0	6	54.5
1975	18	112.5	4	36.4
1976	19	118.8	4	36.4
1977	17	106.3	4	36.4
1978	18	112.5	3	27.3
Mean	17.9	111.7	5.4	48.9

tion of birds in the boundary zone between forest and a more open area, clearly influences the spacing of territories. The open area need not necessarily be large or clear-cut; a small road through the forest or a little sparsely wooded area in the middle of it is enough.

Sex ratio and breeding state. Birds in the hand were sexed according to the shape of the cloacal region and the incubation patch, because there are no known differences in plumage between the sexes (e.g. Svensson 1970). Both sexes have an incubation patch during the breeding season (Efremov & Payevski 1973), but in the male it is not usually as naked as in the female. In the field, the birds could often be sexed according to their behaviour (e.g. song). The sex ratio seemed to be nearly equal. The annual estimates give an average male proportion of c. 51 % (Table 1), although in the individually known part of the population it was c. 54 %.

As the breeding state could not be confirmed for every bird, the number of non-breeding individuals is unclear. However, since some males paired with at least two females during one breeding season (Solonen 1977), there were presumably some non-breeding males in the population. Besides some obviously unpaired territory-holders, some birds caught during the breeding seasons most probably did not own any of the territories recorded. These birds may have been non-breeding stragglers belonging to the so-called floating population (e.g. Enemar 1959), birds which have failed in nesting or are breeding somewhere else. A few females and some males bred twice in a year.

Site tenacity. Of the 164 obviously stationary birds marked in the breeding time in 1972—77, 20 males and 5 females were recovered in later years (Table 3). None of the 201 nestlings ringed in 1972—77 was recorded in the following years. Birds were recovered on new territories in different parts of the area, but also near to their previous territories or in the immediate vicinity of the previous nest site (Table 4). One nest was even found in the very same site, although the birds were not the same. Thus, the nearness of nests in different years not only indicates nest site tenacity in the birds, but also shows the places that meet the nest-site requirements of the species especially well.

Annual mortality of adult birds. The annual mortality was estimated from the non-return rate of marked

TABLE 3. Numbers of stationary Garden Warblers ringed and recaptured in later years in the study area.

		Males	Females	Total
Ringed	*N*	80	84	164
Recaptured	*N*	20	5	25
	%	25.0	6.0	15.2

TABLE 4. Distances (m) between the nests of the same Garden Warbler individuals in different years, in the population of Lammi.

Distance	0—25	26—50	51—100	101—200	201—400	>400	Mean	Range
Males	3	—	4	1	2	1	150	<5—500
Females	2	1	—	—	2	—	130	<5—325

Note: In the study area the greatest possible distance is c. 850 m, and the greatest distance between nest sites was c. 680 m.

birds. In this connection the mortality actually means the disappearance of individuals from the population, thus comprising both deaths and emigration. On average, over 70 % of the estimated total number of adult Garden Warblers were annually ringed or recovered in the study area, and about 62 % of them died (or emigrated) during the next year (Table 5). Differences between years seem to be relatively small, but the annual mortality (turnover) of the females, about 82 %, seems to be significantly higher than that of the males ($\chi^2=20.99$, $P<0.001$). The return rate of the Garden Warblers seems to be lower in the year following recruitment to the population than in later years, when it actually better represents the real survival rate (cf. v. Haartman 1949) and is about 60—70 % (Table 6). The mortality of these birds is thus 30—40 %, averaging 33 %.

TABLE 5. Annual non-return rate (%) of marked (*N*) adult Garden Warblers in the population of Lammi.

	Males		Females		Total	
	N	%	*N*	%	*N*	%
1972—73	20	62	18	83	38	72
1973—74	22	53	22	84	44	67
1974—75	26	47	20	88	46	58
1975—76	16	45	9	74	25	52
Mean	21	52	17	82	38	62

The annual mortality was calculated as follows:

Mortality (%) = 100[1-(recovery rate) : (proportion of the total population caught in 2nd year)].

It was assumed that all the marked birds used in calculations belonged to the local population and that — as in an ideal case — all the surviving individuals returned every year to the study area.

Age structure of population. If the above assumptions are valid and if all immigrants to the population were one year old, about 60 % of the adults in the Garden Warbler population studied were birds born in the previous year (Table 7). The proportions of older birds seem to remain fairly constant year after year. Due to the higher mortality (turnover) of the females, their average age (period spent in the population) is lower than in the males. The oldest bird recorded during the study was a male that reached an age of at least 5 years.

Nesting success and fledgling production. The nesting success of the Garden Warbler population fluctuated heavily during the study. Predation was the most common cause of unsuccessful breeding. In only a small proportion of the nests was failure due to starvation or some other reason (Table 8). Some individuals, males more often than females, participated

TABLE 6. Return rate of the Garden Warblers in relation to age in the population of Lammi, according to calculations based on numbers of ringed and recaptured birds.

Year	x	x+1	x+2	x+3	x+4
	E O	E O	E O	E O	E O
1972	49 (38)	13.8(10)	8.3 (7)	5.8 (3)	3.5 (1)
1973	33.2 (34)	7.1 (6)	5.8 (3)	3.5 (1)	—
1974	35.6 (33)	9.8 (5)	7.0 (2)	—	—
1975	22.6 (14)	7.0 (2)	—	—	—
Total	140.4(119)	37.7(23)	21.1(12)	9.3 (4)	3.5 (1)
Returned %	27	69	66	60	

Note: x = year of recruitment/ringing, E = estimate for whole population, O = uncorrected number based on observations on ringed birds.

in a real second clutch, especially in favourable breeding seasons (cf. Table 1).

The clutch size averaged 4.62±0.78 (*SD, N* 61). About 71 % of the eggs laid hatched, and 46 % produced a fledgling. On average, 7.2 eggs were laid, 5.1 young hatched, and 3.3 young fledged per female per season (Table 9). The average number of fledglings produced per successful breeding was 3.8. The whole population, averaging 46 adult individuals, was estimated to produce about 72 fledglings per year.

Discussion

Population density. The abundance of food and the great number of sheltered nest sites were probably the main factors responsible for the concentration of the Garden Warbler territories in the most luxuriant part of the study area, where the territories were more than twice as dense as in the less fertile part (112 vs. 49 per km²). In the latter area, however, the range of the yearly fluctuations was as much as 93 % of the mean density, as against only 17 % in the luxuriant part. The territories were also smallest where food was abundant and the vegetation rich, as in many other species (e.g. Cody 1974, Cody & Walter 1976).

Territorial behaviour may limit the size of a breeding population if the suitable habitat is restricted, but probably not very effectively (e.g. Lack 1966, Cody 1971, Klomp 1972; cf. however Wynne-Edwards 1962). The effect of territoriality on the population is likely to differ with the species and habitat. It may be insignificant, or it may force some of the individuals to occupy suboptimal en-

TABLE 7. Age structure in the Garden Warbler population of Lammi in 1972—76. Number of individuals in different age-classes.

	Minimum age (years)				
	1	2	3	4	5
1976	24	7	7	4	4
1975	22	10	6	6	
1974	36	7	8		
1973	33	14			
1972	49				

Note: All recruits to the population were assumed to be one year old. In the birds ringed in the first year of study (outermost figures on the right in each year) separate age-classes could not be distinguished.

TABLE 8. Nesting success and causes of failure in the Garden Warbler population of Lammi in 1972—78.

	1972	1973	1974	1975	1976	1977	1978	Total
No. nests	16	20	18	8	12	11	10	95
Unsuccessful (%)	31	20	61	50	75	45	30	45
Predation	19	10	39	38	42	36	20	29
Starvation	6	5	11	—	25	—	—	7
Other causes	6	5	11	13	8	9	10	9
Successful (%)	69	80	39	50	25	55	70	55

vironments, or even prevent them from breeding (v. Haartman 1971). At least in some cases, the high density of Garden Warblers already present may have prevented additional birds from settling in the area and so restricted the potential number of simultaneously breeding warblers (Solonen 1976).

Interspecific competition. Besides intraspecific competition, there is obviously also some kind of interspecific competition with the Blackcap *Sylvia atricapilla.* The two species have many ecological similarities, e.g. habitat preference, feeding behaviour and a considerable overlap in foraging height (cf. Lack 1971, Cody & Walter 1976, Mason 1976). Their territories are at least partly mutually exclusive, either temporally or spatially, although there is some overlap, too. In general, Blackcaps start nesting earlier than Garden Warblers, but the territories of Blackcaps are usually larger, which makes them difficult to defend against the more numerous Garden Warblers. Blackcaps usually breed only in the most luxuriant parts of the study area. In the potential nesting time of both species, vacated territories often immediately attract new breeding pairs, usually Garden Warblers. These may be birds which have failed in their earlier breeding attempts or are about to start their second breeding, or possibly also birds which have so far been prevented from breeding, e.g. by territorial behaviour or lack of a suitable nest site (cf. e.g. Hensley & Cope 1951, Diesselhorst 1968, Harris 1970).

According to Murray (1971), interspecific aggressiveness between similar-sized widely sympatric species that are common in the same habitats is unidirectional — the one attacks and the other retreats. In the present case of the Garden Warbler and the Blackcap, the latter seems to be the more

TABLE 9. Breeding success per female including first, replacement and second clutches in the Garden Warbler population of Lammi in 1972—78.

	1972	1973	1974	1975	1976	1977	1978	Mean
Females	24	23	24	22	23	21	19	22
Eggs laid	6.5	8.1	7.6	8.2	7.0	6.5	6.4	7.2
Eggs fully incubated	6.0	6.7	4.2	5.5	3.9	4.7	6.4	5.3
Eggs hatched	5.6	6.4	3.6	5.2	3.7	4.5	6.4	5.1
Young fledged	4.2	4.9	1.7	3.9	1.2	3.0	4.1	3.3

aggressive. Howard's (1948) observations point to the same conclusion, whereas Raines (1945) reports that the two species are more or less mutually exclusive. Some sibling species may also be different in many respects but compete with each other in certain conditions. In the area where their ranges overlap, the Reed Warbler *Acrocephalus scirpaceus* and the Sedge Warbler *A. schoenobaenus* are generally separated from each other by their feeding or nesting habits, either temporally or spatially, but when they share habitats, their territories are clearly mutually exclusive (Catchpole 1972, 1973).

Site tenacity. Garden Warblers have been found to come back year after year to their old breeding areas both in this south Finnish population and in central Europe (Novak 1959, Bezzel 1963). The study area was too small for definite conclusions about the site tenacity of the birds, but males may be significantly more site tenacious than females (Table 3; $\chi^2 = 8.49$, $P < 0.01$). The distances between the nesting sites chosen by birds in different years also indicate site tenacity (Table 4) (cf. Barlein 1978). The high non-return rate of the females may be caused by their weak site tenacity or high mortality, or both (cf. v. Haartman 1949, 1951, Haukioja 1971). There are no marked differences in catchability or observability between the sexes in the Garden Warbler, like those in some other species (e.g. Hildén 1978). Breeding may strain females more than males and so increase their mortality (cf. e.g. Cody 1971, Bulmer & Perrins 1973). Higher mortality of the females is usual in small passerines (Lack 1954).

Adult mortality. Age-independent mortality is considered typical of adult birds (e.g. Kluijver 1951, Farner 1955, Soikkeli 1970, v. Haartman 1971; see however also Botkin & Miller 1974, Hildén 1978), but the mortality of birds breeding for the first time may be higher than that of older ones, possibly because of their lower social position and inexperience in utilization of environmental resources. The estimated annual mortality of adult Garden Warblers (62 %) exceeds that of a southwest German Blackcap population (54 %) (Barlein 1978) but is within the normal range for passerines (40—70 %) (e.g. v. Haartman 1951, Schmidt & Hantge 1954, Farner 1955, Haukioja 1969).

The mortality figures for the Garden Warbler presented in Table 5 are based on more data and arrived at by slightly different methods than my preliminary values (Solonen 1976, Solonen & Tiainen 1978a, b), and are probably more realistic. However, when the birds had returned once to the study area, the mortality sank to 33 % (cf. Table 6). Thus, the real adult mortality may be noticeably lower than the turnover, because it is unlikely that all old birds (especially females) are site tenacious. Similarly, the proportion of yearlings suggested is obviously too high, because the immigrants may also include birds over one year old. The mortality rates are or may be biased for at least the following reasons: (1) errors made in estimating the population size and sex ratio, (2) the estimates of the proportion of the total population caught may be unreliable because they may include birds not belonging to the local population, (3) the low proportion of birds caught in some years makes the sample size rather small, (4) it is unlikely that all the surviving birds returned to the study area every

year, (5) the study period was short, and (6) the study population was small.

Breeding success. In the Garden Warbler the factors that may affect the production of young, either directly or indirectly, include (1) clutch size, (2) food, (3) predation, (4) weather, (5) brood size and number of broods, (6) time required for nesting, (7) nest site, (8) cover vegetation, (9) time of the breeding season, (10) habitat (includes above-mentioned factors), and (11) population density (Solonen 1976, 1977). In the years when development of the cover vegetation was delayed due to cold weather (1974—77), the losses due to predation were more serious than in other years (Table 8). Predation is in general the most important cause of breeding losses in birds (e.g. Cody 1971, v. Haartman 1971). In the population studied the clutch size was higher (4.62) but the breeding success lower (Table 9) than in British Garden Warblers. The British birds laid 4.44 eggs per clutch, and 57.6 % produced a fledgling (Mason 1976).

Concluding remarks. The heavy fluctuations in the number of young produced by the Garden Warbler were accompanied by fluctuations in population size, but these were small, and the population studied seemed to be in a stable condition. There was a slight positive correlation between the numbers of offspring and the population size in the following year (r = 0.75, not significant). After a year when the production of young was very low (1974), both the population density and the proportion of yearlings/immigrants seemed to be lower than before (Table 7), evidently reflecting low breeding success in the previous year outside the study area as well. Within a longer time sequence or a larger area fledgling production has to compensate the adult mortality, otherwise the status of the species will change. Mostly owing to heavy predation, the production of young in the present population probably failed to compensate for adult mortality in many, if not all, of the study years (cf. Barlein 1978). Theoretically, such compensation seems possible, e.g. if adult mortality does not exceed 50 % and first year mortality 70 %. In practice, it appears that the equilibrium of the population was maintained by immigration of one-year-olds and probably also some older individuals from other breeding areas. The mortality of young birds may also noticeably affect population density (Lack 1966, Murton 1972). However, the environment of the study area is particularly attractive for the Garden Warbler, and in such habitats immigration of birds from other areas very effectively compensates losses caused by mortality and emigration.

Difficulties in estimating the local population size, sex ratio, number of breeding individuals and breeding attempts, mortality, etc. often reflect the diffuse nature of the population (cf. Diesselhorst 1968, Solonen 1977). The Garden Warbler population of the study area is not an isolated unit, and individuals obviously frequently cross the arbitrary boundaries of the area even in the breeding season.

Acknowledgements. I wish to thank Pertti Saurola and Juha Tiainen for help in the early stages of the study and in the field work. Many useful comments on the drafts of the manuscript were made by Heikki Auvinen, Olavi Hildén, Martti Soikkeli, Torsten Stjernberg and Risto A. Väisänen. Pertti Rassi mapped the territories in 1971 and contributed data for 1972—73, and many other persons helped in the field. In 1977 the work was supported financially by the Leo and Regina Wainstein

Foundation and Societas pro Fauna et Flora Fennica.

Selostus: Lehtokertun populaatiodynamiikasta Lammilla

Lehtokertun populaatiodynamiikkaa tutkittiin Lammilla, Etelä-Hämeessä, vuosina 1971—78. Tutkimusalueella (27 ha) oli vuosittain pesimäkauden alkupuolella 21—26 reviiriä, mukana myös ilmeisesti parittomien koiraiden reviirejä. Lehtokerttutiheys, 86 reviiriä/km², osassa aluetta n. 112 reviiriä/km², on poikkeuksellisen suuri verrattuna keskimääräisiin arvioihin Etelä-Suomessa (7—9 paria/km²). Alueen karummassa osassa tiheys oli kuitenkin vain 49/km² ja vaihteli täällä vuosittain enemmän kuin muualla.

Rengastetuista, paikallisista aikuislinnuista (164) noin 15 % (25 % koiraista ja 6 % naaraista) tavattiin uudelleen tutkimusalueella myöhempinä vuosina. Aikuislintujen vuosikuolevuus (vaihtuvuus) oli koirailla 52 % ja naarailla 82 %. Rengastuksen jälkeisenä kesänä linnuista palasi vain 27 %, mutta myöhempinä vuosina keskimäärin 67 %.

Noin 71 % munituista munista kuoriutui ja 46 % tuotti lentopoikasen. Pesimätulos vaihteli vuosittain paljon etenkin petoeläinten ja sääolojen vaihtelevasta vaikutuksesta siten, että lentopoikasia tuotettiin 1.2—4.9 (keskim. 3.3) naarasta kohti. Eräät yksilöt, koiraat useammin kuin naaraat, osallistuivat onnistuneen pesinnän jälkeen toiseen pesintään saman pesimäkauden aikana, mutta yleensä vain suotuisissa olosuhteissa.

Populaation poikastuotto ei ainakaan useina vuosina näytä riittävän korvaamaan aikuiskuolevuutta. Teoriassa se olisi kuitenkin mahdollista, jos aikuiskuolevuus ei ylitä 50 % eikä ensimmäisen vuoden kuolevuus 70 %. Käytännössä sen sijaan on ilmeistä, että tutkimusalueen lehtokerttupopulaatiota pitävät vakaana muilta pesimäalueilta tulevat, enimmäkseen yksivuotiaat, mutta luultavasti osittain myös vanhemmat linnut.

Taulukoissa esitetään seuraavat tiedot: 1. reviirien ja pesintöjen määrä sekä paikallisen populaation koko, 2. reviirien määrä ja tiheys tutkimusalueen rehevässä ja karussa osassa, 3. tutkimusalueella paikallisina rengastettujen ja myöhempinä vuosina kontrolloitujen lintujen määrät, 4. etäisyydet samojen lehtokerttuyksilöiden pesien välillä eri vuosina, 5. tutkimuspopulaation lehtokerttujen vuotuinen vaihtuvuus, 6. palanneiden määrä suhteessa ikään, 7. populaation ikärakenne, 8. pesinnän epäonnistumisen syyt ja onnistuneiden pesien osuus, ja 9. pesintätulos naarasta kohti.

References

ANON. 1970: Recommendations for an international standard for a mapping method in bird census work. — Bull. Ecol. Res. Comm. Nr 9:49—52. — Lund.

BARLEIN, F. 1978: Über die Biologie einer südwestdeutschen Population der Mönchgrasmücke (Sylvia atricapilla L.). — J. Orn. 119:14—51.

BEZZEL, E. 1963: Zum Durchzug und zur Brutbiologie von Grasmücken (Sylvia) nach Fängen und Ringfunden im Ismaninger Teichgebiet, Oberbayern. — Vogelwarte 22:30—35.

BOTKIN, D. & R. S. MILLER 1974: Mortality rates and survival of birds. — Amer. Nat. 108:181—192.

BULMER, M. G. & C. M. PERRINS 1973: Mortality in the Great Tit Parus major. — Ibis 115:277—281.

CATCHPOLE, C. K. 1972: A comparative study of territory in the Reed Warbler (Acrocephalus scirpaceus) and Sedge Warbler (A. schoenobaenus). — J. Zool., Lond. 166:213—231.

CATCHPOLE, C. K. 1973: Conditions of coexistence in sympatric breeding populations of Acrocephalus warblers. — J. Anim. Ecol. 42:623—635.

CODY, M. L. 1971: Ecological aspects of reproduction. — *In* D. S. FARNER & J. R. KING (eds.): Avian biology, Vol. 1:461—512. New York.

CODY, M. L. 1974: Competition and the structure of bird communities. — Princeton.

CODY, M. L. & H. WALTER 1976: Habitat selection and interspecific interactions among Mediterranean sylviid warblers. — Oikos 27:210—238.

DIESSELHORST, G. 1968: Struktur einer Brutpopulation von Sylvia communis. — Bonn. Zool. Beitr. 19:307—321.

EFREMOV, V. D. & V. A. PAYEVSKY 1973: Incubation behaviour and incubation patches of males in five species of genus Sylvia (in Russian with English summary). — Zool. Žurnal 52:721—728.

ENEMAR, A. 1959: On the determination of the size and composition of a passerine bird population during the breeding season. — Vår Fågelvärld, Suppl. 2:1—114.

FARNER, D. S. 1955: Bird-banding in the study of population dynamics. — *In* A. WOLFSON (ed.): Recent studies in avian biology, pp. 397—449. Urbana.

v. HAARTMAN, L. 1949: Der Trauerfliegenschnäpper. I. Ortstreue und Rassenbildung. — Acta Zool. Fenn. 56:1—104.

v. HAARTMAN, L. 1951: Der Trauerfliegenschnäpper. II. Populationsprobleme. — Acta Zool. Fenn. 67:1—60.

v. HAARTMAN, L. 1971: Population dynamics. — *In* D. S. FARNER & J. R. KING (eds.): Avian biology, Vol. 1:391—459. New York.

HARRIS, M. P. 1970: Territory limiting the size of the breeding population of the Oystercatcher (Haematopus ostralegus) — a removal experiment. — J. Anim. Ecol. 39:707—713.

HAUKIOJA, E. 1969: Mortality rates of some Finnish Passerines. — Ornis Fennica 46: 171—178.

HAUKIOJA, E. 1971: Short-distance dispersal in the Reed Bunting Emberiza schoeniclus. — Ornis Fennica 48:45—67.

HENSLEY, M. M. & J. B. COPE 1951: Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. — Auk 68:483—493.

HILDÉN, O. 1978: Population dynamics in Temminck's stint Calidris temminckii. — Oikos 30:17—28.

HOWARD, E. 1948: Territory in bird life. — London & Glasgow.

KLOMP, H. 1972: Regulation of the size of bird populations by means of territorial behaviour. — Neth. J. Zool. 22:456—488.

KLUIJVER, H. N. 1951: The population ecology of the Great Tit, Parus m. major L. — Ardea 39:1—135.

LACK, D. 1954: The natural regulation of animal numbers. — Oxford.

LACK, D. 1966: Population studies of birds. — Oxford.

LACK, D. 1971: Ecological isolation in birds. — Oxford.

MASON, C. F. 1976: Breeding biology of the Sylvia warblers. — Bird Study 23:213—232.

MURRAY, B. G. 1972: The ecological consequences of interspecific territorial behaviour in birds. — Ecology 52:414—423.

MURTON, R. K. 1972: The control of bird populations. — Gerfaut 62:63—81.

NOVAK, L. 1959: Zug beringter Grasmücken der Gattung Sylvia aus der Tschechoslovakei. — Sylvia 16:161—172.

RAINES, R. J. 1945: Notes on the territory and breeding behaviour of Blackcap and Garden Warbler. — Brit. Birds 38:202—204.

SCHMIDT, K. & E. HANTGE 1954: Studium an einer farbig beringten Population des Braunkehlchens (Saxicola rubetra). — J. Orn. 95:130—173.

SOIKKELI, M. 1970: Mortality and reproductive rates in a Finnish population of Dunlin Calidris alpina. — Ornis Fennica 47: 149—158.

SOLONEN, T. 1976: Lammin biologisen aseman ympäristön lehtokerttupopulaatio vuosina 1971—76. — M. Sc. thesis, Dept. Zool., Univ. Helsinki.

SOLONEN, T. 1977: Lehtokertun Sylvia borin pesimäbiologiasta (Summary: Breeding biology of the Garden Warbler). — Lintumies 12:69—78.

SOLONEN, T. & J. TIAINEN 1978a: The study of the bird community in the station area. — Lammi Notes 1:16—18.

SOLONEN, T. & J. TIAINEN 1978b: A bird community study at Lammi Biological Station, southern Finland (in Polish with English summary). — Notatki Ornitol. 19 (1—4):55—63.

SVENSSON, L. 1970: Identification guide to European Passerines. — Stockholm.

TIAINEN, J. & T. SOLONEN 1979: Erään eteläsuomalaisen alueen lintuyhteisö (Summary: The breeding bird community in a south Finnish study area). — Lintumies 14.

WYNNE-EDWARDS, U. C. 1962: Animal dispersion in relation to social behaviour. — Edinburgh.

Received October 1978, revised December 1978