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WITH NOTES ON RELATED SPECIES

BY

STAFFAN ULFSTRAND

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(Report from Falsterbo bird station No. 19)

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1. Introduction

The present investigation was initiated with a view at elucidating the enigmatic migratory movements in the Great Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*). These species appear almost annually at the Falsterbo bird observatory in strongly fluctuating numbers but at the same time may be found wintering in large numbers over their entire ranges within Sweden. Also the Coal Tit (*Parus ater*) exhibits large-scale annual fluctuations at the observatories, but this species has long been counted with the so-called irruption birds, and its movements are known to be correlated with the annual variations in the seed crop of the spruce (*Picea abies*). The Treecreeper (*Certhia familiaris*), the Goldcrest (*Regulus regulus*) and the Longtailed Tit (*Aegithalos caudatus*) also pass through at the observatories, the former two species in all years, the latter only in some years. But little migration is performed by the former two species in daylight and numbers are usually comparatively low in the latter, and therefore their movements have attracted less attention than the more spectacular movements of the Great, Blue and Coal Tits. Other Swedish species of the genus *Parus* are rare or absent at the observatories.

The ecological background to the movements of the Great and Blue Tits is a question that has been almost completely ignored in spite of the strong interest shown by ornithologists for the ecology of these species. The Great Tit is without doubt one of the best known birds of the world, as far as the breeding biology and population dynamics are concerned. The fact that many aspects of the annual cycle of this species have been investigated of course is of great help in an attempt to fill the gaps in our knowledge concerning its migration ecology.

Even if the interest was focussed on the Great Tit from the beginning, it was judged that a comparative study of the nonbreeding ecology of other Swedish species of the genus *Parus* would be necessary. Further opportunities for comparisons were obtained through adding the Goldcrest, the Treecreeper and the Longtailed Tit to the list of species involved in this study. Although systematically more or less unrelated to the true tits of the genus *Parus*, the nonbreeding ecology of these species in several respects resembles that of the *Parus* species. Initially, also the Nuthatch (*Sitta europaea*) was included, but since the study of its feeding habits involved particularly great difficulties (p. 22), it was dropped at an early stage.

Fluctuations in the food supply have been demonstrated to play an important rôle for the migratory system of many species that occur in strongly fluctuating numbers at the bird observatories. With regard to this fact it was considered necessary to undertake a careful study of the feeding habits of the species involved. Such a study of course had to be carried out over at least two or three nonbreeding seasons. The author's field studies on the feeding habits were commenced in November 1958 and discontinued in midwinter 1960/61. It was important to collect information from more than one locality, but after a time the conditions prevailing in deciduous woods attracted the whole interest. However, since the studies were carried out in an area of mixed woodland, it was possible to keep an eye also on those species preferring coniferous trees. At the same time as the feeding ecology was being studied, information was also gathered concerning the activity types of the birds. Such information may indicate the relationship between the birds and the food supply by showing how large a proportion of their time the birds have to devote to food seeking. If this proportion approaches 100 %, it may be assumed that the birds are up against food scarcity.

Seasonal and annual changes in the density of the populations in the investigation area of course had to be closely followed. However, the results obtained only reflect strictly local conditions. Therefore it was necessary to secure information concerning the population density over larger areas, not as absolute figures per unit area, but rather as annual changes in relative density. This information was provided by a cooperative census, performed by several hundred field ornithologists scattered over the southern and middle parts of Sweden.

A rich material concerning the migration of North European birds has been collected at the Swedish bird observatories at Falsterbo in Skåne and Ottenby at the southern tip of the island Öland in the Baltic in the course of the last twenty years or so. This material proved a rich source also for information concerning the migration of tits. The studies at the bird observatories are carried out with two main aims: first to record the visible migration, and second to trap and ring the largest possible portion of the resting migrants. Both techniques have yielded valuable information on the migration of tits.

The basis for this paper was provided by the extensive material gathered at the Falsterbo bird observatory during the last two decades.

2. Description of study areas

Most of the field work concerned with the feeding habits of the birds was performed in the south-central part of the province of Skåne (Scania) in southernmost Sweden (approx. 55° 40′ N. lat., 13° 35′ E. long.). This part of Skåne is a predominantly agricultural district with light sandy soils, There are several lakes, the largest of which is Vombsjön. There are also considerable stretches of meadows, in part dry and uninteresting but elsewhere wet and inhabited by a rich bird life. They are used for grazing cattle. Woods also occupy a prominent position in Central Skåne. They are of two main types: first, there are comparatively "natural" types of deciduous woods, most often with beech (*Fagus silvatica*) as the dominating tree, and second, there are large tracts of planted coniferous woodland. Both types are intensely managed, but some deciduous groves have been allowed to grow old to the great advantage of wildlife.

The main study area was predominantly of the first type. This area, called the Öved wood, is covered with mixed woodland. Beech and oak (*Quercus robur*) are the dominant trees, and both occur in clumps of considerable age. There are also areas of alder (*Alnus glutinosa*) and scattered trees of ash (*Fraxinus excelsior*), birch (*Betula alba*), elm (*Ulmus scabra*), wild cherry (*Prunus avium*) and others. In this area there are also three clumps of pine (*Pinus silvestris*) and spruce (*Picea abies*). Further, there are a number of open areas, partly cov-

ered with shrub of *Salix spp.*, *Sorbus nigra*, *Viburnum opulus* and *Rubus fruticosus*. The Öved wood is delimited to the south by the shore of Vombsjön. Along the shore is a marshy strip, covered by alders. There is also a relatively narrow fringe of reed (*Phragmites communis*), in which scattered willows (*Salix*) occur. To the southeast the wood is delimited by meadows grazed by cattle. Along the edge there is a dense shrub vegetation of for example willows, *Prunus padus* and *Sorbus nigra* as well as young beech. To the east lies an extensive fruit orchard. To the north the study area is delimited in part by dry meadows, in part by cultivated fields and in part by a road, on the far side of which the woodland extends over a considerable area. No woodcutting was going on, whilst my field work was carried out, nor was any significant amount of food added by human interference. The birds thus had to depend entirely on "natural" foods.

The Öved wood is not thoroughly mixed. Rather the trees tend to be separated in pure clumps within the wood: first a group of beech, then a group of oak etc. There is one area, however, of thoroughly mixed pine and spruce and another of beech and oak. Both these mixtures are made up of comparatively young trees. In the pure oak and beech clumps, however, many trees have attained very old age.

It should be pointed out that the Öved study area is not isolated from other woodlands. On the contrary, the bird population is in communication with other populations through a broad area in the north and a narrow passage in the southeast. Particularly in the latter passage, which is made up chiefly of pines, tit flocks have often been seen to enter or depart from the study area. Certain species also frequent the fruit orchards and are by this area in contact with still other tree-covered areas. These opportunities of movements into and out of the area permit of the population being considered representative of the populations from a much larger area than the study area itself. This would hardly have been the case in an isolated grove surrounded in all directions by *e.g.* cultivated fields.

The appearance of the Öved wood is illustrated by Figs. 1 a to c and 2 a. The specific composition of the wood is made clear by Tab. 1.

Certain other woods were visited for special purposes. One was a pure beech wood, the B ö k e b e r g w o o d (Fig. 2 b), situated approx. 30 km SW of the Öved wood. This wood is of moderate to

Tab. 1. Some features of the Öved study area: estimates of the proportion of different vegetation types and of the specific composition of the wood.

See also Figs. 1 and 2.

Whole area:		*Specific composition of the Öved wood:*	
Tree-covered ground without shrub	55 %	Beech (*Fagus silvatica*)	35 %
Tree-covered ground with shrub	25 %	Oak (*Quercus robur*)	20 %
Shrub	10 %	Alder (*Alnus glutinosa*)	5 %
Open areas	10 %	Birch (*Betula alba*)	3 %
	100 %	Spruce (*Picea abies*)	15 %
		Pine (*Pinus silvestris*)	15 %
		Fruittrees (*Pyrus malus et al.*)	2 %
		Various	5 %
			100 %

rather old age and, still more than the Öved wood, is being intensely managed. A completely pure section of the wood was selected for the field work, although there were some small patches of undergrowth of young birch, alder and hornbeam (*Carpinus betulus*). The ground was covered by a thick carpet of beech debris and was almost devoid of herbaceous vegetation. The study area was in all directions surrounded by further beech woods. At a distance of some hundred metres, there were three clumps of spruce. No human habitations occur in this part of the wood.

A third study area was the Vomb wood (Fig. 2 c). To the south of Vombsjön there is an extensive area of coniferous plantations approx. 40 years of age. This wood stands on dry grassy ground and is made up of both pine and spruce. In the northwest corner of this wood, where the field work was carried out, the wood is of pure pine and the trees are of greater and more variable age than in most parts of the large plantation area. The area is cut in sections by narrow paths and broad fire breaks. Along the edges of the latter are narrow borders of birch, rowan (*Sorbus aucuparia*) and willows. The transect through this wood was located so that only pure pine areas were passed through. There were a number of uninhabited summer cottages, which did not attract the birds and where no food was offered to them.

a

b

c

Fig. 1. Öved. (See also fig. 2 a.) a) Clearing in a *Fagus-Pinus* mixed area with *Sorbus nigra* and *Urtica sp.* This place was much frequented by Marsh Tits (*Parus palustris*). The seeds were deposited chiefly in the pines. b) Mature *Fagus* wood on a slope facing south over Vombsjön. No ground vegetation. This habitat is much frequented by Great Tits (*Parus major*) when there is a good mast crop, but much less when there is no mast. c) Mixed *Fagus-Quercus* area with scattered *Picea* trees. — Photo: S. Ulfstrand, February 1961.

a

b

c

Fig. 2. a) Öved. Mixed *Pinus-Picea* area with dense undergrowth of *Sorbus nigra*, *Rubus spp.* and other shrubs. Marsh Tits (*Parus palustris*) frequently collected seeds from *Galeopsis*, *Urtica* and various grasses on the meadow, depositing them in the conifers. This part of the wood was chief haunt of Coal Tits (*Parus ater*) and Goldcrests (*Regulus regulus*). — b) Bökeberg. A pure *Fagus* stand where beech mast, when available, became all-dominant as tit food. Coal Tits frequented this area in some numbers to exploit the mast but were otherwise absent. — c) Vomb. A pure pine plantation, habitat for the Crested Tit (*Parus cristatus*). Goldcrests always were very numerous, whilst the Blue and Marsh Tits (*Parus caeruleus*, *P. palustris*) were only casually recorded. — Photo: S. Ulfstrand, February 1961.

3. Feeding habits of tits, the Treecreeper and the Goldcrest in the nonbreeding season

A. Introductory remarks

In the present chapter the information collected by the author on the feeding habits of the Great Tit, Blue Tit, Marsh Tit (*Parus palustris*), Treecreeper and Goldcrest, in part also the Crested Tit (*Parus cristatus*), in the nonbreeding season is given. The field work has been restricted to the three main study areas described above. The chief aim was to investigate whether there was any kind of food of predominant importance for some or all of the species, and if so, whether this kind of food occurred in strongly fluctuating quantities from year to year.

Several workers have previously studied the feeding habits of tits and the other species mentioned above. PALMGREN (1932) studied the differences in choice of feeding stations (for explanation of this term, see p. 19) between Willow Tit (*Parus montanus*) and Goldcrest and tried to correlate his findings with morphological-functional differences. COLQUHOUN & MORLEY (1943) studied the vertical zonation of certain woodland birds in England, whilst SNOW (1949) performed an interesting, though not extensive, study of the feeding stations in a Central Swedish forest. Later, several British ornithologists have paid close attention to the feeding habits of the tits in English deciduous and coniferous woods. HARTLEY (1953) and BETTS (1955) have published important contributions to this subject, and GIBB's (1954 a) extensive study in several respects has been a model for my own field work. Further, HAFTORN (1953, 1954, 1956 a, b, c, 1959) has performed extremely detailed investigations on the feeding habits of the Norwegian tits inhabiting coniferous forests, paying special attention to their storing habits. In fact, to HAFTORN must go the credit for discovering the extreme significance of food storing for tits wintering in high latitudes. Finally, GIBB (1960) has recently published a most important paper on the food supply, population density and mortality in tits and the Goldcrest in some English pine plantations. L. TINBERGEN (1960), in a study on the feeding habits of tits in Dutch woods, was particularly interested in the impact of bird predation on insect populations.

There are also many brief communications on the feeding habits of tits scattered in the literature. Most often they describe some unusual kind of food or feeding technique. In this connection the remarkable habit of opening milk bottles developed in Great Britain may be mentioned. This phenomenon has been described and discussed by *i.a.* FISHER & HINDE (1949), HINDE & FISHER (1951), CRAMP *et al.* (1960: 180) and GIBB (1960: 204), but no adequate explanation has been found. In Sweden the habit is obviously very rare. Interestingly, STRÖMBERG (1958) found that Great Tits, when offered milk bottles close to a bird-table in a district where the birds could not possibly have any previous experience of such bottles, rapidly acquired the habit of tearing off the capsules. His experiments did not show whether the capacity was acquired by one individual only or by several individuals in rapid succession. This kind of approach to the study of feeding habits on tits would be rewarding.

B. Selected references concerning the food and feeding habits

Swedish ornithological handbooks contain extremely scanty information on the food and feeding habits of the tits, the Treecreeper and the Goldcrest. The statements usually are transcriptions from earlier handbooks. This being so, the most equitable thing to do is to quote the original information supplied by NILSSON (1858) who published a handbook crammed with information, largely derived from own field observations. The following quotations are translations from the Swedish.

Great Tit (NILSSON *op. cit.*: 410—411): "In summer they devour plenty of insects, larvae and insect eggs; in autumn and winter they also consume plant seeds: oats, fruit pips, pine and spruce seeds, beech mast, nuts etc. They often visit carcasses. They do not unshell the seeds but grasp them with their toes and peck the kernel out. In captivity they will eat whatever one offers to them, from the animal as well as from the plant kingdom; in particular they like tallow and meat, both raw and boiled." Under the heading of "Habits and habitat" NILSSON gives the following additional information: "They attack unwell birds not rarely; they open their skull with their pointed beak and peck the brain out. Sometimes they gather in large numbers round birds that have been caught in snares and devour them. (I have once seen them devour a Blackcock (*Lyrurus tetrix*) which had been placed in a box.) When they are in a cage or a small room together with other small birds, they attack them not rarely and kill them, especially if they run short of food. If one throws a piece of meat to them in their cage, they fly with it to a high place, where they peck it in pieces, squeezing it between their toes, and eat it."

Blue Tit (NILSSON *op. cit.*: 423): "In summer, insects, larvae and pupae; in autumn also berries, kernels and plant seeds; in winter insect eggs and pupae, through the destruction of which he is useful particularly in the gardens."

Coal Tit (NILSSON *op. cit.*: 412): "Insects, larvae and pupae; he also takes seeds of pine and spruce etc."

Crested Tit (NILSSON *op. cit.*: 414): "Insects, larvae and insect eggs, and juniper berries and seeds of pine and spruce."

Marsh Tit (NILSSON *op. cit.*: 419): "Insects, larvae and pupae, and plant seeds and berries. In the gardens and woods he rids the trees of many noxious insects; he also devours seeds of thistle, burdocks, cabbages, sunflower and other plants. Among berries he is particularly fond of rowan, and therefore he is often caught in snares put up for small birds in autumn."

Treecreeper (NILSSON *op. cit.*: 182): "Insects, larvae, pupae and insect eggs, which he industriously seeks for in the bark of the trees." In another context: "This small bird devours plenty of noxious insects."

Goldcrest (NILSSON *op. cit.*: 430): "Small insects, larvae, insect eggs and pupae. They pick these items from the twigs and their extreme tips, which they examine from all quarters."

These descriptions, published a hundred years ago, contain almost all that has been recorded about the food of the species in question in Sweden. On the whole, the statements are correct, although there are a few unwarranted generalizations and exaggerations. Thus the murderous inclination of the Great Tit is certainly exaggerated, for it is obviously a rare incident for this species to kill another bird under natural conditions. Preys and carcasses are of no quantitative significance in the food ecology of the Great Tit. HAFTORN (1956 c: 5) found that the Willow Tit had the supply of juniper berries (*Juniperus communis*) to itself: "Neither the Crested Tit nor the Coal Tit utilizes this source of food". This is at variance with NILSSON's statements. Personally I am unable to support that the Marsh Tit shows any preference for rowan berries, but I do not doubt that they are sometimes consumed by this species. But NILSSON points to many essential facts in the food habits too, such as general preference of the Marsh Tit for vegetable foods, the dominant proportion of animal food in the Blue Tit and the completely animal diet of the Treecreeper and the Goldcrest. The omnivorous inclination of the Great Tit is well described, only somewhat too drastically; it is remarkable how NILSSON's opinion of the Great Tit has penetrated in much later literature (but see EDBERG 1962). It is also a point of interest that NILSSON lists

beech mast as a food item for the Great Tit but not for any other species.

The modern handbooks add no novel knowledge on the subject (HOLMSTRÖM *et al.* 1942, SVÄRDSON & DURANGO 1950).

In a recent popular handbook HAFTORN (1959) presents a survey of his findings concerning the food choice of three conifer-dwelling species of tits, *viz.* the Coal Tit, Crested Tit and Willow Tit. He also mentions that the Treecreeper may occasionally take a seed that has happened to cling to the bark. HAFTORN stresses the great importance of vegetable food for all the three tit species in winter. The Willow Tit almost always subsists mainly on vegetable foods in winter, whilst the other species have to depend on animal food to a large degree, when the coniferous seed crop has failed. PALMGREN (1959: 213) confirms that the Goldcrest is almost exclusively insectivorous, and DURANGO (1946) points out the great significance of spruce seeds for the Coal Tit.

Two standard references, although not concerned with conditions in this country, have to be briefly reviewed.

NIETHAMMER (1937) characterizes the food of the Great Tit as "äusserst vielgestaltig" and refers to the great seasonal changes in feeding habits. In spring, summer and autumn the Great Tit is said to subsist mainly on animal food but also "zuckerhaltige, frische Pflanzenteile wie Beeren, Erbsen, reife Birnen und andere Früchte . . . Mit beginnendem Winter wird immer stärker öl- und fetthaltige Nahrung bevorzugt, wie sie viele Samen (Hanf, Sonnenblumenkerne, Walnüsse u. a.) bieten, daneben fette Larven usw." Concerning the Blue Tit, NIETHAMMER states that the food is on the whole very similar to that of the Great Tit, "aber erheblich mehr Insekten". Among vegetable items, seeds are said to be less attractive than berries. For the Coal Tit, insects are said to be of great importance, but coniferous seeds play a significant role in winter. The Crested Tit is stated to live chiefly on insects and to take only a less significant proportion of coniferous seeds. For the Marsh Tit, the food is said to be made up of insects in spring and summer but also of large quantities of small seeds, particularly of herbs, and berries in autumn and winter. The Treecreeper and Goldcrest are said to be almost exclusively insectivorous. It may be added that the Long-tailed Tit also is stated to be exclusively insectivorous.

WITHERBY *et al.* (1948) list many different kinds of food for the Great Tit but present no quantitative information concerning their importance. The Great and Blue Tits are described as being very catholic in their food choice. For the latter species, beech mast is listed as a food item, although only in passing. The British population of Coal Tit is apparently much less dependent on spruce seeds than the Scandinavian birds. For this species, beech mast is also mentioned, as it is for the Marsh Tit. The Goldcrest and Treecreeper are stated to be insectivorous, although there are a few records of seeds being found in their gizzards.

The handbooks from Sweden and abroad thus contain no quantitative information on the food ecology of the species in question. More detailed information is available in some recently published studies devoted to the ecology of tits. They have particularly great interest, since they deal with the same species and similar habitats as the present investigation.

HARTLEY (1953) studied the feeding stations (see below, p. 19) of tits in certain English districts. The habitat consisted of deciduous woodland as well as gardens and plantations. Among details of interest for comparative purposes may be mentioned that the Blue Tit exhibited a clear preference for oak and that all the species involved in his study were capable of exploiting beech mast for food (*i. e.* Great Tit, Blue Tit, Coal Tit and Marsh Tit). The Great Tit took a large proportion of its food from the ground. It is rather interesting to learn that the ground temporarily became the most frequented feeding station for this species, for example when a large quantity of walnuts had dropped to the ground. The Marsh Tit was found to have a comparatively narrow range of feeding stations.

GIBB (1954 a) mentions that "there were unusually heavy crops of hazelnuts and beechmast in the autumn of 1950" and goes on to say that "hazelnuts were a staple food of Great Tits from September to April, and beechmast (taken rather less than hazelnuts) from September to March". The Great, Blue, Coal and Marsh Tits all took beech mast, but the Willow and Longtailed Tits did not. GIBB too noted that oak was much preferred by Blue Tits. He points out the variety of feeding stations visited by Marsh Tits and the preference shown by this species for vegetable foods.

BETTS (1955) focussed her interest on the relationship between bird and insect populations and used chiefly the technique of gizzard analysis, supplemented by field studies on the habits. She found that beech mast was preferred as food to other similar kinds of vegetable products, such as acorns and sweet chestnut (*Castanea sativa*). Particularly the Great and Marsh Tits were found to exploit the beech mast supply extensively. In a comparison BETTS reached the conclusion that "the Marsh Tit shares certain features with both the Great and Blue Tits, but in many ways its diet is nearer to that of the Great Tit" (*op. cit.*: 304). As will be presently shown, the findings in the study areas in Skåne agree closely with those of BETTS. The latter author found a much higher proportion of "nut tissue" in the Great and Marsh Tits than in the Blue Tit. Seeds of certain ground herbs were absent or nearly so from the Blue Tit, but frequent in the other two species. Rather unexpectedly from a Swedish view-point, such seeds were fairly well represented in the stomachs of Coal Tits. Birch seeds, on the other hand, were restricted to the Blue Tit, which extensively exploited this source of food from September to January. Moss sporogonia were frequent in the Blue Tit but absent from the other species. It would carry to far to cite the multitude of interesting findings reported by BETTS concerning the preferences shown by different tit species in their choice of insect food etc.

These quotations are intended to provide a background for the following descriptions of the feeding habits in South Swedish deciduous woods.

C. Study technique

In order to investigate the food ecology of a natural bird population several methods are conceivable. One is to kill a sufficient sample of the population and examine the gizzard contents in the laboratory. However, this method has important disadvantages for the study of the feeding habits of tits. Since great annual, seasonal, local and individual differences are to be expected, the sample would have to be so large that the population would be unsuitable for further study. Besides, the gizzard analysis method has serious inherent drawbacks, as discussed by HARTLEY (1948: 362) and VAN KOERSVELD (1951).

In the present study the aim was not to obtain complete lists of all the kinds of food consumed by the different species. No more was required than an adequate picture of what foods play quantitatively significant rôles for the different species. The degree of interspecific segregation also had to be examined. Neither of these problems can be tackled using the gizzard analysis method only. For example, if two species are found to have consumed the same kind of food even in large quantities, this does not prove that they are in competition, for they may have taken the food in different sections of the habitat, for instance on the ground and among the twigs, respectively.

Although subject to certain limitations, it was decided to use a simple observational technique for the study of the feeding habits of the tits, the Treecreeper and the Goldcrest in the South Swedish woods. Instead of collecting the birds, one has to carry out intense and large-scale field observations concerning their feeding habits. What is recorded in the field are the feeding stations of the birds, *i.e.* at what places within the habitat the birds are seeking food. It may be assumed that the frequency of visits by food seeking birds to a given feeding station approximately reflects the importance of the food provided at this feeding station. Often it can be directly seen what kind of food the birds are taking, and in other cases this may be inferred from circumstantial evidence. Even if a bird was not actually seen to find and swallow some food particle, its feeding station was recorded and included in the computations. It might be argued that only birds actually seen consuming some food were to be included. But this distinction is not possible to uphold in the field. Many of the particles taken are so minute that they are invisible to the human observer. Such tiny particles, *e.g.* aphids, are also often taken

at such a rate (*cf.* GIBB 1960: 175) that the process has been aptly called "browsing". The tiny size of the items and the rapid movements of the birds render it impossible to distinguish between food seeking and actually feeding (*s. str.*) individuals. However, it is in most cases very easy to see if the birds are food seeking (*s. l.*) or if they are intent on other activities. If all birds not actually seen eating were to be neglected, the observation material collected would grossly overestimate the proportion of vegetable food, which often occurs in larger particles and at more conspicuous places. Therefore, it was judged to be necessary and permissible to include also the records of birds not actually seen consuming food particle(s).

As a matter of course, the kind of food taken was always noted when possible. Most often it was possible to distinguish between vegetable and animal food, but the latter category was not subdivided. The former group, on the other hand, was divisible into several different classes: beech mast, herbaceous seeds etc. The technique of food seeking and of preparing the food is very different for animal and vegetable particles.

The classification of the feeding stations had to be different in different habitats (see tables). In the mixed wood at Öved each species of tree was one feeding station, all the kinds of shrub vegetation were lumped to one feeding station, and ground again was one feeding station. In the tables, visits to the less common trees were lumped in one group ("various"), to which also visits to heaps of cut wood, to the roof and walls of an old uninhabited cottage and to the tyres of a parked car (!) etc. were referred. It may seem that this is a very rough classification. However, although not apparent from the primary tables, the information obtained by the field studies was much more detailed, since additional data were noted about most of the food seeking birds. These additional data have been fully utilized when preparing the specific accounts.

At this stage it must be pointed out that the finding of an identical or nearly identical range of feeding stations in two or more species is not proof that these species are competitors for food. It is possible that two species may visit similar feeding stations but take completely different kinds of food. The concept of feeding station is a spatial one, describing the position of the bird within the habitat. In itself, it does not supply information on the food.

It is of course necessary to collect as homogenous a material of observations as possible. For the present purpose it appeared adequate to adopt the method of repeated standard observations (GIBB 1954 a: 513—514). A similar technique has been employed by most other students of woodland bird ecology. During a slow walk along a selected route careful observations on every individual of the species concerned were made, the activity of the bird during approx. 5 to 10 secs. being the basis for the classification of its status: kind of activity, kind of food sought for etc. Birds heard in the distance were neglected. The canopy, the trunks of the trees and the ground were closely watched, so that also silent birds may be discovered. Notes were taken immediately about every bird. When performing the field work in the Öved wood, the following data were usually recorded:

a) species; b) type of activity during the standard observation (food seeking, calling, preening etc.; see Chapter 4); c) if food seeking, feeding station visited; d) when possible, kind of food taken; e) relation to other birds (if member of a flock and composition of flock etc.); f) special observations of behaviour, food seeking technique, intensity of activity etc.

The statement above that every individual discovered was recorded as one standard observation needs qualification, for two kinds of observations were constantly omitted:

a) those birds, the behaviour of which was obviously influenced by the presence of the observer;

b) those which were impossible to classify, *e.g.* birds shifting from one feeding station to another in the middle of the observation or from one kind of activity to another etc.

A special check in March and November 1960 revealed that less than 3 % of the birds were omitted for the latter reason. The former reason caused the discarding of an extremely small proportion of the records and is entirely without significance.

If possible it was avoided to record a given individual more than once, but it was impossible to adhere strictly to this principle in case of large tit flocks rapidly roaming through the canopy. Days with unfavourable weather generally were avoided. All field work was performed between one and six hours after sunrise.

At first a major problem seemed to be the fact that some species of tits habitually transport larger food particles some little distance before chopping up and actually devouring them. This habit was so common in the Nuthatch that the species had to be discarded from the investigation. It is also rather frequent in the Great Tit and Marsh Tit and less so in the Blue Tit and Coal Tit. The difficulty involved, however, proved to be less important than first thought. If a bird picks up a food particle on one branch and moves to the next, no classificatory trouble arises, for it remains in the same feeding station all the time. The problem begins when a bird moves from, say, a beech, where a beech nut has been found, to a near-by pine to eat it. Very often in such cases it could be seen that the bird was in fact eating a beech nut, and then this was of course remarked in the notes. Beech mast was the food item most often transported. Therefore, the importance of this food may periodically have been underrated, for some birds moving over to a near-by tree of some other species with a beech nut may have been classified as feeding in these other kinds of trees. In September to October 1960 a special check revealed that the habit of transporting food particles caused uncertainty in 5 % of the standard observations concerning the Great Tit. Since beech mast was being consumed with greatest intensity at that time, this figure surely represents a maximum. Hence it may be concluded that the habit of food transports does not usually introduce a significant error in the material. However, the proportion of birds feeding on beech mast at feeding stations other than beech will have to be taken be into account for example when comparing the significance of this food supply for different species (p. 48 *et seq.*).

BETTS (1955: 283) reports a number of cases of disagreement between feeding stations, as recorded in the field, and the contents of the gizzards of the same birds, which were collected after having been watched for a longer or shorter period in the field. BETTS followed a party of tits through a pure oak grove for a fairly long period, but upon autopsy the gizzards were found to contain almost exclusively beech mast, presumably devoured before the birds had entered the oak grove. However, such cases must be exceptional. It is bound to be very unfavourable for the birds to spend much time food seeking in an environment that does not reward their efforts.

A special case of food transporting is f o o d s t o r i n g (HAFTORN 1954, 1956 a, b, c, 1959 and other works). This phenomen will

be returned to in several contexts later. It may sometimes be difficult to decide if a bird seen on a branch is busy storing a food particle or looking for one. In most cases, however, it is possible to decide whether storing or food seeking is being performed. As also recorded by GIBB (1960: 177), a characteristic feature is the moment of hesitation before the bird flies off from the site of storing — it is as though it wanted to make sure that the morsel had been sufficiently well camouflaged. The problem is that if a bird collects a food particle for instance in an elder bush and flies up to a near-by oak to store it, it may be recorded as feeding in oak. Such errors have certainly been made from time to time. However, in a way it is correct to say that a bird hiding an elder berry in an oak is feeding in oak. It is obvious and will be further discussed below that the storing places have to be specifically characteristic (p. 60). Therefore it is likely that a food particle hidden by for example a Coal Tit will be retrieved by a Coal Tit, if it is retrieved at all. A bird hiding food is not depleting but rather augmenting the food supply at a feeding station. A record of storing is hence of equal value as one of exploitation of a food source from the viewpoint of comparing the feeding stations of different species.

Birds of course are more conspicuous in some feeding stations than in others. Moreover, the feeding stations vary seasonally with regard to their density of cover. Thus, in September it is difficult to discover a Blue Tit feeding in the beech canopy, whilst in winter the same bird may be extremely conspicuous even in the top of a very tall beech. It has not been possible to contrive a method to account for these discrepancies. However, with experience the observer becomes more and more efficient and comes to know "where to look", which tends to level off the irregularites produced by the different feeding stations. In this connection it may be mentioned that in the winter of 1957/58 the author made a good deal of preliminary work on tit feeding habits in a district in Central Skåne. These studies provided opportunities for practising the skill to discover tits in the canopy, and thanks to this training the efficiency of the observer may be assumed to have been the same right from the beginning of the field work upon which the present paper is based.

With regard to these facts it seems admissible to conclude that the technique employed is of sufficient accuracy for the aims of the present investigation. Finally it may be pointed out that sometimes various kinds of information were collected on separate occasions. On a

first walk through the wood for example the feeding habits were paid close attention to, whilst on an immediately following second walk the birds were accurately counted and their general activity was studied. This explains numerical discrepancies found between tables of *e.g.* census results, feeding habits and activity types.

The transect through the Öved area took on average 2 hrs. 15 min., that through the Bökeberg wood 1 hr. 50 min., and that through the Vomb wood 3 hrs. 10 min.

Finally, it may be mentioned that the material condensed in Tabs. 2 to 9 inclusively consists of no less than 21.280 standard observations.

D. Specific accounts

I. *Öved*

For a description of this locality, the reader is referred to Chapter 2.

a) Great Tit (Tab. 2). — In the late autumn of 1958, when the present study was started, there was a heavy crop of beech mast. In November this supply made up by far the greatest proportion of the food of the Great Tit. Much of the beech mast was still hanging in the trees, and although there was also a great deal of beech mast lying on the forest floor, the Great Tits preferred utilizing the portion still remaining in the trees. This preference is extremely marked, for after the turn of the year only a small fraction of the cupulae on the trees contain nuts, and yet the birds diligently searched for these rather than exploited the ground where nuts were plentiful. The frequency of visits to beech gradually decreased, but up to and including February beech was visited in about or more than 33 % of the cases. In November to February, incl., 90 % of the visits to beech were concerned with the exploitation of beech mast. If it is added that some of the feeding stations other than beech were also partly concerned with beech mast (ground and shrub), it is apparent that beech mast played an extremely significant rôle for the whole food situation of the Great Tit in the winter of 1958/59.

The second most frequented feeding station was the shrub vegetation. Here the Great Tits were obviously exploiting several different kinds of food. In the elder bushes, the berries were freely taken; this supply was largely depleted already by the end of November. When exploiting the elder bushes and other species of shrub vegetation for animal food, the Great Tits concentrated on the main stems and parti-

cularly on the forks between the primary branches and the main stems. The feeding intensity was often recorded to be low in this feeding station. Often the Great Tits would move downwards in the bushes and examine the debris collected between the lowest branches. From there, they often moved out on the ground. Besides the shrub vegetation, the ground was the most important feeding station. Most often the Great Tits were recorded on the ground below beech trees, and they were taking a great deal of mast, as was strikingly apparent from their behaviour. It was also directly seen in many cases that they were feeding on smaller particles, not beech mast, and because of the complete absence of herbaceous vegetation, the conclusion is justified that these smaller particles were mainly animals. On some days after heavy gales, it was noted that plenty of beech mast had dropped down from the trees. This was particularly conspicuous when the ground was snowcovered. However, Great Tits were scarcely ever recorded to feed on mast on top of the snow.

Other feeding stations made up less than 10 % of the monthly totals. As mentioned above (p. 20), the category called "various" consists of records from the scarce tree species and from a variety of odd places. Even the tyres of a car parked at the road-side were examined. This refers to probably two different Great Tits which in October 1960 seemed to make a routine of examining the tyres of the author's car which was parked at the road-side!

In the winter of 1959/60 beech mast was practically absent. Because of the great significance of this food for the Great Tits in the preceding winter, this was bound to have brought about an entirely different food situation for the species. The main task, therefore, was to examine what alternative food sources were exploited by the birds.

In early September 1959, nearly 50 % of the food seeking Great Tits were recorded in beech. The behaviour of the birds revealed that they were hunting insect food which was abundant in the dense foliage. Special attention was paid to the leaves which were examined from all sides. When the birds were trying to examine the leaves from below they would sometimes hover for a couple of seconds, but they are not expert in this technique. In the course of October the Great Tits virtually abandoned beech as a feeding station. For the rest of the winter this feeding station occupied a relatively unimportant position. This situation should be compared with that prevailing in the preceding winter (Tab. 2). In the winter of 1958/59, the proportion

Tab. 2. Percentage distribution of Great Tits on feeding stations in the Öved area.

Year	1958		1959									1960							
Half-month	II	II	I+II	I	II+I	II	I	I	II	II	II	I+II	I+II	I+II	II	II	I+II	I+II	II
Month	11	12	1	2	3+4	4	9	10	10	11	12	1	2	3	4	9	10	11	12
Fagus	52	42	33	36	30	24	49	37	12	15	11	15	24	11	16	60	64	58	65
Quercus	6	8	3	9	6	10	11	22	18	18	6	19	19	10	7	6	6	4	8
Alnus	2	3	3	6	2	4	7	3	4	1	13	5	6	8	9	2	—	3	2
Betula	—	1	1	—	2	2	—	—	2	—	—	—	—	1	1	—	—	—	1
Picea	5	7	7	12	5	10	3	6	6	2	4	9	3	7	1	9	5	7	3
Pinus	6	9	9	8	6	6	7	9	10	9	4	5	8	7	1	2	5	4	7
Ground	8	4	13	10	28	18	4	12	21	36	45	25	18	21	18	12	15	10	10
Shrub	15	24	29	19	20	22	18	12	23	19	17	22	22	29	43	8	5	14	4
Fruittrees ..	3	2	2	—	1	3	—	1	3	1	—	—	—	1	5	—	—	—	—
Various	3	1	1	—	—	—	2	1	1	1	—	—	—	6	1	1	—	—	—
Standard observations:	280	672	929	282	438	276	267	270	245	155	53	123	63	151	106	370	354	312	296

Total: 5.642

of Great Tits feeding in beech never dropped below 33 %, whilst in 1959/60 the average figure was less than half this minimum value, *i.e.* a drastical change. The tits recorded in beech in the latter winter were seeking food on the branches and main trunks, particularly on outgrowths and around the openings of cavities. Obviously the birds were subsisting almost exclusively on animal food.

Beech mast was not substituted by other kinds of vegetable food, at least not in a quantitatively significant degree, but by animal food which was taken in deciduous trees, on the ground and in the shrub vegetation. At the last two feeding stations some vegetable food was also taken. In early autumn, elder berries were freely eaten. By comparison with the preceding winter, the feeding stations that showed the most marked increase are the oak and the ground. In November and December approx. 40 % of the Great Tits were recorded in the lastmentioned feeding station.

The general pattern of the feeding habits of the Great Tit in the Öved wood is thus quite different in these two winters. In the first of them, beech mast made up a dominating part of the food, in the latter the birds subsisted chiefly on animal food.

In the autumn of 1960 and up to the turn of the year the Öved wood was carrying a still richer crop of beech mast than in 1958. If the period November to December 1960 is compared with the same period in 1958, the resemblances are striking. In 1960 approx. 62 % of the feeding stations were in beech, as compared with 47 % in 1958. Direct observations showed that 82 % of the visits to beech were concerned with the exploitation of the mast crop. This figure was 90 % in the winter of 1958/59. Thus, in relation to beech mast all other food sources were reduced to secondary importance. The conclusion is inevitable that when beech mast is available it quickly becomes the staple food of the Great Tit. Second to mast came the shrub vegetation and the ground, which is again a corroboration of previous findings.

To a limited extent the Great Tits in the winter of 1959/60 found and consumed one year old beech nuts in the ground. It was observed on several occasions in December to February 1959/60 that Great Tits flew up from the ground with a largish particle in the bill and proceeded to prepare it on a branch in the way typical for

birds feeding on beech mast and similar large vegetable particles. In the present connection it was of course of extreme importance to try and find out what objects the birds were finding. In four cases it was possible to prove the suspicion that the tits were in fact feeding on one year old beech mast. On 11 and 19 December 1959 and on 2 and 22 February 1960, I managed to scare the bird at just the right moment, *i.e.* when the bird was just about to start hammering the particle to pieces and was squeezing it between the toes, and then retrieve the morsel as it fell to the ground. In all four cases the particle was found to consist of a beech nut, much decayed and shrunken but still easily recognizable. It was difficult to assess accurately if the old beech mast supplies had any quantitative significance for the Great Tits. The behaviour described above, however, is a conspicuous feature and would surely have been recorded, had it occurred to a significant extent, particularly as much attention was paid to studying the rôle of beech mast for the birds in question.

In April 1960 the proportion of Great Tits feeding in the shrub vegetation rose to a peak. This was caused by the attraction exerted by early flowering willows and other bushes. Whether the birds were feeding on bud tissue or on insects gathering around the flowers or both was not ascertained.

In the Öved wood the author made some interesting observations concerning f o o d p a r a s i t i s m in the Great Tit. At the time of those observations I was not aware of the fact that a similar type of behaviour had previously been recorded from England. LONG, OWEN and SOUTHERN (according to RICHARDS 1958: 499) and HART (1958) have seen Great Tits, and more rarely Blue Tits, systematically robbing stores deposited by Coal and Marsh Tits. According to RICHARDS (*loc. cit.*) the Great Tit "spends much of its time watching Coal Tits and trying to find the nuts they have hidden. More often than not the bird is frustrated by the efficiency with which the food is concealed . . . It would seem that the Great Tit is something of a parasite; it stores no food itself but keeps company with birds that do, and so benefits by their industry".

My own experience of parasitic habits in the Great Tit is restricted to repeated observations on six different days, *viz.* on 12, 26 and 27 January and 14, 23 and 26 February, all in 1960. The course of events was almost identical in all cases. A few Marsh Tits were busy storing *Galeopsis* seeds, chiefly on oak limbs, covered by lichens.

Two Great Tits were also present. On several occasions in each of the six days I saw a Great Tit fly up to exactly the same spot where a Marsh Tit had been a moment earlier and stored some food particle. The Great Tit usually was there within approx. 30 secs. after the Marsh Tit had departed. The Great Tit poked with its bill among the lichens, sometimes so violently that pieces of debris were seen falling down. Whether it found the food particle hidden by the Marsh Tit or not could not be conclusively proved, but in several instances it was possible to see that the Great Tit picked up some particle and swallowed it. This was seen on at least seven occasions from three different days. Of course it is not impossible that the Great Tit found something else to eat on the spot, but in all probability it was the particle deposited by the Marsh Tit that was found and eaten. In three cases the Great Tit flew up on the branch, whilst the Marsh Tit was still there, busy selecting a storing place. The Marsh Tit flew off with no particular hurry, when the Great Tit performed a "half-hearted" threat display. In all probability the Marsh Tit took with it the morsel to be stored, and the Great Tit was not rewarded — in fact it also departed immediately. This incident seems to be half-way between a "supplanting attack", as defined by HINDE (1952: 22), and food parasitism, as described above. It seems quite reasonable that the robbing of food stores has developed from the technique of supplanting attacks.

Food parasitism, as performed by the Great Tit, is not easy to detect under natural conditions. The experience of the author does not justify any detailed estimation of its quantitative significance. It seems certain, however, that the Great Tits were robbing stores of deposited food only rather occasionally, or at least, that this habit had been acquired by only a few individuals. The latter possibility perhaps seems more probable, for the technique was perfect in the tits attempting the robberies. Those individuals certainly were not robbing stored food for the first time, when they happened to be caught in the act. It may be significant that all the observations of food parasitism were recorded in the winter of 1959/60, when beech mast was absent and the birds probably had some difficulty in satisfying their food requirements. In the autumn and early winter of 1960/61, no case was discovered, although special importance was attached to assess the significance of this habit.

b) Blue Tit (Tab. 3). — In the winter of 1958/59, when beech mast was plentiful, a considerable proportion of the feeding stations of the Blue Tit were situated in beech. Up to and including January about 45 % of the feeding stations were in this tree, later the figure dropped to about 30 % but rose again in April. The portion of Blue Tits visiting beech in order to exploit the mast was much lower than in the Great Tit (p. 24). In November to February, inclusively, 39 % of the birds recorded as food seeking in beech were working at the mast. The increase in the frequency of visits to beech in April was caused by birds feeding at the buds. It was not established whether they were taking bud tissue or insects or both. The Blue Tit is known to show a stronger preference for bud tissue than the other tits (*e.g.* BETTS 1955).

It is obvious that the Blue Tit exploited the beech mast to a much lesser degree in this winter than the Great Tit.

Oak was the second most often recorded feeding station, although the monthly percentages show considerable fluctuations. In February, oak even surpassed beech, although with a very narrow margin. With regard to my field observations, however, I am inclined to believe that the rôle of oak was rather underestimated. If one were to measure the importance of different feeding stations by the total time spent in them, oak would almost certainly have scored a higher figure than beech. There are many notes in my field diaries about the long time spent by Blue Tits in oaks, and their apparent success and energy in these trees. It was also noted on several occasions that when a mixed tit flock moved through a mixed wood, the Blue Tits often got "stuck" in the oaks, whilst the other tits moved on. In the oaks the Blue Tits were often recorded as examining extremely carefully the dead branches, particularly their ends, where the birds would hang upside down, hammering at the decaying wood so that the chips flitted about. Also the tips of live branches and twigs were searched for food, and in spring the Blue Tit exhibited a strong interest in the buds. Even if a bird was seen to linger at such a feeding station for a quarter of an hour, this would yield only one record. The long periods spent in oak therefore will be underrepresented in the material.

The only other feeding station of significance for the Blue Tit was the shrub vegetation. Here the birds were most often recorded as hanging upside down at the end of the twigs. There is no record to

Tab. 3. Percentage distribution of Blue Tits on feeding stations in the Öved area.

Year	1958		1959									1960							
Half-month	II	II	I+II	I	II+I	II	I	I	II	II	II	I+II	I+II	I+II	II	II	I+II	I+II	II
Month	11	12	1	2	3+4	4	9	10	10	11	12	1	2	3	4	9	10	11	12
Fagus	42	47	43	28	33	38	46	45	43	34	29	37	37	28	19	50	49	46	36
Quercus	30	19	10	30	17	18	18	29	20	47	45	31	39	24	9	20	16	13	30
Alnus	4	5	7	9	8	11	8	1	4	6	8	3	10	16	3	7	5	8	6
Betula	—	1	4	3	7	6	1	—	2	1	2	6	4	7	8	—	1	2	2
Picea	2	8	6	4	5	6	9	3	5	2	2	2	—	2	3	1	4	3	3
Pinus	4	7	9	7	5	5	5	3	4	3	4	2	4	4	—	2	4	1	—
Ground	2	1	3	1	1	2	—	7	4	1	—	—	—	1	3	—	—	4	2
Shrub	10	11	13	11	14	9	14	10	14	4	10	15	6	12	49	16	18	17	20
Fruittrees ...	5	2	4	6	10	6	—	3	2	3	—	1	—	5	6	3	3	4	1
Various	1	1	1	1	—	—	—	—	4	—	—	2	—	2	—	1	—	2	—
Standard observations:	164	322	292	215	314	266	195	148	200	180	49	94	51	101	90	189	296	212	146

Total: 3.524

show that the Blue Tits ever fed on elder berries, but it is possible that they sometimes did, particularly in early autumn when this crop was abundant.

Other feeding stations were visited only more or less casually. There was a certain interest in alder, birch and fruit trees in comparison with other tit species. Coniferous trees were still less frequented by this species than by the Great Tit.

In the winter of 1959/60 the feeding habits of the Blue Tits were basically similar to those described above. Beech and oak together attracted approx. 60 to 75 % of the food seeking Blue Tits, and from November onwards, oak was about as often visited as beech. With regard to the underestimation of the feeding stations situated in oak (*cf.* above) this fact indicates that oak was in fact of primary importance for the species. The food sought for in these deciduous trees was largely composed of insects. When beech mast was not accessible, the Blue Tit seemed to resort to an almost purely animal diet.

Annual differences in feeding habits were, on the whole, slight by comparison with the Great Tit. This was borne out by the studies in the autumn of 1960. The birds were found in deciduous trees, often frequenting the top third parts but also at lower levels. The absence of beech mast in the winter of 1959/60 superficially at least seemed to cause little change in the feeding habits of the Blue Tit. The rôle of this food supply, however, should not be underestimated. A considerable proportion of the feeding stations were concerned with the exploitation of this food, the value of which to the birds is further increased by its large proportion of fat and its ready accessibility. The birds are able to satisfy their needs by means of beech mast at the expenditure of comparatively little energy. Therefore, it seems to be a nearly perfect "reserve" food supply. In the years when beech mast is unavailable, the Blue Tits have to compensate by feeding on other items, and as this alternative supply is largely made up by insect food, which is not at all so readily exploited, the food situation no doubt is much improved for the Blue Tits when beech mast is abundantly available. These facts which will be returned to in several contexts are not fully represented in the tables. The significance of beech mast for the Blue Tit is further discussed below (pp. 48—56).

No signs of food storing nor food parasitism have been discovered in the Blue Tit. Certain tendencies towards storing were described

for the Blue Tit by HINDE (1952: 25), whilst HART (1958) recorded attempts at parasitism of food stored by other tits.

c) Coal Tit (Tab. 4). — There is little to say about the feeding habits of the Coal Tit in the Öved wood. In the winter of 1958/59 Coal Tits were present throughout the winter. More than 80 % of the feeding stations were situated in conifers, this figure in some months rising to almost 100 %. Spruce dominated over pine, sometimes markedly so, and as the birds are rather more conspicuous in pine than in spruce because of the greater average height of the latter tree in the Öved wood, the rôle of spruce is underestimated if anything. Coal Tits were often recorded as clinging to the cones, and it was obvious that spruce seeds composed a part of their diet. In November to December and again in March quite a considerable proportion of the birds were seen in beech. In autumn they were largely feeding on the beech mast. In spring the increased frequency of visits to beech coincided with a passage through the area of migrating Coal Tits, which passed through the beech woods during occasional food seeking.

In the winter of 1959/60 the Coal Tits virtually abandoned the area in the course of October. There was an extremely poor crop of spruce seeds in this autumn, as was the case over a large part of Southern Sweden (FALL 1959). A few individuals remained in a nearby spruce area and casually trespassed into the study area but were too few to provide material on the feeding habits. As in the previous year there was a tendency of increasing frequency of visits to deciduous trees in the migration seasons.

The observations in the autumn of 1960 added no novel aspects on the habits of the Coal Tits. The species became scarce in the course of the autumn but did not disappear completely. In Southern Sweden the cone crop was poor, although not so extremely so as in the previous autumn (FALL 1960). Besides, the birds had access to a supply of beech mast, which was utilized to some extent, as discussed below (pp. 44 and 55).

d) Marsh Tit (Tab. 5). — In the winter season of 1958/59 the Marsh Tit was found to be exploiting the beech mast for food in a considerable degree. In November to December about 40 % of the total number of feeding stations were situated in beech. This

Tab. 4. Percentage distribution of Coal Tits on feeding stations in the Öved area.

Year	1958		1959									1960							
Half-month	II	II	I+II	I	II+I	II	I	I	II	II	II	I+II	I+II	I+II	II	II	I+II	I+II	II
Month	11	12	1	2	3+4	4	9	10	10	11	12	1	2	3	4	9	10	11	12
Fagus	8	19	4	1	9	—	16	2	·	·	·	·	·	(27)	(—)	10	14	10	—
Quercus	1	4	2	—	—	1	2	4	·	·	·	·	·	(7)	(—)	1	4	—	—
Alnus	—	—	2	—	—	—	—	—	·	·	·	·	·	(—)	(—)	—	—	—	—
Betula	—	—	1	—	—	—	—	1	·	·	·	·	·	(—)	(—)	—	—	—	—
Picea	52	44	59	61	66	72	60	60	·	·	·	·	·	(60)	(87)	60	57	55	77
Pinus	33	33	25	38	19	27	21	33	·	·	·	·	·	(7)	(13)	29	24	35	23
Ground	4	—	1	—	1	—	—	—	·	·	·	·	·	(—)	(—)	—	1	—	—
Shrub	2	—	5	—	—	—	—	—	·	·	·	·	·	(—)	(—)	—	—	—	—
Fruittrees ..	—	—	1	—	5	—	—	—	·	·	·	·	·	(—)	(—)	—	—	—	—
Various	—	—	—	—	—	—	—	—	·	·	·	·	·	(—)	(—)	—	—	—	—
Standard observations:	82	278	258	111	125	98	98	131	Not present					(30)	(15)	79	200	99	52

Total: 1.611 (+45)

Tab. 5. Percentage distribution of Marsh Tits on feeding stations in the Öved area.

Year	1958		1959									1960							
Half-month	II	II	I+II	I	II+I	II	I	I	II	II	II	I+II	I+II	I+II	II	II	I+II	I+II	II
Month	11	12	1	2	3+4	4	9	10	10	11	12	1	2	3	4	9	10	11	12
Fagus	40	42	31	24	23	23	24	29	29	19	11	17	17	18	18	42	50	30	42
Quercus	10	8	5	11	10	14	4	15	22	40	16	20	10	9	18	12	19	16	28
Alnus	4	4	5	6	8	6	2	—	1	6	—	8	8	9	5	3	—	2	6
Betula	2	4	3	3	1	5	2	—	1	1	—	4	2	5	6	—	—	—	4
Picea	8	3	5	5	5	6	6	7	5	1	13	9	2	5	—	4	1	6	2
Pinus	8	4	1	2	4	9	3	5	1	3	3	4	—	8	2	7	5	8	2
Ground	12	6	8	10	13	8	27	21	17	15	21	9	15	9	5	14	10	21	10
Shrub	16	28	38	29	35	29	30	20	21	15	37	25	33	37	27	18	15	16	6
Fruittrees ..	—	—	4	8	2	1	—	2	1	1	—	4	10	—	21	—	—	1	—
Various	—	1	—	2	—	—	2	1	1	—	—	—	2	1	—	—	—	—	—
Standard observations:	108	183	280	177	221	192	113	137	179	158	38	109	48	79	63	129	198	202	140

Total: 2,754

figure later decreased. Special observations revealed that on average 65 % of the visits to beech were concerned with the exploitation of the beech mast (November to February, incl.). The corresponding figures were 90 % and 39 % for the Great and Blue Tits, respectively. The Marsh Tit, thus, was intermediate between these two species with regard to the degree of exploitation of beech mast.

Much of the beech mast was not consumed immediately but stored for later use. No exact quantitative information was gathered concerning the proportion of the food that was stored at different seasons of the year. Some food was stored in the beeches but much was transferred to oaks, which seemed to be preferred to other trees for storing purposes. Also, the surface of the oak branches with their many crevices in the bark and the rich carpet of lichens seemed to be much more suitable for hiding objects than the smooth surface of the beech bark. Therefore, in point of fact, some of the feeding stations recorded in oak might actually refer to food emanating from the beech. Further, many of the feeding stations on the ground and some of those in conifers, alder, birch etc. were concerned with the deposition or exploitation of food stores composed by beech mast. With regard to these facts, the conclusion seems justified that the rôle of beech mast for the Marsh Tit was very great indeed (*cf.* p. 50).

Other feeding stations of significance were the ground and the shrub vegetation. In the shrubbery the birds were mainly concerned with vegetable food, particularly elder berries but also wild raspberries and blackberries etc. To a certain extent, animal food was also taken. The visits to the ground had two aims. In this winter the principal aim was to collect beech mast that had dropped from the trees. The secondary aim was to collect seeds from herbaceous plants, particularly *Galeopsis sp.* These food supplies of course occurred in different areas, for below the beech the floor was devoid of flowering plants. This difference in localisation also caused that beech mast and *Galeopsis* seeds were usually stored in different species of trees: the former mainly in oak and beech, the latter in pine and to some extent in spruce. Elder berries were also stored in large numbers. As the richest supply of such berries was available in an area covered by pine and spruce trees, most of the berries were stored in these trees.

The Marsh Tit was on the whole fairly wide in its choice of feeding stations. The observations, however, warrant the conclusion that

much the largest part of the food consisted of vegetable matter.

With respect to the great importance of beech mast for the food ecology of the Marsh Tit in 1958/59, it was of course important to examine which alternative food source this bird has to resort to in the absence of this kind of food. Field observation in 1959/60 showed that several kinds of food gained in importance to make up for the failing supply of beech mast. In September to early November and in a lesser degree also later in autumn and right into January, the Marsh Tits were very active storing seeds of herbaceous plants, particularly of *Galeopsis* but also of *e.g. Urtica*, certain grasses, *Lamium album*, and *Plantago major*. These seeds were stored in various species of trees with a certain preference for oak among the deciduous species and for pine in comparison with spruce. Some food was also hidden at the main stems of elder bushes. It is somewhat difficult to compare with the preceding season, as observations were then not started until November. Yet it is clear from the records from November onwards that the intensity of storing of herbaceous seeds was much greater in 1959/60. Virtually all the birds recorded on the ground were exploiting the seed supplies of herbaceous plants, which is in marked contrast to the preceding winter when a majority of ground-seeking Marsh Tits were taking beech mast.

In November and December 1959 oaks were visited to a greater extent than in the previous winter. The birds were taking small particles, in part probably stored previously, and most of this food consisted of small animals. However, I was early led to suspect that the Marsh Tits to some extent were feeding on beech mast, deposited a whole year earlier, and soon it was possible to obtain proof of this. In the first place the birds were obviously eating some fairly large particles, for they went through the procedure of fastening the morsel between their toes, hammering at it and devouring it in pieces. This is indicative but not proof of consumption of beech mast. In nine cases, however, distributed over four days in December 1959 and four days (five cases) in January 1960, I succeeded in scaring the bird at just the right moment so that it dropped the food as it flew off. In seven of these cases the food was retrieved and found to be a beech nut, much shrunken and decaying but easily recognizable. In the remaining two cases only fragments of unidentified vegetable tissue were found, and although it was judged very likely that these

fragments were pieces of beech mast tissue, this was not established with certainty.

In the autumn of 1960 the Marsh Tits were again showing great interest in the tremendous beech mast crop. The relatively large proportion of feeding stations in oak was connected with the storing activities. Like the Great Tit the Marsh Tit obviously prefers exploiting the beech mast in the trees to that lying on the ground; in point of fact the Marsh Tit is even less inclined to seek food on the ground. In some cases a Marsh Tit collecting beech mast on the forest floor was recorded to store the mast in or near the ground: among the debris below a mixed oak and beech area (two cases), in a dead oak branch lying on the ground (three cases in rapid succession, obviously by the same individual), under moss on dead oak and beech stumps at a vertical distance from the ground of approx. 12 cm (five cases on three different days, all in the same area and thus possibly by the same individual) and below moss on a heap of cut wood at a vertical distance from the ground of 5 and 24 cm, respectively (two cases in rapid succession by the same individual). On a few occasions, storing in the ground proper was suspected but was not proved. There has also been reason to suspect storing of food near the base of elder bushes, but it was not established. It is surprising that such a habit occurs in a district where snow covers the ground for a considerable time in most years, rendering the supplies inaccessible in times of greatest need. However, the habit of storing in the ground is not common.

Although a detailed study of the storing habits of the Marsh Tit was not on the programme, my notes permit the conclusion that this species intensively stores food from September (when my field work has begun) to late February, occasionally also in March, with a peak of intensity in September to late October, possibly extending into November when beech mast is available for the storing purposes. The start of the storing activities has not been established.

e) Treecreeper (Tab. 6). — The Treecreeper is specialized to a narrow range of feeding stations, *i.e.* the surface of tree trunks and major semi-vertical limbs. This specialization has marked the whole morphology of the bird. It has interfered with its capacity to avail itself of periodically abundant vegetable food supplies. By this rigidity it differs abruptly from all the species of the genus *Parus*. Eco-

Tab. 6. Percentage distribution of Treecreepers on feeding stations in the Öved area.

Year	1958		1959									1960							
Half-month	II	II	I+II	I	II+I	II	I	I	II	II	II	I+II	I+II	I+II	II	II	I+II	I+II	II
Month	11	12	1	2	3+4	4	9	10	10	11	12	1	2	3	4	9	10	11	12
Fagus	30	26	40	25	36	36	53	32	33	27	3	21	20	22	14	22	44	40	26
Quercus	17	21	19	20	18	22	18	27	16	40	22	16	10	21	20	18	26	21	22
Alnus	5	2	3	3	3	3	4	—	1	3	—	2	—	10	8	4	—	1	6
Betula	—	1	1	—	1	1	—	1	—	—	—	—	3	3	7	—	—	—	—
Picea	20	25	13	22	20	18	11	21	28	12	36	41	33	17	17	16	18	26	15
Pinus	28	25	22	30	22	20	14	19	17	15	36	19	35	20	23	27	12	12	21
Ground	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Shrub	—	—	1	—	—	—	—	—	1	—	3	—	—	1	7	—	—	—	4
Fruittrees ..	—	—	1	—	—	—	—	—	—	—	—	—	—	4	7	2	—	—	5
Various	—	—	—	—	—	—	—	—	3	3	—	1	—	3	—	1	—	—	1
Standard observations:	54	125	187	83	122	134	73	92	93	60	36	90	40	77	30	79	111	128	89

Total: 1.703

logically speaking, the Treecreeper is also much more strongly specialized than the woodpeckers, for example, which, although primarily adapted to a similar range of feeding stations, have retained the possibility to utilize various other feeding stations and therefore have a much wider range of foods at their disposal.

In the Öved wood, the Treecreeper was found to frequent all kinds of trees. However, it did not visit its feeding stations at random. If so, the frequency of visits to the different tree species would have been proportional to the relative abundance of the trees (Tab. 1). This was not the case. Also, the frequency with which different trees were visited showed irregular and so far inexplicable changes from month to month. This demonstrates that the Treecreepers were positively selecting certain trees in favour of others. Illustration of this is to be seen in Tab. 6. The proportion of all visits devoted to beech for example varied between 53 % (September 1959) and 3 % (December 1959).

f) Goldcrest (Tab. 7). — Superficially the Goldcrest is in many ways similar to a small tit, but systematically it is more remote from the *Paridae* than both the Treecreeper and the Nuthatch, being a member of the subfamily *Sylviinae* of the *Muscicapidae* (VAURIE 1959: 298).

This similarity may be seen in the feeding habits of the Goldcrest which resemble those of the smaller tits, particularly those of the Coal Tit. Like this species, it shows a strong preference for coniferous trees. Whilst the Coal Tit was shown to prefer spruce to pine, this did not strictly apply to the Goldcrest within the present study area. In autumn this species was about equally attracted to both spruce and pine, but later there was a gradual change in favour of the spruce. This may be due to the revival of territorial behaviour patterns, for in the breeding season, or rather for nest building purposes, the Goldcrest clearly prefers spruce to pine (PALMGREN 1932, 1959).

The most important ecological difference between the Goldcrest and the Coal Tit from the nutritional point of view is that the former is apparently restricted to animal food, whilst the latter is able to draw upon the supplies of spruce seeds as well. In the course of the present investigation, no indication was found that the Goldcrest ever touches vegetable foods.

Tab. 7. Percentage distribution of Goldcrests on feeding stations in the Öved area.

Year	1958		1959									1960							
Half-month	II	II	I+II	I	II+I	II	I	I	II	II	II	I+II	I+II	I+II	II	II	I+II	I+II	II
Month	11	12	1	2	3+4	4	9	10	10	11	12	1	2	3	4	9	10	11	12
Fagus	3	1	—	—	4	—	5	13	17	2	—	3	—	—	3	11	15	7	—
Quercus	—	—	—	—	5	—	3	5	7	2	—	1	—	—	6	1	6	4	—
Alnus	—	—	—	—	—	—	—	1	—	—	—	—	—	—	8	1	—	—	—
Betula	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Picea	47	49	61	44	55	72	68	35	41	47	57	57	63	66	43	61	42	58	54
Pinus	50	46	39	56	32	28	25	46	32	49	32	40	37	29	41	24	37	28	43
Ground	—	—	—	—	3	—	—	—	—	—	6	—	—	—	—	—	—	—	—
Shrub	—	3	—	—	1	—	—	1	1	—	5	—	—	6	—	2	—	2	3
Fruittrees ..	—	—	—	—	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Various	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
Standard observations:	193	201	89	115	150	103	106	261	288	134	108	161	73	91	79	164	219	131	149

Total: 2.815

During the migration periods, the Goldcrest was often found in deciduous trees as well as in the shrubbery. This was found to apply also to the Coal Tit (p. 33). However, sometimes the Goldcrests seemed to show a temporary preference for such vegetation, in which they spent considerable periods, apparently seeking food with great efficiency. This is in contrast to the Coal Tits, which seemed to visit the deciduous vegetation more in passing (except when feeding on mast, p. 44). The ability of the Goldcrest to obtain food from deciduous vegetation at a satisfactory rate was strikingly illustrated by observations in January to April 1960. In this period the author spent much time in a grove approx. 10 km. N of Lund, which was wholly made up of oak with an admixture of alder and other deciduous trees (but no beech). There was also a dense undergrowth of hazel (*Corylus avellana*), but not a single coniferous tree. In this grove a group of four Goldcrests spent the whole period of approx. 4 months during which the area was studied. In February there were very cold periods with morning temperatures down to —12° C. The fact that the Goldcrests were able to sustain life there shows that they are capable to find food at a sufficient rate in pure deciduous vegetation, even when the climatical conditions are very strenous indeed.

On a few occasions Goldcrests were watched seeking food on the ground and in herbaceous vegetation. Unfortunately, it was not recorded what they were taking.

II. *Bökeberg* (Tab. 8)

For a description of this locality the reader is referred to Chapter 2. The studies at this locality were intended to provide further information on the importance of beech mast for the different species.

a) Great Tit. —The Bökeberg beech wood was investigated for the first time in January 1959 and was at that time carrying a rich crop of beech mast. Part of this mast was still hanging in the trees, whilst most of it had dropped to the ground and was being consumed on a large scale by numerous flocks of Bramblings (*Fringilla montifringilla*), as well as by smaller numbers of other birds, particularly Chaffinches (*F. coelebs*).

It was found that approx. 58 % of the feeding stations of the

Tab. 8. Percentage distribution on feeding stations in the Bökeberg beech wood in January 1959 and 1960.

Species	Year	Bole	Primary branch	Secondary branch	Twigs	Mast	Shrub	Ground	Standard observations
Great Tit	1959	5	9	2	3	58	13	10	639
	1960	7	29	17	2	—	26	19	137
Blue Tit	1959	—	2	10	33	24	27	4	259
	1960	3	5	27	36	—	27	2	134
Coal Tit	1959	8	1	—	9	76	3	3	129
	1960	·	·	Not present			·	·	—
Marsh Tit	1959	1	6	8	19	29	30	7	297
	1960	3	6	13	19	—	44	15	142
Treecreeper ...	1959	92	8	—	—	—	—	—	74
	1960	91	9	—	—	—	—	—	33

Total: 1.844

Great Tit were directly concerned with the exploitation of beech mast in the trees. However, since a considerable proportion of the birds recorded as feeding on the ground and also some of those in the shrub vegetation, were also eating beech mast, this figure has to be increased to approx. 70 %. Just as in the Öved wood, thus, the Great Tits were to a large extent subsisting on beech mast, and another similarity is that they preferred utilizing that part still hanging in the trees to that which had dropped to the ground.

Those feeding stations that were not concerned with the exploitation of beech mast were scattered throughout the wood, from the ground up to the higher parts of the tall trees. The Great Tit always demonstrated a certain preference for the central parts of the trees, particularly favouring the forks between the trunk and the primary branches and also all sorts of unevennesses at the surface of the trunks.

The Bökeberg wood was again studied in January 1960, when there was no beech mast. Because of a lower number of visits and, more important, a much lower number of standard observations secured per visit, the material was much less extensive than in the preceding winter. The restricted material shows that the Great Tits were feeding largely on insect food, collected from the boles, forks, primary branches and to some extent the peripheral parts of the

beeches. No indication was found that the Great Tits were feeding on one year old beech mast, although decaying beech nuts were not uncommon in the debris on the ground.

On the whole the studies in Bökeberg fitted in with the results obtained by the more extensive results from the Öved wood. In both places, the beech mast was the staple food of the Great Tit in those years when it did occur, and in both places the birds had to resort to a more or less pure diet of invertebrate animals in its absence.

b) Blue Tit.—In January 1959 the Blue Tits were to a considerable degree exploiting beech mast for food. Nearly one quarter of the feeding stations were found to be directly concerned with this food. Some birds recorded at other feeding stations were also consuming beech mast. In some cases the observations suggested that Blue Tits working at the beech mast in the trees were examining the cupulae and the mast for insects and not primarily taking the nut tissue. Although this fact introduces a certain source of error in the computations, it most probably was not of great significance, but it does render the evaluation of the importance of beech mast to the Blue Tit less easy to determine. In all probability this was of the same order of size in Bökeberg as in the Öved wood.

The Blue Tit, in contrast to the Great Tit, showed a clear preference for the peripheral parts of the trees, hanging at the tips of twigs and examining leaf buds. Also the shrubbery was visited to some extent. Other feeding stations were visited only more or less casually.

In the following winter the Blue Tits were spread over three classes of feeding stations, *viz.* secondary branches, twigs and shrub vegetation.

The observations in pure beech wood thus essentially confirm the results obtained in the Öved wood, namely that the Blue Tit exploits the beech mast to a considerable degree, although much less than the Great Tit, and that in case of its absence it resorts to an almost pure animal diet. No vegetable food, except beech mast, seemed to play a significant rôle for the Blue Tit.

c) Coal Tit.—A considerable number of Coal Tits was found in the pure beech wood area at Bökeberg in 1959. The birds were almost exclusively feeding on beech mast. No less than 76 % of the feeding stations were directly concerned with the exploitation of this food, and with regard to birds recorded at other feeding stations but feeding

on mast this figure should be still more increased. Thus four fifths of the birds were in fact exploiting the beech mast. The Coal Tits recorded in the beech wood, however, were there only on brief visits. It was often witnessed how a small group of Coal Tits departed from the beech wood making for the nearest spruce plantation. They were only raiding the beeches for food and then returning to their proper habitat. Nevertheless it is obvious that beech mast played a considerable rôle for at least part of the Coal Tit population in the winter of 1959/60.

In the following winter no Coal Tits at all were present in the same area. A few individuals were noticed in the surrounding spruce plantations, but no particular attention was paid to those birds.

d) Marsh Tit. — In January 1959 the Marsh Tits spent most of their time consuming beech mast. Although only approx. 30 % of the feeding stations were situated in direct contact with the beech mast in the trees, this figure has to be increased for certain reasons. In the first place, most of the Marsh Tits recorded at the ground and in the shrubbery were also devoting their attention to beech mast, and second, part of the birds recorded in the trees, although not at the mast, were preparing beech mast before consuming it. The Marsh Tit, apart from the mast, frequented a range of feeding stations intermediate between those of the Great and the Blue Tit, although more similar to that of the former species.

It was rather remarkable that no storing at all was going on in spite of the abundance of food. In the Öved wood, beech mast was a preferred object for storing by the Marsh Tit. This may in part be explained by the season, but it should be remembered that a considerable storing activity was going on in the Öved area also in midwinter.

In January 1960 the feeding stations were spread through the wood in a pattern strongly resembling that found in the Great Tit but with certain differences. The most frequented station was the shrub vegetation, in which about 44 % of the feeding stations were situated. Here the Marsh Tits sometimes employed a technique like that of the Blue Tit, *i.e.* examining the buds hanging upside down, but sometimes they examined the stems like Great Tits. Comparatively many Marsh Tits were also found on the ground. With partial exception of the last-mentioned feeding station, most of the food taken was obviously animals. No signs of storing or of exploitation of stores of beech mast

were discovered. This may possibly confirm that little food storing has taken place in the locality in the previous year.

e) Treecreeper. — The Treecreeper only frequented the trunks and sometimes the larger limbs. It is unable to deal with beech mast.

f) Goldcrest. — This species was never recorded in the pure beech wood although common in the spruce plantations.

III. *Vomb* (Tab. 9)

For description of the locality, see Chapter 2.

a) Great Tit. — The Great Tit was unexpectedly found to occupy a very narrow range of feeding stations in the pure pine plantation at Vomb. In the first place, the species was numerous in the narrow borders of deciduous vegetation around the blocks of pine trees. Its habits in this vegetation were not examined. In the pines the species was only moderately numerous but sufficiently so to permit the collection of a satisfactory material of standard observations.

Nearly two thirds of all feeding stations in the pines were situated at the primary branches, and particularly the ramification between the bole and these branches was a much frequented place. In these forks, small heaps of twigs, needles and other debris had often accumulated, and the Great Tits often poked among this material so that pieces fell to the ground. Like GIBB (1954 a: 522) I found that the Great Tits also were much attracted by Squirrel (*Sciurus vulgaris*) dreys but also by old nests of Wood Pigeon (*Columba palumbus*),

Tab. 9. Percentage distribution on feeding stations in the Vomb pine wood in January 1959.

Species	Bole	Primary branch	Secondary branch	Twigs, needles	Hovering	Ground	Standard observations
Great Tit	12	64	17	3	—	5	317
Coal Tit	—	1	19	78	2	—	161
Crested Tit ...	2	21	66	12	—	—	204
Treecreeper ...	96	4	—	—	—	—	88
Goldcrest	—	0,3	2	82	16	—	617

Total: 1.387

Crows (*Corvus corone cornix*) and other birds. Only to a very slight extent did the Great Tits enter the peripheral zone of needles and twigs. It was obvious that the Great Tits were exclusively taking animal food in these surroundings.

b) Blue Tit. — The Blue Tit was only casually recorded in the pines. When met with, it was usually travelling at considerable speed through the area, sometimes in mixed flocks, sometimes in small pure groups. Their intensity of food seeking usually was very low. In the fringes of deciduous vegetation round the pine blocks the Blue Tit was more numerous, and here the species was often seeking food with great energy. These observations illustrate how much more closely tied to deciduous vegetation the Blue Tit is than the Great Tit.

c) Coal Tit. — In January 1959 the Coal Tit was rather numerous in the pine plantations at Vomb. Just as in the Great Tit, its narrow range of feeding stations was a matter of some surprise. No less than 78 % of the records refer to the zone called "twigs, needles", *i.e.* the extreme quarter of the branches. Nearly all the remaining records were obtained in the next inner part of the branches.

d) Crested Tit. — The Crested Tit was met with only in the Vomb wood. Although the distance between this locality and the Öved wood, which was so intensively studied, is only approx. 4 km over the lake and 9 km round the shore, no single record was ever obtained of Crested Tits in the latter area. This illustrates the extreme stationariness of the Crested Tit (*cf.* DURANGO 1954: 11—12, HAFTORN 1958). Because of the relatively sparse occurrence of this species in Central Skåne, the number of records remained relatively low.

The narrow range of feeding stations was as conspicuous in the Crested Tit as in the Great and Coal Tits. About two thirds of all the records refer to the zone of secondary branches, with a certain amount of entering into the surrounding zones. Thus the Crested Tit occupied the interspace between the Great Tit and the Coal Tit.

e) Marsh Tit. — This species was recorded only on a few occasions in the pines and was relatively scarce also in the surrounding deciduous vegetation. This demonstrates not only the clear preference of the species for deciduous vegetation, which caused the bird to keep nearly completely clear of the Vomb area, where the large tracts of

pines and spruces strongly dominate over the deciduous vegetation, but also its extremely stationary habits (*cf.* DURANGO 1944).

f) Treecreeper.—As expected, the species was confined to the trunks and the adjacent parts of the largest branches.

g) Goldcrest. — The Goldcrest was abundant in the pine plantations in January 1959. This species occupied the most peripheral zone of the pines, *i.e.* the needles and twigs at the extreme ends of the branches. In contrast to all other species involved in this study, the Goldcrest is in the habit of hovering outside the branch tips and thereby has an opportunity to examine the needles from an angle, from which other birds are unable to inspect them. Apart from this peculiarity, however, the feeding stations lie within the same range as those of the Coal Tit. It should be remembered that this fact does not prove that the birds are taking the same kind of food (*cf.* GIBB 1960). In fact, it is almost certain that many differences exist between the food choice of these species. For one thing, the Goldcrest takes only insects, whilst the Coal Tit takes a great deal of coniferous seeds, when available. Second, the latter species has evolved the habit of storing food. Thus, when the two species are seen food seeking together, it is likely that the Coal Tit in part subsists on discovering stored food, a possibility not open to the Goldcrest. In spite of these arguments, however, it is likely that the two species have several food resources in common (*cf.* GIBB *op. cit.*).

E. Ecological comparisons between the species inhabiting deciduous woods

I. *Öved*

The species studied in the Öved area may be divided in three groups with respect to their ecological characteristics. In one group is placed the Treecreeper by itself, for reasons explained above (p. 38). In a second group can be placed the Goldcrest and the Coal Tit, both of which show strong preference for coniferous trees. In a third group, finally, we find the Great Tit, Blue Tit and Marsh Tit, all of which prefer deciduous vegetation, this being most marked in the Blue Tit. In the present section these three species will be compared.

In the specific accounts it was repeatedly pointed out that the significance of the beech mast crop for these species was not equally

great and that they turned to different alternative foods when beech mast was not available. With regard to the great significance of the presence/absence of beech mast for these birds, a comparison must be made of the relationship of the three species to this food. The basic figures, upon which the following discussions are founded, may be found in Tabs. 2, 3 and 5. Restricting our attention to the period from November to February (incl.) in 1958/59, we find the following approximate average figures for the feeding station classified as "beech":

Great Tit	Blue Tit	Marsh Tit
40 %	40 %	35 %

These figures, however, have to be adjusted for a number of reasons, the details of which were largely presented in the specific accounts. Beech, as a class of feeding stations, comprises records of birds feeding on mast as well as on animals. These groups were generally possible to tell apart in the field, although this is not indicated in the primary tables. Of all the birds recorded as food seeking in beech, the following average percentages concern birds consuming mast:

Great Tit	Blue Tit	Marsh Tit
90 %	39 %	65 %

Thus of all birds, the following proportions were occupying themselves with the exploitation of beech mast:

Great Tit	Blue Tit	Marsh Tit
36 %	16 %	23 %

Furthermore, some visits to feeding stations other than beech were also concerned with the consumption of beech mast. Thus, part of the Great Tits feeding on the ground were seen to eat beech nuts, and several Marsh Tits were seen busy storing beech mast on oak branches. To account for these circumstances it is necessary to introduce a factor of some uncertainty in the computations. In the two species mentioned above the figures have to be substantially increased. In the Blue Tit, however, there is the additional difficulty that some of the birds seen at the cupulae may in fact have been looking for insects. There are some indications that this did happen, but there is

not the slightest cause for assuming that it was the chief attraction. Further, the Blue Tit is less inclined to transfer food from the place of discovery to some other place before eating it. Therefore, several factors act upon the figure of the Blue Tit in different directions, and the best thing to do is to keep its figures at the level directly found in nature, only rounding them off. The following figures, thus, are estimations, although based on a substantial factual basis:

Great Tit	Blue Tit	Marsh Tit
approx. 50 %	approx. 15 %	approx. 35 %

This means that no less than every second food seeking Great Tit, every third Marsh Tit and every sixth or seventh Blue Tit, were exploiting beech mast for food at the time of the observations. For all the species, thus, beech mast was of considerable significance, most so for the Great Tit and least so for the Blue Tit, whilst the Marsh Tit occupied an intermediate position.

These conclusions were tested in the autumn of 1960, when there was again a heavy crop of beech mast. This time the figures for the period of September to December are used.

The proportion of all food seeking birds recorded in beech was on average:

Great Tit	Blue Tit	Marsh Tit
62 %	45 %	41 %

The proportion of the visits to beech concerned with exploitation of beech mast was observed to be:

Great Tit	Blue Tit	Marsh Tit
86 %	47 %	70 %

From these figure we may determine that of all birds the following percentages were occupied with beech mast in the beeches:

Great Tit	Blue Tit	Marsh Tit
53 %	21 %	29 %

Making the additions necessary to account for birds feeding on mast outside the beech trees we obtain the following figures:

Great Tit	Blue Tit	Marsh Tit
approx. 65 %	approx. 20 %	approx. 40 %

The results obtained in the autumn thus closely fit in with those from the preceding winter. Beech mast was of the same relative importance to the three species. For all of them, a higher percentage was feeding on the mast in the autumn of 1960. This was probably correlated with the fact that mast was still more plentiful this year and that the studies were carried out at an earlier season, when a greater proportion of the mast was still available in the trees. After it has fallen to the ground, it is inaccessible to the Blue Tit and much less attractive for the other two species. Further, it may be of significance that the autumn months are the peak season for storing in the Marsh Tit, which therefore was working not only to satisfy its immediate food requirements but also to deposit stores, and as may be recalled, beech mast is a preferred storing item for this species.

Next, it is of importance to compare what food sources the different species utilized to supplement their diet of beech mast. In the Great Tit, the ground and the shrub vegetation were the most often recorded supplementary feeding stations. Some of the birds recorded at these stations were taking mast, particularly on the ground. Apart from beech mast it is apparent that the shrubbery furnished most of the food to the Great Tit. Here the birds were taking both vegetable and animal foods, although in midwinter the latter was of primary importance, the rich harvest of elder berries having been already depleted due to the efforts of several other bird species. The remaining portion of the feeding stations was distributed over many trees, including the conifers, and were largely, if not wholly, devoted to the exploitation of animal food.

In the autumn of 1960 beech mast occupied such a predominant position for the food ecology of the Great Tits that all other food sources became insignificant.

The Blue Tit, as pointed out above, was much less attracted by the beech mast. The largest proportion of the feeding stations of this species was devoted to the exploitation of insects in deciduous trees, with a distinct preference for oak, and also possibly a certain quantity of bud tissue and similar vegetable substances from deciduous vegetation. In birch and alder Blue Tits were seen at work on the catkins, but this was not a frequent feeding station. The only feeding station where the species came into immediate contact with the Great Tit was the shrubbery. However, as pointed out in the

specific accounts, the two species differed in their distribution within this class of feeding stations. The Great Tit concentrated upon the central parts of the bushes, whilst the Blue Tit was usually recorded from the most peripheral ones. The conclusion is certainly warranted that apart from beech mast the Blue Tit feeds in the main on animal food, supplementing it occasionally with birch and alder seeds and bud tissue.

These findings were confirmed by the studies in the autumn of 1960. Apart from beech mast most of the food consisted of insects collected from deciduous vegetation, particularly oak, beech and shrubbery, supplemented with minor quantities of vegetable food from various sources.

The Marsh Tit utilized beech mast on a large scale. Among secondary food sources, the shrub vegetation was of greatest significance. In this class of feeding stations, the Marsh Tit exhibited a pattern of distribution and techniques that was intermediate between those of the Great and Blue Tits. The visits to deciduous trees, when not concerned with the exploitation of mast, were to supplement the predominantly vegetarian diet with some animal food. In beech and oak, the Marsh Tit preferred the lower third of the trees and particularly searched the larger limbs, poking with its bill among the lichens. In part, it was obviously exploiting stored food supplies. The studies in the autumn of 1960 yielded no novel aspects on the ecology of the Marsh Tit.

In order to conclude the preceding discussion, the following points may be set forth:

1) There are marked differences in the degree of utilization of beech mast between the three species involved in this study. With regard to their rates of exploitation of this supply they may be ranked in the following order: Great Tit, Marsh Tit, Blue Tit.

2) With regard to food sources other than mast exploited under conditions of mast abundance, the Great and Marsh Tits are more similar to each other than either is to the Blue Tit. In the diet of the latter species beech mast is never of predominant importance. This fact, however, in no way precludes beech mast being very significant in the ecology of this species (*cf.* p. 32). Apart from beech mast, the Blue Tit subsists on

an almost pure insect diet, whilst the Great Tit is less specific and the Marsh Tit more inclined to turn to other sources of vegetable food. Also the Marsh Tit has its stores of food largely to itself. The Great Tit shows greater inclination to ground feeding than the other species. In the shrubbery and also in the deciduous trees, the feeding stations of the Great and the Marsh Tit are rather similar, although with certain distinctions.

Next the ecological characteristics of the three species must be examined in the absence of beech mast. For this purpose the data from the winter of 1959/60 are available.

The Great Tit was most often recorded in the shrub vegetation and on the ground. Together these two classes make up approx. 40 to 65 % of the total number of feeding stations. The habits in the shrubbery have been described above. In midwinter the food taken there chiefly consisted of animals, but in autumn a great deal of elder berries was also taken. The ground seemed to furnish most of the food compensating for the absence of mast. Although it is somewhat difficult to establish what kinds of food are taken by ground seeking birds, there can be no doubt that only a limited proportion of the food was made up of vegetable matter. Large vegetable particles are almost always treated in the wellknown characteristic way, and herbaceous plants were largely absent on the ground below the beeches, where most of the ground feeding was performed. The conclusion is inevitable that the birds were largely taking animals. In late January and February the Great Tits moved up into the deciduous trees, where the food again was predominantly of animal origin. This change was at least partly caused by the snow and by the very wet conditions in the ground. Oak and beech together made up approx. 40 % of the total number of feeding stations in the period in question, having earlier (November to early January) provided only 17 to 33 % of the feeding stations.

Thus, in the absence of beech mast the Great Tits resorted to mainly animal food from the ground and the deciduous trees. There was no noticeable increase in the frequency of visits to the shrubbery.

Since the Blue Tit was shown to devote a much smaller proportion of its time to the exploitation of beech mast, it was to be expected that the differences in habits between years with and without mast would be relatively small in this species. This was also found to be the case. In the absence of beech mast the Blue Tit was feeding

almost exclusively on small animals. The feeding stations were generally situated in deciduous trees, particularly oak, where, as described above, the Blue Tit appeared to seek food with special efficiency. To a limited extent, the animal food was supplemented with vegetable tissues from buds, galls etc. Apart from the deciduous trees, the only class of feeding stations of quantitative significance was the shrub vegetation. Here again the food collected was made up almost exclusively of animals.

In the absence of beech mast, the Marsh Tit showed increased interest in oak as a feeding station. It apparently subsisted extensively on stored supplies. In the autumn and up to December, there was also a marked increase in the proportion of ground feeding Marsh Tits. This was caused by the attraction exerted by the rich supplies of herbaceous seeds, which were being consumed and stored on a very large scale. The previous year's mast crop was also available to a certain degree (p. 37), but in all probability vegetable and animal food from the same year was of predominant importance. The winter food doubtless consisted to a large extent of plant seeds stored in the preceding autumn.

Thus, the three species turned to largely different sources of food when beech mast was not available (Tab. 10): 1) the Great Tit changed to predominantly insectivorous habits, taking most of its winter food from the ground and from deciduous trees, as well as from the shrubbery; 2) the Blue Tit remained an inhabitant of deciduous trees, where almost all the food was made up of animals; 3) the Marsh Tit, in contrast to the other two species, remained a vegetarian by using stored supplies of herbaceous seeds, berries and (to a small extent) one year old beech mast. This diet was supplemented with a proportion of lower animals, in part found "naturally", in part stored.

II. *Bökeberg*

In Tab. 8 (p. 43) the material concerning the feeding habits in the Bökeberg wood is condensed. The study in this area was intended to provide points of comparison with the results obtained in the Öved wood.

The importance of beech mast for the different species was very different indeed. Approximately 70 % of the Great Tits were exploit-

Tab. 10. Interspecific comparison of the chief feeding stations and food sources (arranged in approximate order of importance) in the Öved area in midwinter of 1958/59 and 1959/60, showing reduction of segregation when beech mast is available.

1958/59		
Great Tit: Beech (90 % mast) Shrub (mainly animal food) Ground (largely mast)	Blue Tit: Beech (39 % mast) Oak (insect food) Shrub (insect food)	Marsh Tit: Beech (65 % mast) Shrub (mainly vegetable food) Ground (mainly vegetable food) Oak (largely stored food, *i. a.* beech mast)
1959/60		
Great Tit: Ground (animal and some vegetable food) Deciduous trees (animal food) Shrub (mainly animal food)	Blue Tit: Deciduous trees (particularly oak; animal food) (Shrub)	Marsh Tit: Shrub (vegetable and animal food) Deciduous trees (largely stored food, particularly herbaceous seeds) Ground (vegetable food)

ing this source of food, and the corresponding figures for the Blue and Marsh Tits were approx. 20 to 25 % and 40 to 45 %, respectively. The relative interest taken in beech mast is thus the same as found in the Öved wood for the same winter. The figures are generally somewhat higher, which is to be expected with regard to the fact that foods other than mast were probably scarce in the pure beech wood area in Bökeberg. The Coal Tit obviously went into the beech area solely attracted by the mast, as demonstrated by the high percentage of birds exploiting this supply (approx. 80 %). The same was probably partly true also for the other species, *i.e.* they were raiding the beech woods although not spending all their time there.

Secondary feeding stations for the Great Tit were the shrub and the ground, for the Blue Tit the twigs and the shrub, for the Marsh Tit the twigs, the shrub and the ground and for the Coal Tit surprisingly often the tree trunks. In this country the Coal Tit is reputed to be rather strictly confined to conifer woods (*cf.* DURANGO 1946),

Tab. 11. Interspecific comparison of the chief feeding stations and food sources (arranged in approximate order of importance) in the Bökeberg area in January 1959 and 1960. Note the pronounced segregation in 1960.

January 1959		
Great Tit: Beech mast (70 %)	Blue Tit: Beech mast (20 to 25 %) Twigs Shrub	Marsh Tit: Beech mast (40 to 45 %) Shrub
January 1960		
Great Tit: Primary and secondary branches (mainly animal food) Shrub (mainly animal food) Ground	Blue Tit: Secondary branches and twigs (animal food) Shrub	Marsh Tit: Shrub (mainly animal food) Secondary branches and twigs Ground (vegetable and animal food)

Note: The Coal Tit which was present in the former winter and was then largely feeding on mast was absent in the latter winter.

but in England it is much less specialized, often spending much time in deciduous groves. It is interesting to learn that the English Coal Tits also are in the habit of seeking food at tree trunks (see especially BETTS 1955: 305—307).

Just as in the Öved wood, the Marsh Tit was found to be intermediate between the Great and the Blue Tit with regard to its range of feeding stations.

In January 1960 the Bökeberg wood was devoid of mast. The choice of feeding stations was then a matter of great interest. It was found that the Great Tit frequented the primary branches, the shrub, the ground and the secondary branches in this order of importance. The Blue Tit was most often recorded at the twigs, on the secondary branches and in the shrub. The Marsh Tit frequented the feeding stations in the order shrub, twigs and ground. All three species thus differed with regard to their chief feeding station. All were, however, in contact in the shrub vegetation, which was found to be the chief zone of overlapping also in the Öved area. However, there were differences in the way of examining the shrub, and thus at least partly different resources were drawn upon.

On the whole, therefore, the conclusions drawn from the data collected in the Öved area, were confirmed by the less extensive material from the Bökeberg wood. This particularly applied to the rôle of beech mast for the Great, Blue and Marsh Tits. The relationship between these three species will be further discussed in the following section. The differences between the winter with and the one without mast are summarized in Tab. 11.

F. Ecological segregation in different habitats

I. *Deciduous woods*

LACK (1954: 141—153) in a comprehensive discussion of the rôle of food in the natural regulation of bird populations makes use of GAUSE's principle as an argument in favour of the theory that food is in fact the chief agent for limitation of natural bird populations. GAUSE's principle and ecological segregation of species are related concepts. The following quotation from LACK (*op.cit.*: 148) contains the essential part of the argument:

"A third reason for thinking that birds are limited in numbers by their food supply is that each species living in the same region depends on primarily different foods. If food were not limiting numbers, it is hard to see why such differentiation in feeding habits should have been evolved, but its evolution is essential to survival if foods is limiting, since if two species compete for food, the chance of both being equally well adapted is negligible, so that one will eliminate the other. Such differentiation in feeding habits has been found in every case in which a detailed analysis has been made. Thus in closely related passerine species, both in the simple conditions on oceanic islands and in the more complex environment of western Europe, each species was found to take mainly different foods, and none competed for the same food . . . Either the species concerned lived in separate (though often adjacent) habitats, in which case they might feed on similar types of food, or, if they occurred together in the same habitat, they fed on different types of food, differing either in feeding methods or the shape or size of their beaks."

LACK points out that there are exceptions to this rule, but then always when two or more species feed together on a temporarily very rich food supply.

In this context it is of interest to examine whether ecological segregation exists between the species involved in this study and if

this segregation is unequally well pronounced at different periods. By this means it is possible to obtain a clue to the food situation prevailing, assuming that strict ecological segregation is an adaptation to food scarcity, and that reduction of segregation is an indication of a very rich supply, competition being t e m p o r a r i l y suspended.

In deciduous and mixed woods ecological segregation largely broke down between the Great Tit, Blue Tit and Marsh Tit in the presence of beech mast. In certain areas, also the Coal Tit shared the beech mast supplies. It may be mentioned parenthetically that also many other kinds of birds and mammals were taking a full share of the beech mast.

Among the feeding stations other than beech mast a partial segregation is discernible, as set forth in Tabs. 10 to 11. The Blue Tit was comparatively isolated from the other two species, being largely restricted to animal food which was collected chiefly in deciduous trees (particularly oak) and in shrub. The chief zone of contact was the shrub vegetation. However, as repeatedly pointed out in the specific accounts, the fact that the birds were recorded together in the shrub does not mean that they were subsisting on identical foods. In fact, there is evidence to support the contention that the actual overlap in food choice was of rather unimportant extent.

In the absence of beech mast the segregation became much more conspicuous. The birds in the Öved as well as in the Bökeberg wood resorted to specifically different primary feeding stations. In certain classes of stations a certain overlap occurred. Detailed study of the behaviour of the birds revealed, however, that most often the species were drawing upon different resources.

From these data the following conclusion may be drawn: The species in question are adapted to endure conditions of scarce food supplies, as shown by the clear interspecific segregation demonstrated in both of the habitats investigated. However, in the presence of beech mast this segregation is suspended, indicating that beech mast is a food source allowing exploitation by several species without causing competitive relationships between the species involved.

A reduction of the ecological segregation between tits in the presence of rich crops of beech mast and similar vegetable products was established also by Hartley (1953) and Gibb (1954 a).

II. *Coniferous woods*

In the specific accounts it was repeatedly pointed out that the ranges of feeding stations of the different species were exceptionally narrow in the pine plantation at Vomb. This held for the Great, Crested and Coal Tits and for the Goldcrest, whilst the Treecreeper is scarcely comparable in this respect. Not only were the ranges of feeding stations remarkably narrow, but there was also a comparatively slight amount of overlapping. Thus, ecological segregation had reached a high degree of perfection. The relevant data are presented in Tab. 9.

The primary feeding station of the Great Tit attracted 64 % of the birds, whilst the corresponding figure for the Coal Tit was 78 %, for the Crested Tit 66 % and for the Goldcrest 82 %. It may be pointed out that these high figures were obtained in spite of the fact that the classes of feeding stations were narrowly delimited. It is very difficult to compare the relative frequencies with those found in other habitats. But it may be pointed out that in the winter without beech mast the primary feeding stations of the different species in the deciduous woods attracted much lower percentages (between approx. 25 and 45 %). The chief difficulty of comparing the importance of a single primary feeding station for a species in different habitats may be illustrated by the following example: If the feeding habits of the Goldcrest are studied in a pure pine wood, nearly all the birds are recorded in one single feeding station, *i.e.* the peripheral zone of twigs and needles in the pines. If the observer moves into a mixed pine and spruce area, half of each, the birds spread over both pine and spruce but remain in the peripheral zone of the twigs. In that case the percentage recorded in the most frequented feeding station will fall, theoretically to 50 % of that recorded in a pure wood. This is especially true for highly specialized species. For tits it probably has less relevance. Although one has to keep this fallacy, inherent in the classificatory principles, in mind, the conclusion seems to be justified that t h e e c o l o g i c a l s e g r e g a t i o n i s v e r y p r o n o u n c e d i n c o n i f e r o u s w o o d s.

This was also found by HAFTORN (1956 c), who studied the feeding habits of tits, the Goldcrest and the Treecreeper in a spruce forest in Southern Norway. Moreover, the picture obtained by HAFTORN

on the distribution of the different species within spruce is strikingly similar to that found by the present author in pine plantations in Southern Sweden. The resemblances are illustrated in Fig. 3. The feeding stations of the Treecreeper, Crested Tit, Coal Tit and Goldcrest seem to be nearly identical in the two areas, whilst the zone occupied by the Willow Tit in Norway closely corresponds to that of the Great Tit in Skåne.

The strict segregation found in coniferous woods probably is a consequence as well as a prerequisite of food storing. It seems evident that selection would strongly counteract storing, if the stores of a given species were to a large extent utilized by another species. The storing birds would waste energy on a purposeless undertaking. In other words storing becomes selectively valuable only if other species do not find and exploit the stores deposited by a given species. Moreover, the stores have to be placed in such a way that they may be later retrieved by food seeking birds of the same species, for as HAFTORN (1954: 111) points out: "It is clear that the real value of a store depends entirely on how much of it may be used." The members of a given species have to increase the food supplies within the range of feeding stations that is typical for the species in question. (It is generally considered improbable that there is an individual "memory" of stores (*cf.* HAFTORN *op. cit.*: 113).) Thus the storing sites have to be concentrated within a limited zone of the trees, and the narrower this zone is, the better are the chances that the stores will later be found and utilized. For a discussion of the food finding mechanisms of tits the reader is referred to L. TINBERGEN (1960).

Such considerations seem to provide a satisfactory explanation of the strict segregation found in Scandinavian coniferous woodland, where several species, all with storing habits, are found side by side. Efficient storing activities seem to be of vital importance for them (*cf.* HAFTORN 1954: 117—120). The narrow ranges of feedingstations and the comparatively slight amount of overlapping between the ranges of different species are probably adaptations to the improvement of the yield of storing activities. The common evolution of storing habits and of strict ecological segregation in coniferous habitats seem to indicate that food is generally scarce in this habitat.

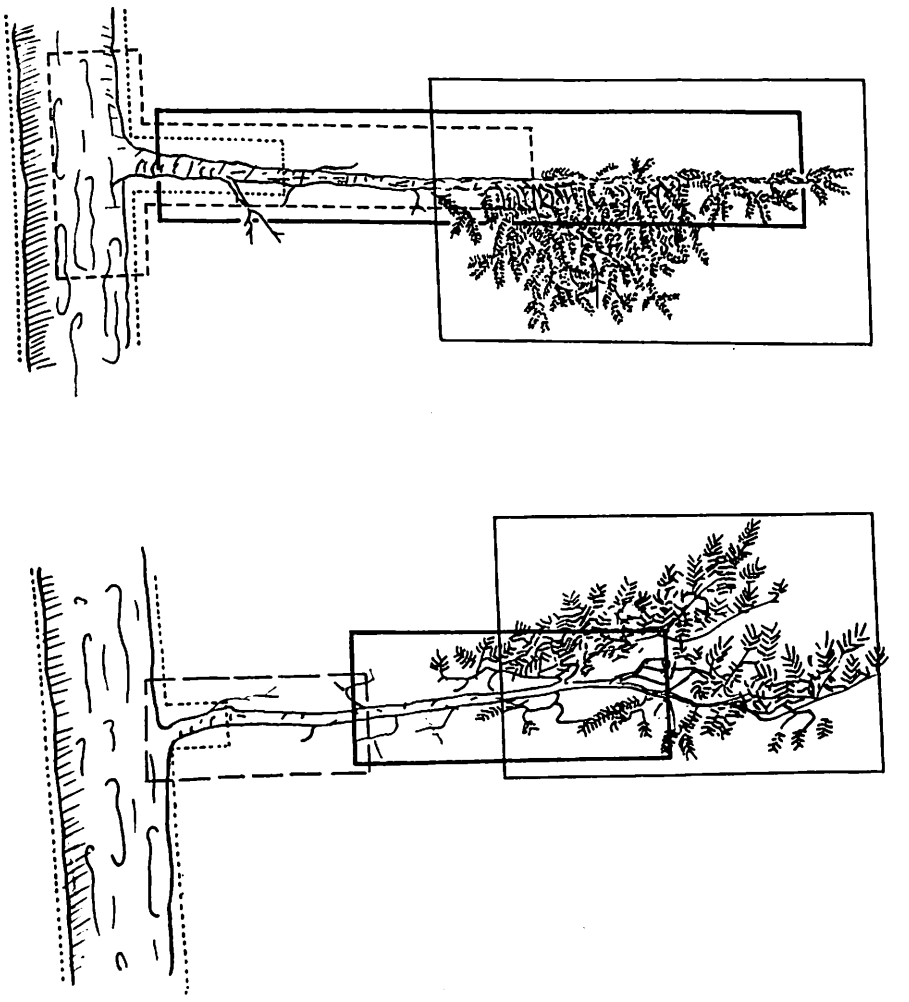

Fig. 3. Ranges of feeding stations in spruce (upper) after HAFTORN (1956 c) and in pine (lower), according to own observations.

——— Goldcrest and Coal Tit
▬▬▬ Crested Tit
- - - - - - - Willow Tit
— — — — Great Tit
. . . . . Treecreeper

4. The intensity of food seeking and the occurrence of aggressive behaviour

A. Introductory remarks

It may be argued that "if food is short, this should be reflected in the urgency with which birds feed" (GIBB 1954 a: 515). Also the frequency of aggressive encounters over food may indicate the general food situation. LACK (1954: 151) used the occurrence of aggressivity over food in winter bird flocks as additional support for the theory of the predominant significance of food for the regulation of vertebrate populations. Therefore, studies on these activity types were included in the investigation programme. Information concerning the activity types was sometimes gathered at the same time as data on food seeking habits, but sometimes on separate occasions, when the standard observations were restricted to the activity studies. The field methods were identical.

Field studies on the intensity of different activities in bird populations have been performed by several authors, who have, however, usually paid attention to one species only. An ethological analysis, containing much useful information, of the Great Tit was presented by HINDE (1952). Questions relating to social dominance and aggressivity have been discussed by *i.a.* BUTTS (1931), COLQUHOUN (1942), HAMERSTROM (1942), ODUM (1942) and DIXON (1949). The only study comprising a number of species simultaneously under observation is that published by GIBB (1954 a).

The material upon which the present chapter is based consists in approx. 21.000 standard observations.

B. Classification of activity types

The following classification was adopted:

food seeking;
flying;
interspecific aggressivity;
intraspecific aggressivity;
singing and sexual behaviour;
other activities.

Generally there were no difficulties in classifying a given individual with regard to its activity types. Food seeking birds, for instance, usually show quite distinctive movements from birds having other occupations "in mind". A bird was classified as "flying" only when seen flying for a distance of at least 30 to 40 metres. Thus, this class approximately corresponds to what GIBB (1954 a: 520) called "distant flight". A bird fluttering from one branch to the next or even from one tree to the next would not be included in this group. Rather it would be classified with regard to its activity before and after this short movement. Aggressive behaviour includes both actual fights, when the birds are in physical contact, and threat postures (*cf.* HINDE 1952). Singing is unambiguous. Sexual activities include copulation, courtship feeding, nest-hole inspection and other phenomena directly concerned with reproduction. The group called "other activities" includes several less clearly defined kinds of activities, the most frequent of which were "sitting passive" and "calling". Here also birds recorded as "preening" and "bathing" were included. The figures in this class tend to show a peak in the early reproductive season, when birds were often seen sitting motionless on a bough or heard calling intensely. There was also a rise in this group in October 1959, when birds were often calling excitedly (particularly the Great Tits; p. 126).

Of course individuals were sometimes seen which could not be easily grouped with any of these categories. In some cases, birds sitting passively were lumped with the "other activities" category, although they were in fact performing a mild version of territorial threat behaviour. When this posture is fully developed, it is certainly unmistakable, but when only imperfectly presented, it is much less striking.

An obvious source of error is the different conspicuousness of different activity types. Thus, a food seeking bird is much more conspicuous than one sitting motionless in the canopy, and a singing bird more than either of these. Of course, if a Goldcrest takes a rest, sitting still or preening in the tangle of twigs of a pine, it is most unlikely to be recorded at all. However, all the tits are approximately equally conspicuous, taking each class of activities separately, so that interspecific comparisons are justified, and the conspicuousness of the different activities is only slightly variable from month to month,

which permits seasonal comparisons. Such comparisons are the main object of the activity studies.

Even if a bird is seen at close quarters, it might be difficult to assign it to any of the above-mentioned classes. For instance, it may suddenly change activity type. Sometimes it is very obvious which of two activities simultaneously performed is the dominating. In such cases where this was impossible to decide, the individual was grouped with "other activities". Such dubious cases were found, on a special check, to make up 2 and 4 % of all records in November 1959 and December 1960, respectively.

C. Intensity of feeding activities

Due to the relationship between body volume and body surface and the consequent correlation between either and heat economy, it is to be expected that the smaller the body weight of a species, the more intense its food seeking activities. This rule will, however, hold true only if the foods of the species compared have approximately the same calorific value per unit effort expended by the birds. GIBB (1954 a: 515) found a close correlation between decreasing body weight and increasing food seeking intensity.

In Tab. 12 the proportion of food seeking birds to all birds observed is calculated for November to January (incl.) in 1958/59 and 1959/60, based on observations in the Öved wood. For comparison, the corresponding results found by GIBB (*op. cit.*) are also set forth, as are the

Tab. 12. Average food seeking intensity in midwinter in Öved 1958/59 and 1959/60 and in England (according to GIBB 1954 a), and body weights.

Species	Food seeking intensity (%)			Body weight (g)	
	1958/59	1959/60	GIBB (1954 a)	GIBB (1954 a)	NIETHAMMER (1937)
Great Tit	74	72	73	18	18,5
Blue Tit	79	82	81	10—11	11
Coal Tit	88	—	91	8—9	(8,5)
Marsh Tit ...	81	81	88	10—11	10,8
Treecreeper ..	88	90	—	—	8,5—9,5
Goldcrest	91	92	99	5	5—6

Note: For the Coal Tit, GIBB's figure refers to the period October to February. All other figures are averages for November to January, incl.

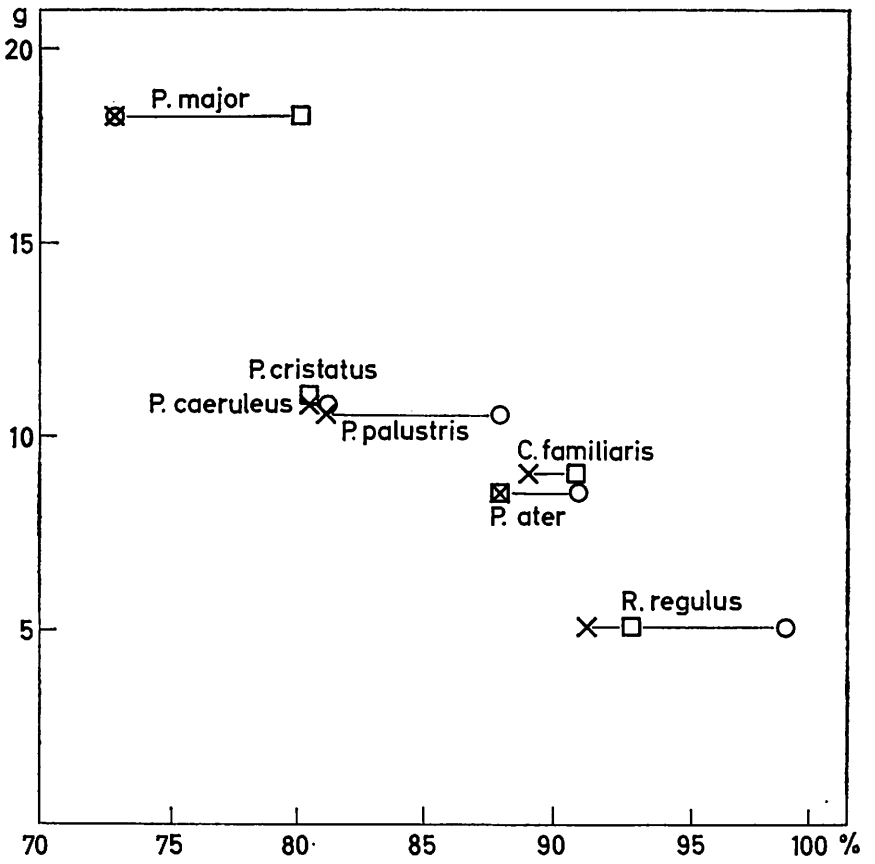

Fig. 4. The correlation between body weight and food seeking intensity in midwinter. Circles = data from GIBB (1954 a), crosses = data from the Öved area, squares = data from the Vomb area.

body weights of the species in question. In the first place it may be pointed out that also in my own material the inverse relationship between body weight and feeding intensity is very obvious, as set forth in Fig. 4. Second, it may be pointed out that the annual differences are so small as to be negligible. Third, a comparison between my own results on the one hand and those of GIBB on the other, reveals farreaching similarities, although there are certain discrepancies. For the Goldcrest this may probably be explained by different classificatory principles: it may be, for example, that I have been more inclined to place the birds in the "flight" or "singing"

groups than GIBB. For the Marsh Tit the discrepancy is marked and may hardly be interpreted as a consequence of classificatory fallacies. It may be suggested that since the storing habits of this species are only mentioned in passing in British tit studies, the British population may have a poorly developed storing instinct and thus may have to work more intensely in midwinter in Britain than in South Sweden, where the birds have access to extensive supplies. With regard to the body weight relationships, the Marsh Tit would be expected to exhibit a food seeking intensity comparable to that of the Blue Tit. This is true in my own material but not in that of GIBB (see Fig. 4). However, apart from the quality of the food there is one more important variable factor, *viz.* the insulating efficiency of the plumage. If this power is very different in different species, their energy requirements will differ. In point of fact, in some preliminary experiments GIBB (1957) found that the Blue Tit had disproportionately low energy requirements and suggested that this was due to the insulation efficiency of its plumage.

Similar comparisons from the Vomb pine plantation show that the Crested Tit is in agreement with results obtained from the Coal Tit, the Treecreeper and the Goldcrest (Tab. 13 and Fig. 4). In this study area, on the other hand, the Great Tit, contrary to expectation, has relatively high intensity both in comparison with the Crested Tit for example and with Great Tits in other areas. This will be returned to below.

The seasonal changes in food seeking intensity are illustrated in Fig. 5, based on numerical values of Tab. 15 to 20. As found also by

Tab. 13. Food seeking intensity in the Vomb pine plantation, January 1959.

Species	% of standard observations referring to food-seeking birds	No. of standard observations
Great Tit	80	398
Coal Tit	88	183
Crested Tit	80	255
Treecreeper	91	97
Goldcrest	93	509

Note: According to NIETHAMMER (1937: 225) and HAFTORN (1956 c: 41) the body weight of the Crested Tit is about 11 g.

GIBB (1954 a), the intensity reaches its maximum value in midwinter, sometimes perhaps slightly earlier than might be expected. Thus in 1959/60 the Great Tit showed greatest food seeking intensity from late October to December. The Treecreeper in both 1958/59 and 1959/60 attained its maximum value in December. Generally speaking, however, the peak fell in December to January, when the days are at their briefest.

The Marsh Tit seems to be at some variance with this general trend. At least the midwinter peak is much less pronounced in this species, which has instead a protracted period of equally high food seeking intensity. This is obviously correlated with its storing activities. The Marsh Tit, so to speak, has to work hard in times of relative abundance to be able to survive periods of scarcity.

The diagrams and tables also illustrate the relatively slight annual variations in food seeking intensity, as was found already on the basis of midwinter data only. The differences that do exist generally are of too slight extent to justify elaboration. There is no over-all trend to increase or decrease at any particular season, the different species fluctuating independently. There is one conspicuous difference, which seems to be of significance. Midwinter intensity in food seeking was in the Great Tit attained as early as in mid-October in 1959 but not until December in 1960. The change was a sudden one, causing a rise in the percentage figure of food seeking birds from 63 to 73 % in the course of October. This would indicate that the Great Tits were able to satisfy their food requirements quicker in 1960 than in 1959, and this most probably was correlated with the presence of beech mast in the former year. That the food situation is in fact reflected in the urge with which birds seek food is further illustrated by the fact, mentioned above (p. 66), that the food seeking intensity of Great Tits in pine wood was remarkably high.

In September 1960 a special study was undertaken to elucidate the influence of beech mast on the food seeking intensity of the Great Tit. The food seeking intensity was studied in two different deciduous groves in Central Skåne, differing in their composition. One consisted of pure beech with a few patches of alder, the other of a mixture of oak, alder, lime (*Tilia*) and birch (but no beech at all). The results are presented in Tab. 14. The Great Tit obtained a much lower figure in the mast area than in the other wood, where this food was not available. The opposite was true for the Coal Tit,

Tab. 14. Food seeking intensity in two different deciduous groves in late September 1960.

Species	Beech wood area		Mixed wood without beech	
	% food-seeking birds	standard observations	% food-seeking birds	standard observations
Great Tit	52	222	63	147
Blue Tit	61	109	63	106
Coal Tit	80	51	53	79
Marsh Tit	76	142	73	117
Treecreeper	80	60	78	46
Goldcrest	(73	26)	83	98
		584(+26)		593

for these birds remained in the beeches to have a meal of mast but travelled through the other deciduous area without stopping, feeding only as they went. The other species show no appreciable differences. However, the material is not so extensive as to permit detailed analysis.

Against this background it may seem peculiar that the food seeking intensity of the Great Tit in Öved was not lower in midwinter when mast was present than when it was not (Fig. 5). The explanation is suggested that this was caused by the strong urge to food seeking after the winter nights, the birds making up for the long starvation in the morning, when the field work was always performed. Differences would possibly have been detectable in the intensity in the afternoon or in the time of the day when food seeking was discontinued and the birds entered their roosts (*cf.* LEHTONEN 1947, KLUIJVER 1950: 111).

To summarize the findings presented above, it may be pointed out that:

1) the specific differences in food seeking intensity in mid-winter were found to be in accordance with expectation on physical grounds,

2) the food seeking intensity was at its peak in mid-winter,

3) local differences in food seeking intensity in the Great Tit were sometimes possible to correlate with probable food availability (beech mast vs. no mast, deciduous wood vs. pine plantation),

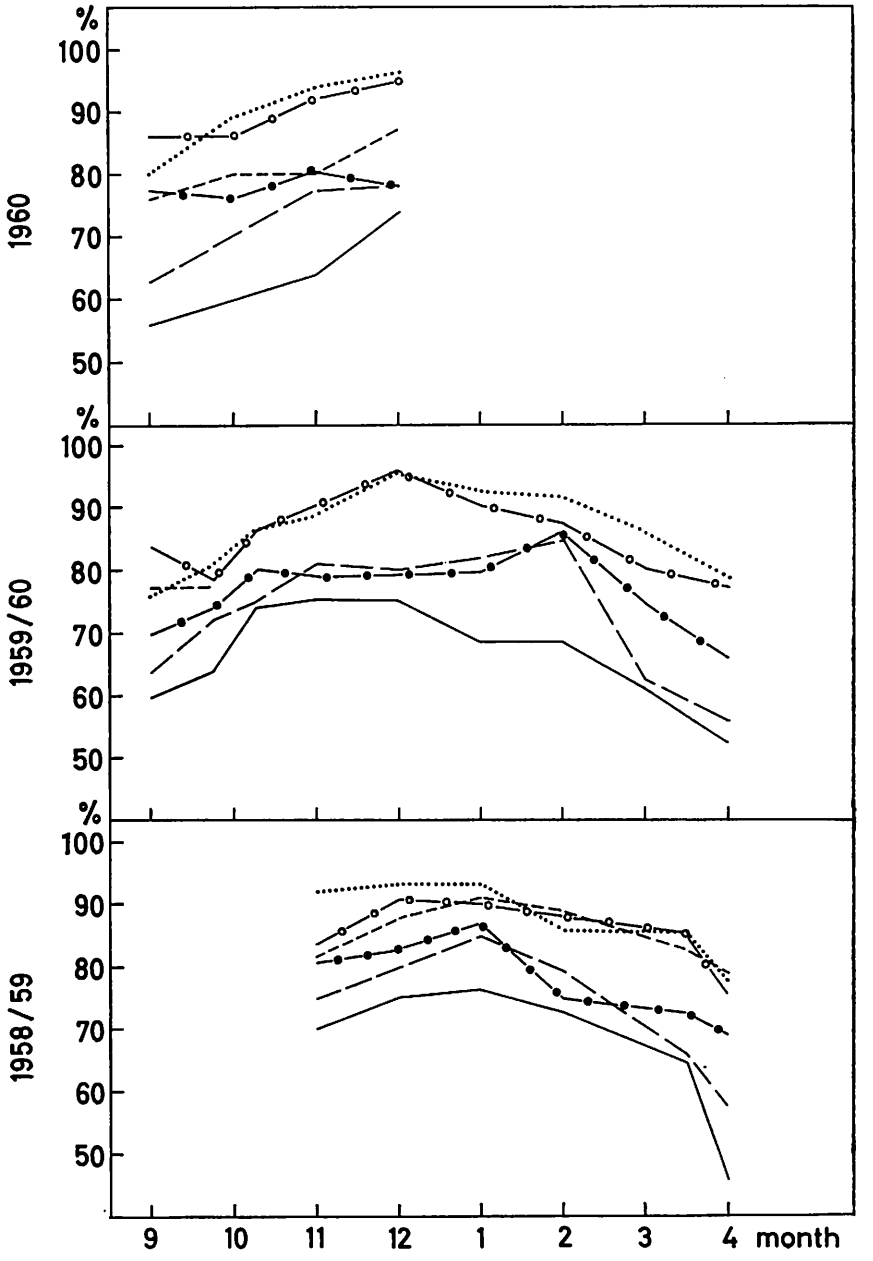

Fig. 5. Seasonal changes in food seeking intensity.

..... Goldcrest
— ∘ — ∘ — Treecreeper
— • — • — Marsh Tit
——— Great Tit
- - - - - - - - Coal Tit
— — — — Blue Tit

4) the Marsh Tit has a protracted period of great intensity, caused by the storing activities,

5) important annual differences in the food seeking intensity in autumn were found in the Great Tit, correlated with the presence/absence of beech mast,

6) possible annual mid-winter differences in food seeking intensity in the Great Tit were obscured by other factors, as yet unknown.

D. Aggressive types of behaviour

Aggressive tendencies may find their expression by several different postures and actions. Direct combats with physical contact between the fighters are rare events, only witnessed eight times by the present author. Four of these cases concerned Goldcrests and were recorded in November, January (twice) and March. The other four cases were fights between Blue Tits and were all recorded in April, having obviously a territorial background.

The most common kind of aggressive behaviour were threat displays (*cf.* HINDE 1952), sometimes followed by pursuits in the trees or in the air. There is no need to describe the different postures, since this has been done by HINDE (*op.cit.*). The encounters varied strongly in intensity: from lengthy "disputes", the two participants assuming a variety of postures, to brief displays by one bird against another flying past. Food was rarely involved. The type of encounter called "supplanting attack" and defined by HINDE (*op.cit.*: 22) thus: "In a supplanting attack for a food object, the aggressor flies at the possessor of the food, causing the latter to fly off, and feeds in his place", was a rare incident in my study areas (*cf.* p. 29). In fact, the threat postures were often assumed without apparent "reason" — they seemed to be caused by some kind of general excitement, one might say "irritation". I was often impressed by the infectiousness of aggressivity. In some days I witnessed sudden outbreaks of aggressive postures and calls, often subsiding after a couple of minutes. On the other hand, hours and days could pass without a single record of aggressive behaviour.

The seasonal and interspecific differences in aggressive behaviour are set forth in Tabs. 15 to 20, where also the other activity classes are included. In the Great Tit there was a prominent peak of aggressive kinds of behaviour in October 1959 (p. 126). Here the "infectiousness"

Tab. 15. Activity types of the Great Tit in the Öved area.

Year	1958		1959									1960							
Month	11	12	1	2	3+4	4	9	10/I	10/II	11	12	1	2	3	4	9	10	11	12
Food seeking	70	75	77	73	64	46	60	63	73	74	74	69	69	61	52	56	60	64	73
Flying	12	10	8	5	7	6	12	18	13	10	9	8	5	8	11	9	11	10	4
Interspec. aggression .	1	1	1	1	—	3	—	3	3	—	—	1	2	—	2	—	—	—	1
Intraspec. aggression .	2	1	2	2	1	—	1	4	4	1	1	—	—	—	—	—	1	1	2
Singing	1	—	2	12	13	25	1	2	1	—	—	3	7	6	24	—	5	—	2
Other activities	14	13	10	7	15	20	26	10	6	15	16	19	17	25	11	35	23	25	18
Standard observations:	402	326	239	386	688	604	442	428	336	207	72	180	91	249	204	660	590	487	376

Total: 6.967

Tab. 16. Activity types of the Blue Tit in the Öved area.

Year	1958		1959									1960							
Month	11	12	1	2	3+4	4	9	10/I	10/II	11	12	1	2	3	4	9	10	11	12
Food seeking	75	80	85	76	66	57	64	72	74	81	80	82	85	62	56	63	70	77	78
Flying	17	9	9	12	7	8	8	11	14	5	7	8	9	12	10	6	7	9	9
Interspec. aggression..	1	—	2	—	3	3	—	3	1	—	—	—	1	1	2	—	1	—	1
Intraspec. aggression .	2	—	—	1	2	—	—	2	1	—	—	—	—	—	4	—	—	1	—
Singing	—	—	1	9	16	27	—	1	—	1	—	2	2	10	21	2	1	—	—
Other activities	5	11	3	2	6	5	28	11	10	13	13	8	3	15	3	29	21	13	12
Standard observations:	219	116	161	283	474	470	306	206	271	222	61	117	60	162	162	300	423	275	240

Total: 4.528

Tab. 17. Activity types of the Coal Tit in the Öved area.

Year	1958		1959									1960							
Month	11	12	1	2	3+4	4	9	10/I	10/II	11	12	1	2	3	4	9	10	11	12
Food seeking	82	88	91	89	83	79	77	77	·	·	·	·	·	·	·	76	80	80	87
Flying	8	8	6	1	—	1	6	10	·	·	·	·	·	·	·	12	13	8	5
Interspec. aggression .	2	1	—	1	2	1	—	—	·	·	·	·	·	·	·	1	1	—	—
Intraspec. aggression .	4	1	2	—	2	—	—	1	·	·	·	·	·	·	·	2	—	2	2
Singing	—	—	1	8	14	19	2	2	·	·	·	·	·	·	·	—	—	2	3
Other activities	4	2	—	1	1	—	15	10	·	·	·	·	·	·	·	9	6	6	3
Standard observations	100	77	69	111	152	124	127	170	Not present							104	250	124	98

Total: 1.506

Tab. 18. Activity types of the Marsh Tit in the Öved area.

Year	1958		1959									1960							
Month	11	12	1	2	3+4	4	9	10/I	10/II	11	12	1	2	3	4	9	10	11	12
Food seeking	81	83	87	75	73	69	70	74	80	79	79	80	86	75	66	77	76	80	78
Flying	5	5	2	11	2	1	6	7	7	8	4	4	7	10	13	7	7	10	10
Interspec. aggression .	—	—	—	1	4	3	—	1	—	—	2	—	—	3	5	—	—	—	1
Intraspec. aggression .	—	—	—	—	2	1	—	—	—	—	1	—	—	2	2	—	—	—	—
Singing	—	—	—	6	11	16	—	—	—	—	1	1	2	1	11	1	—	—	3
Other activities	14	12	11	7	8	10	24	18	13	13	13	15	5	9	3	15	17	10	8
Standard observations:	134	103	87	236	302	263	161	194	227	201	48	128	56	105	95	168	261	253	202

Total: 3.224

Tab. 19. Activity types of the Treecreeper in the Öved area.

Year	1958		1959									1960							
Month	11	12	1	2	3+4	4	9	10/I	10/II	11	12	1	2	3	4	9	10	11	12
Food seeking	84	91	90	86	85	76	84	78	86	90	95	90	87	80	77	86	86	92	94
Flying	6	5	5	5	4	5	3	9	11	6	5	3	4	10	9	10	10	4	3
Interspec. aggression .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Intraspec. aggression .	6	—	3	—	1	4	3	1	3	2	—	2	—	1	7	4	4	1	2
Singing	—	—	—	9	10	14	—	1	—	—	—	—	6	9	7	—	—	—	1
Other activities	4	4	2	—	—	1	10	11	—	2	—	5	3	—	—	—	—	3	—
Standard observations:	64	42	62	97	128	148	87	125	108	67	38	98	48	96	59	80	90	71	46

Total: 1.554

Tab. 20. Activity types of the Goldcrest in the Öved area.

Year	1958		1959									1960							
Month	11	12	1	2	3+4	4	9	10/I	10/II	11	12	1	2	3	4	9	10	11	12
Food seeking	92	93	93	86	85	78	76	80	86	89	95	93	92	86	79	80	89	94	96
Flying	2	3	3	2	2	2	5	6	4	7	4	3	3	2	9	9	4	1	1
Interspec. aggression .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Intraspec. aggression .	4	4	4	3	3	—	2	6	4	—	—	4	4	8	6	6	2	2	3
Singing	—	—	—	8	9	18	4	2	2	—	—	—	1	4	6	—	2	1	—
Other activities	2	—	—	1	1	2	13	6	4	4	1	—	—	—	—	5	3	2	—
Standard observations:	209	163	176	134	176	132	139	325	333	150	114	175	79	106	100	210	222	175	140

Total: 3.258

of aggressivity was particularly conspicuous. Other seasonal changes are hardly distinguishable. The interspecific aggression was directed against many species of birds, although most often against the Blue Tit. This is certainly not correlated with some "antipathy" for this species, but simply with the fact that these birds tend to occur in the same places. In the Blue Tit there was also a certain increase in the frequency of aggressivity in October 1959, but this species in addition shows increasing aggressivity in spring, at the beginning of the reproductive season. Interspecific aggression was most often directed against the Great Tit, but also against other tit species, as well as more casually against other birds such as Treecreeper, Nuthatch, finches and thrushes. The material concerning the Coal Tit hardly contains any information of interest. The Marsh Tit shows a clear peak of aggressivity in the early breeding season but is very "peaceful" at other times. The Treecreeper, on the other hand, is much inclined to quarelling but always directs its aggression to members of its own species. The same is true also for the Goldcrest, in which there was in 1959/60 a clear rise in aggressivity in the early breeding season.

Aggressive types of behaviour are frequent, although scarcely ever leading to actual combat. The *Parus* species freely threat each other, and also species outside the genus, but the Treecreeper and the Goldcrest were never found to indulge in interspecific aggression. In the study area where this work was carried out, t h e b i r d s d i d n o t l o s e o r g a i n a n y s i g n i f i c a n t a m o u n t s o f f o o d b y f i g h t i n g, which is at variance with the findings published by GIBB (1954 a). There was no noticeable increase in aggressivity in the mast-less winter in comparison with the winter with a rich mast supply, further supporting the contention that aggression in the bird populations studied had little to do with food conditions.

5. Seasonal and annual population fluctuations in the Öved wood

A. Introductory remarks

In the previous chapters the food situation for the tits inhabiting the Öved wood has been studied from different angles, and it was shown that the winter of 1959/60 differed from the other winters in

several respects, all of which are probably to be correlated with the absence of beech mast. This may be expected to lead to changes also in the numbers of birds spending the winter in the locality, for the increase in food supply caused by the beech mast crop must have improved the "carrying capacity" of the locality. Therefore, it was from the beginning decided to pay close attention to differences in population density between seasons and between years. The results yielded by this census work are presented in this chapter.

B. Study technique

While the methodology of census work on breeding populations of passerine birds has recently been discussed in detail by ENEMAR (1959), we are lacking a similar treatment for nonbreeding (although more or less stationary) populations. Presumably the properties of nonbreeding populations are in various respects different from those of breeding populations. The chief difference from the present point of view seems to be that birds are closely tied to a territory of limited extent during the breeding season, whilst this is true to a much lesser degree during the nonbreeding season (*cf.* KALELA 1954). For although KLUIJVER (1951) and other workers have shown that many Great Tits pair and maintain some kind of territory from the beginning of the autumn, it is nevertheless true, as pointed out by many authors, that their daily cruising radii in winter are usually much greater than in the breeding season. Also Great Tits which are paired and have selected a territory are known to abandon this area temporarily and join tit flocks roaming through the district. I agree with HAFTORN (1958) that the extent of the movements in winter of North European tit flocks has been grossly overestimated by many naturalists, but nevertheless the individuals are much less tied to a restricted area in winter.

During the breeding season most passerine birds manifest their territories by song. The song may be extremely persistent, and the counting of singing males is the generally accepted technique of estimating breeding populations. In winter song is largely inhibited. That is another difference.

Therefore, as pointed out by PALMGREN (1936: 160), a simple line transect technique is justifiable for assessing winter populations. The aim is not to establish the absolute number of birds inhabiting a

given area, for the simple reason that there is no such absolute figure. The aim is rather to obtain an average figure on the number of birds seen along a given route. On the assumption that the census procedure is kept as constant as possible, this allows interannual, interseasonal and (with especial care) interlocal comparisons. It may be that the theory of line transect surveys presented by YAPP (1956) is much more readily applicable to winter populations than to breeding populations (*cf.* discussion by ENEMAR *op.cit.:* 86 *et seq.*).

When studying winter populations it is thus permissible simply to count all the birds met with along a given route, care being taken to avoid duplications. If the route is extended over a considerable distance, it is found that the number of birds of different species is subject to relatively small daily fluctuations. Very often, however, within a series of such censuses, one or two days diverge strikingly from all the other days. This may be caused be temporary changes in local distribution, caused by meteorological or other factors, as described by JOHNSTON (1942). To justify comparisons between two periods or localities, it is of course necessary to perform a large number of transects.

The results of the census work in the Öved wood are presented in Fig. 6. The figure for any given period is based on at least six and up to 14 daily transects. The census work was sometimes performed at the same time as the taking of standard observations or other studies, but more often on separate occasions. The same route was always strictly adhered to.

C. Results and discussion

The Great Tit population was very dense in the winter of 1958/59, in average 65 birds being counted per transect in November. Later there was a gradual decrease, the lowest figures being obtained in January to February. In March to April there was a clear increase, followed by decrease in late April when the breeding population alone remained. It was estimated that not less than 15 pairs were nesting in the area, the additional birds counted being visitors from surrounding areas.

The autumn of 1959 opened with a fairly high figure, although it was low enough to indicate that most of the year's production had already left the area. In the course of October the population dropped

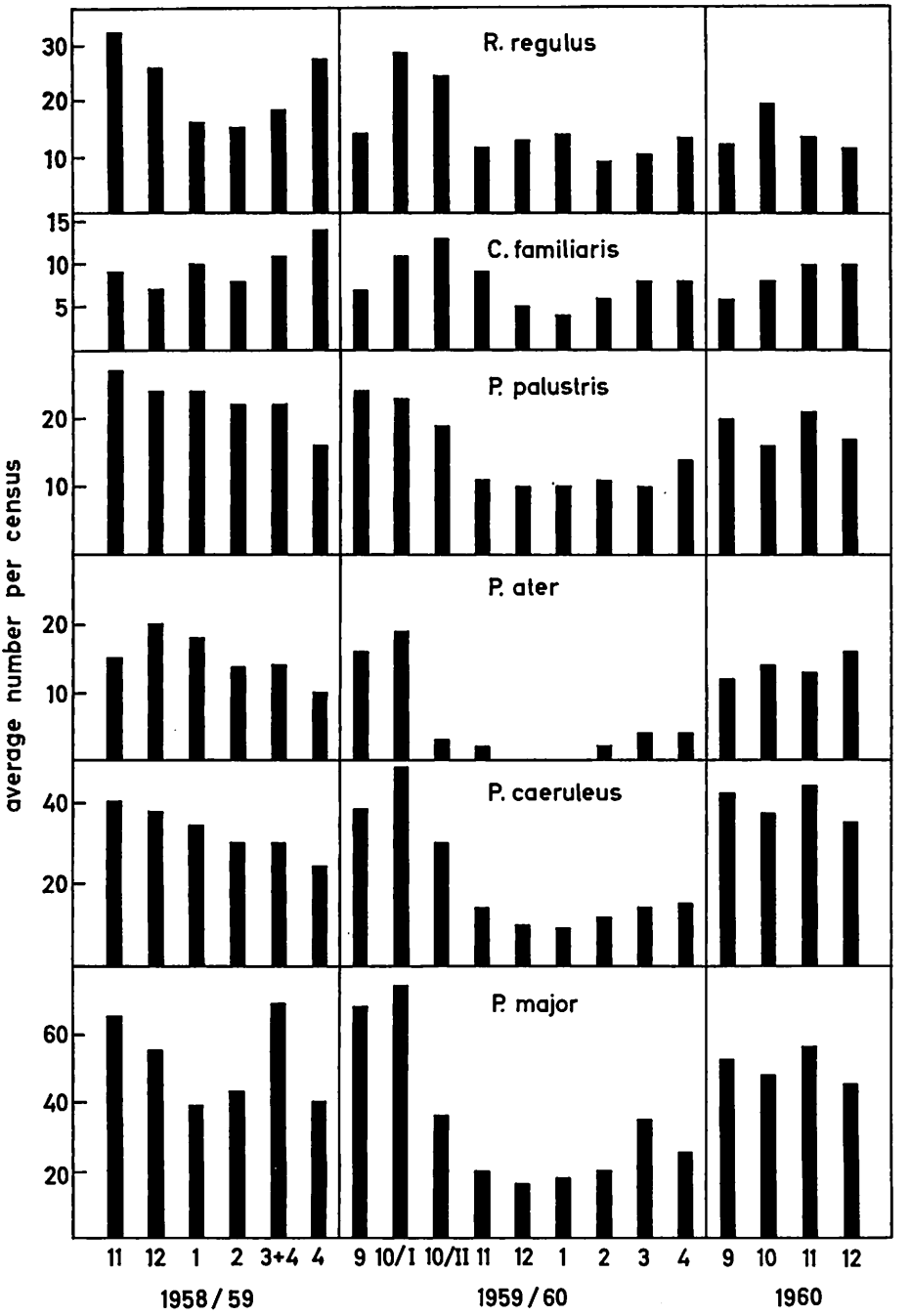

Fig. 6. Population changes in the Öved area. Average values based on 6 to 14 censuses.

rapidly, a further decrease had occurred in November, but then the figure remained comparatively stable until March, when a considerable increase occurred, followed by a decrease in April. Nine or ten pairs nested in the area in this spring.

The autumn of 1960 opened with a lower figure than the preceding autumn, but then the numbers of Great Tits remained remarkably constant until the turn of the year, when the studies were discontinued.

The December populations may be compared for the three winters to illustrate the extent of the differences in the midwinter populations: December 1958 55, December 1959 16 and December 1960 45 birds/census. The 1959 midwinter population, thus, was only about one third of that of the other winters. It may be recalled that this was the winter without beech mast. See also p. 131.

The changes in the population density in the Öved area are obviously correlated mainly with movements in and out of the area, rather than mortality. There is evidence for a first exodus in the summer months, for the September population is far from corresponding to the total of the breeding birds and their progeny. Several workers have by special techniques demonstrated a rapid dispersal of the young Great Tits within the first weeks after their leaving the nest (PLATTNER & SUTTER 1946/47, GOODBODY 1952: 285, GIBB 1954 b: 44).

In the autumn of 1959 there was a further heavy exodus, without correspondence in 1960. This occurred in October. The November population was only approx. 27 % of that of early October. Since this exodus was synchronous with the mass movement of Great Tits recorded at Falsterbo and elsewhere (p. 99), it seems certain that it represented the true "autumn migration".

Possibly a third kind of exodus occurred in the winter of 1958/59 when the numbers of Great Tits suddenly decreased between December and January. In the same time of the following winter, the population seems to have been comparatively stable. A midwinter reduction of the tit population was found by GIBB (1954 b: 41—43) and may be interpreted tentatively as caused by local movements and habitat changes, released by climatical factors. It is a commonplace experience that in the event of cold weather tit populations round human habitations may suddenly increase in midwinter.

It is also noteworthy that the data indicate a considerable reduction of the breeding population in 1960, following the large autumn exodus

in October 1959. However, it is of interest that there is a return of birds in spring, indicating that part of the departed birds do come back or at least that there exists a "spring migration" in the Great Tit (*cf.* ULFSTRAND 1959 b: 46).

The changes in the Blue Tit population were closely parallel with those described above for the Great Tit. Thus the midwinter population of 1959/60 was less than one third of that of the other two winters (using the December averages). This decrease was correlated with a tremendous exodus in October 1959, the November population being only approx. 25 % of that counted in early October. The data for September indicate that there is a rapid dispersal of Blue Tits after breeding, exactly as in the Great Tit.

The Coal Tit was entirely absent from the study area in part of the winter of 1959/60. The December figure is much lower in 1960 than in 1958. A sharp decrease occurred in October 1959, but there was no trace of such a feature in 1960.

The Marsh Tit occurred in comparatively stable numbers. In the spring of 1959 there was a certain decrease, probably caused by dispersal of the birds that had spent the winter in the area, attracted by the beech mast. In the autumn of 1959 there was nothing like the decrease established for the Great and Blue Tits, but rather a gradual decrease beginning in late October and reaching stable conditions in December. There was no noticeable increase in spring. The spring population was considerably lower in 1960 than in 1959. Obviously there was a successive exodus from the area in the winter of 1959/60 but probably this did not involve any distant movements. Therefore it is surprising that there was not a back-movement into the area in spring.

The figures obtained concerning the Treecreeper and the Goldcrest do not seem to require any comments.

For the species of special interest, *viz.* the Great, Blue and Marsh Tits, it was thus possible to show that

1) the last differed from the first two species by having a more stable population,

2) the first two species inhabited the area in much lower numbers when beech mast was not available whilst the difference was much smaller in the last,

3) there was a return movement by Great and Blue Tits into the area in spring, and

4) there are probably three "waves" of exodus, although all may not be developed in every year, *i.e.* a summer dispersal, an autumn off-movement and a midwinter disappearance of local extent. The autumn movements will be subjected to closer examination in Chapter 7. Whether the annual differences were purely local or extended over larger areas, will be examined in Chapter 6.

Finally, it may be pointed out that the low figure in the winter of 1959/60 may have been caused by two kinds of changes, *viz.*

1) that the locally breeding population and its progeny had departed in autumn and that no birds arrived from other areas, and/or

2) that birds arriving from other areas did not stay but passed through the area.

6. Annual and regional differences in the density of the mid-winter populations of the Great, Blue and Marsh Tits

A. The organisation of the Winter Bird Census and the reliability of its results

Quantitative studies on the entire winter avifauna over larger areas have rarely been undertaken. They are extremely time-consuming and therefore hardly possible to carry out by a single worker. In the United States a large-scale attempt at nation-wide "Christmas Counts" was made, and the work continued for many decades. The results were, however, apparently difficult to analyse, for few papers have emerged from the wealth of data assembled (see *e.g.* WING 1941). In recent years Finnish ornithologists have started a cooperative quantitative survey of the winter bird fauna, and the preliminary data for the first seasons covered by this study have been published by KOSKIMIES & RAJALA (1957, 1958) and by RAJALA & TÖRNROOS (1960).

In a way, cooperative investigations on the winter bird fauna are comparatively easy to perform, for the census technique may be very simple (*cf.* pp. 75—76). The elaborate technique required for the study of breeding populations has seriously hampered such work. But in winter the observers are only to be requested to keep detailed

account of all birds seen during their field trips. Personal differences in visual acuity, choice of habitat for the field work, time of day, influence of weather etc. are largely smoothed out, provided that the extent of the field work and the number of participants are sufficiently large. The results must not be expressed in absolute numbers per unit area but are always relative (for example numbers of birds seen per unit distance travelled or per unit time). Such relative values may be utilized for comparative work between districts, between years and, with particular care, between habitats.

With these points in view it seemed worth while to attempt a cooperative investigation of the winter bird fauna of Sweden. Mr. I. LENNERSTEDT joined in the project, and we have since the autumn of 1957 been organising the work together. The procedure is briefly as follows:

Every year in November an appeal is issued to some hundreds of field ornithologists, requesting them to make as accurate counts as possible of all birds observed during their field trips in the period 23 December to 8 January, incl. Together with quantitative lists of species for each separate field trip the observers are requested to send in information concerning time spent in the field, approximate distances covered, chief types of habitat visited in the course of the field trips, weather conditions, snow and ice, presence or absence of food supplied intentionally or unintentionally by man and any other item of importance.

The reports are of very variable extent. Usually a few have to be discarded due to erroneous procedure on the part of the observers, incomplete information on some crucial point etc. The great majority of the reports, on the other hand, are of a very high standard of accuracy and completeness. The extent of the field work upon which they are based varies from a few hours to daily line transects of impressive duration. Some reports are based on the field work of a single person, but many are the outcome of coordinate efforts by a group of ornithologists. The number of birds seen per unit time varies tremendously, due partly to the geographical site of the study area and partly to the variety of habitats examined. In addition to quantitative lists many reports include "point observations" from particularly favourable localities etc., and this additional information is of great interest for the studying of the geographical distribution of the winter fauna. Much useful information on food habits and

similar questions may also be found in the comments offered by the participants.

Northern Sweden was poorly covered by this system of observers and has therefore had to be omitted from the following account. Southern and Central Sweden up to approx. 61° N. lat. was, for the purpose of regional comparisons, divided into five districts, comprising the following provinces (map in Förteckning över Sveriges fåglar 1958):

District I: Skåne, Halland and Blekinge.
District II: Småland and Öland. (Very few reports were received from Öland.)
District III: Västergötland, Bohuslän and Dalsland.
District IV: Östergötland, Södermanland and Uppland.
District V: Västmanland, Närke, Värmland, Dalarna, Gästrikland and Hälsingland.

These districts approximately correspond to the division of Sweden in "stand type regions" by foresters (see *e.g.* Atlas över Sverige 1959), although there are certain discrepancies. Rough average figures on the composition of the forests in the different districts are presented in Tab. 21.

It is obvious that material gathered in this way suffers from considerable sources of error. In the first place, the result obtained from a given census depends entirely on the choice of habitat for the work, and if two workers, even in nearby areas, select to work in sharply different habitat types, such as for example deciduous wood and open meadows on the one hand and coniferous forests in hilly areas on the other, they will obtain very different lists of species observed. However, since all the reports from one district are pooled, such differences should be largely smoothed out. Large reports covering perhaps 75 field hours in themselves represent a large variety of habitats, and the participants are always urged to spread their census work over many different habitats. Yet this potential source of error makes it necessary to be very careful when comparing different districts and also when comparing different years within one and the same district, for if a large, annually recurring census drops out, this may affect the figure for the whole district.

Further, it is clear that the figures are more reliable for numerous species than for scarce species and for euryoecious than for stenoecious species. There is one more factor to keep in mind, *viz.* the differential

Tab. 21. Approximate percentage composition of woodlands in south and middle Sweden. From Atlas över Sverige (1959).

District	Pine	Spruce	Mixed I	Mixed II	Deciduous
I	12	21	4	23	39
II	23	21	19	29	9
III	21	23	16	29	12
IV	28	20	17	26	9
V	26	24	21	25	4

Mixed I = less than 10 % deciduous trees
Mixed II = 10 to 70 % deciduous trees

gregariousness. If a species is strongly gregarious, the population of a given area tends to become concentrated in a few groups at a few particularly favourable localities, but in a species which tends to occur as solitary individuals or in very small groups only, the birds are more evenly scattered over the suitable habitat (*cf.* LENNERSTEDT & ULFSTRAND 1959: 217). Tits are definitely gregarious but seldom concentrate in very large flocks, and therefore they may be considered favourable for quantitative work, particularly as they are among the most numerous members of the winter fauna. All this, however, applies less to the Longtailed Tit than to the *Parus* species.

As a matter of course great individual differences occur in an assemblage of several hundred workers, as far as field efficiency, training and scrupulousness are concerned. However, these sources of error may be considered rather constant from year to year and from district to district. The gradual increase in number of participants is not likely to have caused a decrease in average competence. The increase has not been caused by accepting less competent coworkers but has been due to a widening of knowledge about the project. The participants of the first year's work did not make up some kind of élite but was a random sample of the contributors of notes to the journal of the Swedish Ornithological Society (*Vår Fågelvärld*). Later this sample became greater, but its properties have not changed in any appreciable way.

This cooperative project, called the Winter Bird Census, has been performed four times. The results from the first occasion, however, are not included, as the work was then of a preliminary

nature and the extent of the field work involved much less than in later winters. It may also be pointed out that the Winter Bird Census will be repeated in years to come and that the methodology of this kind of census work will be discussed in a separate context. In the present connexion some tendencies found in the Great, Blue and Marsh Tits will be set forth, since they seem to offer interesting clues to the problem of the winter ecology of these species and to provide supporting evidence for the findings presented in the preceding chapter. The results yielded by the Winter Bird Census are presented briefly below, but their evaluation is largely deferred to the concluding discussion (Chapter 8).

B. Results

First it may be pointed out that on the basis of quantitative work on breeding populations, SIIVONEN (1948) was able to show that violent fluctuations are the rule rather than exceptions among passerine birds, and KLUIJVER's (1951) magnificent research on the Great Tit amply supports this opinion. Of all species whose population dynamics have been satisfactorily investigated, the Great Tit showed the most rapid fluctuations (LACK 1951: 415). Thus, the finding of large-scale annual fluctuations in population density, both in migratory and in stationary species, is to be expected, and an annual change of *e.g.* 30 to 40 %, perhaps much more, may perfectly well be real and must definitely not be *a priori* explained as due to sampling errors.

The numerical values obtained in the Winter Bird Census are summarized in Tabs. 22 to 24. The relative densities are throughout expressed as number of birds seen per 10 hrs. of field work.

a) Great Tit.

The annual total of Great Tits comprised in the Winter Bird Census has amounted to 9.000 to 14.000 birds.

In District I there was a moderate decrease amounting to approx. 15 % between 1958/59 and 1959/60. This is in agreement with the studies in the Öved area (p. 78 and Fig. 6), although the overall decrease was considerably smaller than that recorded in my own study area. From 1959/60 to 1960/61 there was an increase of approx. 65 % in the density of the Great Tit population. Although too much importance should not be attached to the absolute figure, the tendency is very obvious indeed. The increase was definitely not

Tab. 22. Results of the Winter Bird Census in 1958/59.

District		Hours	Great Tit	Blue Tit	Marsh Tit
I:	Total	167	1.512	296	270
	per 10 hrs.		90,5	17,7	16,2
II:	Total	356	2.369	285	594
	per 10 hrs.		66,5	8,0	16,7
III:	Total	401	2.332	516	425
	per 10 hrs.		58,2	12,9	10,6
IV:	Total	313	1.154	480	315
	per 10 hrs.		36,9	15,3	10,1
V:	Total	303	1.775	224	280
	per 10 hrs.		58,6	7,4	9,2
I to V:	Total	1.540	9.142	1.801	1.884
	per 10 hrs.		59,4	11,7	12,2

Tab. 23. Results of the Winter Bird Census in 1959/60.

District		Hours	Great Tit	Blue Tit	Marsh Tit
I:	Total	142	1.095	215	244
	per 10 hrs.		77,1	15,1	17,2
II:	Total	358	2.472	356	583
	per 10 hrs.		69,1	9,9	16,3
III:	Total	411	2.705	728	538
	per 10 hrs.		65,8	17,7	13,1
IV:	Total	510	2.495	853	531
	per 10 hrs.		48,9	16,7	10,4
V:	Total	239	2.022	225	156
	per 10 hrs.		84,6	9,4	6,5
I to V:	Total	1.660	10.789	2.377	2.052
	per 10 hrs.		65,0	14,3	12,4

caused by the considerable increase in the amount of field work involved, as has been checked in some study areas which were studied in both years. A great increase in the midwinter population was found also in the Öved area. As additional evidence that the increase was not caused by some "artificial factor" (such as changes in the composition of the group of coworkers) may be pointed out that the Marsh Tit showed no similar change, although this species inhabits similar habitats as the Great Tit.

Tab. 24. Results of the Winter Bird Census in 1960/61.

District		Hours	Great Tit	Blue Tit	Marsh Tit
I:	Total	360	4.603	1.691	618
	per 10 hrs.		127,9	47,0	17,2
II:	Total	428	2.180	300	755
	per 10 hrs.		50,9	7,0	17,6
III:	Total	396	2.943	458	550
	per 10 hrs.		74,3	11,6	13,9
IV:	Total	419	1.910	559	302
	per 10 hrs.		45,6	13,3	7,2
V:	Total	332	2.356	472	167
	per 10 hrs.		71,0	14,2	5,0
I to V:	Total	1.935	13.992	3.480	2.392
	per 10 hrs.		72,3	18,0	12,4

The highest relative densities in 1960/61 were recorded from three study areas in the interior of the province of Skåne and one from the coastland in Blekinge. All these studies were performed largely in beech woods or in mixed woods with a prominent proportion of beech. These reports were all of considerable extent, particularly the one from Blekinge.

District II compares favourably with District I with respect to the constancy and the extent of the field work involved (360 to 430 hrs.). The population tendencies follow a completely different pattern from that found in District I. Between the first two winters there was a slight increase (to be rated as *status quo*), whilst between the last two winters there was a considerable decrease, amounting to approx. 25 %.

District III is also favourable with regard to the amount and constancy of the field work involved (approx. 400 hrs.). In this area there were slight increases between the first and the second as well as between the second and the third winters.

District IV has produced sufficiently extensive data, but the annual changes in the group of observers have been relatively large. Between 1958/59 and 1959/60 there was a considerable increase, and between 1959/60 and 1960/61 a very slight change, equal to *status quo*.

District V is very large. Therefore the material obtained is probably much less homogenous than that of the other districts. The extent of the field work is satisfactory, fluctuating between 240 and 330 hrs., but between the first and the second winter there was an unusually heavy "turn-over" of the participants, many giving up the work and many entering the project. In particular, the addition of some areas with very dense population in the second winter seems to have caused an unduly large increase in the average figure. Probably the change in this district was of the same magnitude as in the other districts. There was a moderate decrease between the second and the third winters.

The changes are, thus, very different in the different districts. However, the main line of divergence is between District I, on the one hand, and all other districts on the other. Between the first two winters there was a considerable decrease in District I, as confirmed by my own field work in the Öved and Bökeberg areas, whilst in all other districts there were slight changes or certain increases, in no case any decrease at all. The exceptional increase in District I between the second and the third winters has no counterpart whatsoever in the other districts, in which there were slight and unimportant changes in various directions — except in District II, lying immediately to the north of District I, where there was a considerable decrease.

With regard to the great regional differences in tendency, it is of limited value to compute the overall changes. Combining all districts we find an increase of approx. 10 % between the first and the second as well as between the second and the third winters.

b) Blue Tit.

Annual totals of 1.800 to 3.500 Blue Tits have been counted in the Winter Bird Censuses.

In District I there was a decrease of approx. 15 % between 1958/59 and 1959/60. In 1960/61 a tremendous increase was found, amounting to more than 200 %. This is a quite amazing change, and there is no doubt that the figure reflects a true change in the density of the Blue Tit population wintering in the district, as in the Great Tit. An examination of those reports that contain particularly high figures shows that the underlying field work was most often carried out in beech woods or in mixed woods with beech, just as in the

Great Tit. Some records of considerable gatherings of Blue Tits in the reed beds of eutrophic lakes were also sent in. Many participants spontaneously commented upon the abundance of Blue Tits, and pure flocks of considerable size were frequently recorded, otherwise an uncommon sight except during migratory movements. The increase is very large also in comparison with that found in the Great Tit. Thus, whilst the the Blue Tit density in District I in 1958/59 and in 1959/60 amounted to approx. one fifth of that of the Great Tit, this proportion had in 1960/61 risen to two fifths.

District II shows a certain increase between the first two winters, and an equally large decrease between the second and the third winters. There is thus a great difference between Districts I and II. On the other hand, the regional changes are similar to those found in the Great Tit.

District III and IV are rather similar to District II, whilst District V diverges by showing a certain increase between the first and the second as well as between the second and the third winters. The relatively low density found in the latter district probably reflects the fact that the Blue Tit is a comparatively southerly species in this country (*cf.* ENGSTRÖM 1952: 29). This scarcity of course tends to render the figures less reliable.

On the whole the picture obtained of the changes in the Blue Tit is closely similar to that found in the Great Tit. In both species, District I diverges sharply from the rest of the area. Not only do the changes run in opposite direction, but they seem to be of a different order of magnitude too. The overall tendency in the Blue Tit is one of increase, but between 1959/60 and 1960/61 this was caused solely by the change in District I, the tendency in all the other districts being one of decrease.

c) Marsh Tit.

This species was counted to the extent of 1.900 to 2.400 individuals a year. The most remarkable thing with the Marsh Tit is its extraordinary overall stability. Closer examination, however, shows that considerable changes within the districts have occurred, particularly in the more northerly districts. This may be partly due to the lower figures obtained in these districts, where the Marsh Tit population is beginning to thin out. This species, like the Blue Tit, has a distinctly

southerly distribution in Sweden (Förteckning över Sveriges fåglar 1958). It may be pointed out that the fact of the increases and decreases tending to counterbalance each other should by no means be used as an argument that the changes depend on inter-district movements. Such long-distance movements are entirely unknown in the Marsh Tit, as pointed out in Chapter 7.

In the Marsh Tit, there are no large-scale changes at all in District I. This is of considerable interest, for it strongly supports the idea that the changes found in the Great and Blue Tits are real and not caused by changes in the distribution of the participating ornithologists or similar "unnatural" factors. Such factors would obviously have influenced the figures also of the Marsh Tit, which occurs in similar habitats.

The changes in other districts will not be taken up to discussion in the present context.

7. Autumn movements of tits as recorded in Southern Sweden, particularly at Falsterbo

A. Introductory remarks

As pointed out in the Introduction, the present study of the non-breeding ecology of the tits was initiated in order to try to elucidate the autumn movements of the Great and Blue tits, as recorded at the Swedish bird stations at Falsterbo, southwestern Skåne (55° 23′ N. lat., 12° 50′ E. long.), and also at Ottenby on the island of Öland in the Baltic (56° 12′ N. lat., 16° 24′ E. long.). For approximately fifteen years several hundreds of Swedish ornithologists have cooperated in the study of bird migration at these places, the work being organized by Sveriges Ornitologiska Förening (the Swedish Ornithological Society). This programme of intensive migration research was initiated by RUDEBECK's (1950) studies at Falsterbo in the autumns of 1942 to 1944. In the course of all this work a tremendous amount of information concerning the migratory habits, the time course of migration and many other aspects has been secured. Some obscure points have emerged from the data, and one concerns the migration of the Great and Blue Tits. Several people have remarked upon the similarities between their occurrence and that of certain other species, usually called "irruption species", but nobody has ever suggested what might

be the background of their movements. That is to say that nobody thought it possible that their migratory movements might be correlated with some food factor in a similar way as in the classical "irruption birds", to which *i.a.* the Coal Tit belongs. A correlation between increasing population density and increasing tendency to movements has been conclusively demonstrated by KLUIJVER (1951) and has been called upon by CRAMP *et al.* (1960) to explain some of the recent large-scale movements of the species in question. However, the issue is confused, and the migratory movements have remained enigmatic.

In the present chapter the evidence bearing upon the autumn movements of tits in Southern Sweden will be reviewed. This evidence consists not only of the observational data collected at the bird observatories but also of ringing recoveries, in part from the bird stations but chiefly from the national ringing schemes of Sweden, Norway and Finland. Certain other sources are also available, so that the picture may be fairly fully presented.

B. Critical examination of the information gathered at the Swedish bird stations

As a great deal of our knowledge concerning the autumn movements of tits is derived from the data assembled at the bird stations, it is necessary to discuss the qualities of this material before it may be evaluated. In this connection it is fortunate that the author has had the favour of participating in the work both at Falsterbo and at Ottenby.

The research activities at the observatories are carried out along two main lines. One consists of the observational studies on visible migration. During the chief autumn migration period, one or two observers have been watching the migration, making as accurate counts as possible of all birds seen leaving land and moving out over the sea, together with notes on flight direction, altitude, behaviour etc. At Falsterbo such work was performed in 1942 to 1944 (RUDEBECK 1943, 1950) and from 1949 onwards (with a break in 1951) under the auspices of Skånes Ornitologiska Förening. For the latter period annual reports have been published, but for the study of tit migration it has usually been necessary to examine the field diaries or daily summary sheets prepared on the spot by the observers. At Ottenby observations on the diurnal migration were carried out from 1947 to

1956 (incl.). In this case the review of the material has been restricted to the annual totals, which are published in the annual reports.

The observers usually begin their work before sunrise and continue either until the migration activity for the day has waned or until dusk. The latter has been the case when more than one observer has been available. For tits it does not matter which of the routines is adhered to, for these birds are on the move in the morning hours when general migratory activity is at its peak.

This simple method yields important information concerning many aspects of the migration of diurnally active birds. The chief source of error depends of course on the fact that the observer is able to cover only a small section of the area of migratory activity, although the observations sites have been chosen to permit the observation of the maximal possible part of the bird stream. The fact that only a sample of the stream of migration birds is surveyed does not in itself interfere with the results, but the difficulty is that the geographical location of the chief passage is subject to considerable daily fluctuations, correlated with wind and possibly other environmental conditions (*cf.* RUDEBECK 1950, ULFSTRAND 1960). This may cause an underestimation of the passage of a given species, if its migratory peak days (pp. 103—106) happen to fall on days with unfavourable winds from the observers' point of view. The only method to account for this uncertainty is to check with the ringing figures for the same species and to keep an eye on the wind conditions. For the tits, the effect of wind conditions is reduced by the fact that these birds tend to move on very calm days (own observations) but augmented by the circumstance that their migration flight is usually condensed to a few days in the whole autumn. Also the tits usually occur in an "all or none" annual rhythm at the bird stations, *i.e.* either they are numerous or they are practically absent. Such fluctuations are of course not liable to become completely obscured by wind conditions.

The second chief type of activities at the Swedish bird observatories is the trapping and ringing of resting birds. It would carry to far to describe all the methods adopted for this purpose. It may be mentioned that at Ottenby ringing has been performed in full scale from 1948 and onwards, whilst at Falsterbo this activity was not fully developed until 1952.

The potential errors inherent in the ringing figures are on the whole of a different nature from those of the observation material.

Local deviations of the passage due to wind conditions will hardly cause any serious errors in the ringing material, for the birds are likely to get trapped when resting irrespective of meteorological conditions. Large scale deviations may cause aberrations in the ringing figures, but tits are strongly influenced by guiding lines (p. 107) and will hardly be deviated over larger distances. The passage of a tit population through for example the Falsterbo peninsula usually has a duration of many weeks, which reduces the impact of temporary weather conditions still more. Therefore, if the movement is of considerable extent the tits are extremely likely to get caught in certain numbers and thus the movement will become reflected in the ringing figures. Hence the conclusion seems justified that on the whole the ringing figures are a more reliable guide to the annual changes in migration activity of tits than the observation totals.

On the other hand, there are certain disadvantages inherent in the ringing figures. The chief source of error depends on the circumstance that the experience and energy of the ringers exert a considerable influence on the results and further that certain changes in trapping equipment have been undertaken, aiming at better efficiency. These difficulties, fortunately, may be largely overcome thanks to the detailed notes entered in the ringing diaries concerning areas worked, equipment used and people participating.

As a whole it may be said that both the study techniques discussed above have their advantages and their disadvantages but that they, taken together, provide an adequate picture of the annual fluctuations of the tit migration and also of the migration periods etc. The following generalisations seem to be justified:

1) If the ringing and observation totals are both high for a given species, this is strong evidence for a large-scale movement over the area in question.

2) If the ringing total is high but the observation total low, this also indicates a considerable movement, for meteorological conditions may have reduced the observation figures.

3) If the observation total is high but the ringing figure low, careful scrutiny of the material is necessary. There may be some factor causing the ringing figure to fall unduly, such as too few ringers, damages to traps etc. If no such factors are found, the situation indicates a small-sized movement or at least a wave of birds hurrying past the area with extraordinary speed.

4) If both ringing and observation totals are low, this is good evidence that no important movement was in process in the year in question.

C. Migratory movements recorded at Falsterbo bird station

I. *General occurrence of the different species*

The annual totals of migrating and ringed tits at Falsterbo are presented in Tabs. 25 and 26, respectively. The period of observation is not exactly the same in the different years, but on the other hand the most important months, September and October, are usually fully covered (except in 1942, 1949 and 1960). The migration in November is kept apart, for this month was studied only in some years. As far as the evidence goes, little tit migration occurs in November.

An important fact borne out by the tables of the tit migration at Falsterbo is the almost complete absence of the Marsh, Willow and Crested Tits. The last-mentioned species used to breed, or at least occur regularly, in some pine plantations on the Falsterbo peninsula, but has only in rare exceptions been seen to undertake any wanderings outside of these plantations. In later years it has been less regularly recorded in these plantations and may have disappeared as a breeding bird. The other two species do not breed in the immediate vicinity of Falsterbo; it is not known exactly how close to the peninsula the nearest breeding localities of the Marsh Tit are, but the distance most probably does not exceed 30 km. The Willow Tit, as pointed out previously, is absent as a breeding bird in a large area in south and west Skåne. The only records that have come to my knowledge of Marsh Tits at Falsterbo are an observation of my own of three birds on 5 November 1947, a flock of about 10 birds in the light-house garden on 21 September 1953 (M. MARKGREN 1955) and one bird making abortive migration attempts on 17 September 1961 after the period with which we are primarily concerned (own observation). There may be a few additional records hidden in the diaries. The Willow Tit is still rarer, and I have never seen it myself in the area in spite of a couple of hundred days spent there in the course of the last fifteen years. As shown in Tab. 26, however, one bird was ringed in 1957 and two in 1959.

The Longtailed Tit in some years occurs in considerable numbers but is completely absent in other years. There is evidence for con-

Tab. 25. Annual totals of tits recorded on visible migration at Falsterbo bird station.

Year	Period	Great Tit	Blue Tit	Coal Tit	Marsh Tit	Willow Tit	Crested Tit	Longtailed Tit	*Parus sp.*
1942	13.8.–22.10.	–	–	–	–	–	–	–	–
1943	1.8.–31.10.	416	–	–	–	–	–	–	–
1944	1.8.–31.10.	52	–	–	–	–	–	–	–
	1.11.–12.11.	–	–	–	–	–	–	–	–
1949	1.8.–17.10.	402	1.113	66	–	–	–	11	440
1950	1.8.–29.10.	288	98	–	–	–	–	–	101
1952	1.8.–31.10.	2	455	27	–	–	–	–	320
1953	1.8.–31.10.	19	154	18.439	–	–	–	–	–
1954	1.8.–31.10.	4	9	2	–	–	–	–	–
1955	1.8.–31.10.	143	699	–	–	–	–	–	–
	1.11.–30.11.	–	–	–	–	–	–	–	–
1956	1.8.–31.10.	1.453	102	1.972	–	–	–	89	–
	1.11.–26.11.	–	–	–	–	–	–	33	–
1957	1.8.–31.10.	890	5.612	452	–	–	–	177	–
	1.11.–30.11.	40	51	–	–	–	–	8	–
1958	1.8.–31.10.	4	7	–	–	–	–	–	–
	1.11.–30.11.	–	–	–	–	–	–	–	–
1959	1.8.–31.10.	7.535	3.573	7	2	–	1	10	64
	1.11.–15.11.	–	–	–	–	–	–	–	–
1960	1.8.–17.10.	10	7	–	–	–	–	–	–

Sources of information: for 1942 to 1944 RUDEBECK (1950), and for later years unpublished data in the archives of Skånes Ornitologiska Förening as well as published annual reports of the Falsterbo bird station (Vår Fågelvärld, *seriatim*). For 1961, see pp. 130–131.

siderable movements in 1956, 1957 and 1959. The situation in 1949 is uncertain, for the low numbers of migrating birds were inconclusive and not supported by ringing activities. My own field diaries indicate that there was also a considerable movement in October to November 1948. The Longtailed Tits are usually late, and a proportion of the birds may pass as late as in November and may therefore have been overlooked. However, that any large numbers are overlooked for that reason is contradicted by the negative findings in the years when the observation activity was continued throughout November. More detailed information concerning the Longtailed Tit movement in 1959 will be presented in another connexion (ULFSTRAND in preparation). The species does not breed locally.

Tab. 26. Annual totals of tits trapped and ringed at Falsterbo bird station.

Year	Period	Great Tit	Blue Tit	Coal Tit	Marsh Tit	Willow Tit	Crested Tit	Longtailed Tit
1952	1.8.–31.10.	35	37	3	–	–	–	3
1953	27.8.–6.10.	10	5	177	–	–	–	–
1954	1.8.–11.10.	15	6	1	–	–	–	–
1955	1.8.–31.10.	54	90	–	–	–	–	–
	1.11.–30.11.	–	1	–	–	–	–	–
1956	1.8.–31.10.	53	21	24	–	–	–	21
1957	1.8.–31.10.	101	524	21	–	1	–	40
	1.11.–30.11.	82	26	–	–	–	–	19
1958	1.8.–31.10.	21	13	–	–	–	–	–
1959	1.8.–31.10.	93	102	2	1	2	–	85
	1.11.–15.11.	3	2	–	–	–	–	–
1960	1.8.–31.10.	63	7	2	–	–	–	–

Sources of information: for 1952 to 1953 ENEMAR (1955), for later years the ringing diaries of Falsterbo bird station deposited in the archives of Skånes Ornitologiska Förening. The Great Tit figures for November 1957 and for 1960 were augmented due to special efforts of the ringers. See p. 97.

The Coal Tit is similar to the Longtailed Tit in its extremely irregular occurrence. In many years it has been completely absent, *viz.* in 1942 to 1944, 1950, 1955 and 1958 and almost so in 1952, 1954, 1959 and 1960. In 1949 the position is unclear. In 1953, 1956 and 1957 large quantities of Coal Tits were on the move. Particularly the first-mentioned of these three years was quite outstanding. Both the ringing and observation figures exceed many times the added totals of all other years.

The position of the Great and Blue Tits is more complicated, and these birds will be subjected to a more detailed consideration. The Great Tit has been observed on migration in all years except in 1942 and the Blue Tit in all years except 1942 to 1944. The numbers have, however, shown extremely large fluctuations.

The observation figures of the Great Tit show that l a r g e s c a l e m o v e m e n t s w e r e p e r f o r m e d i n 1 9 5 6, 1 9 5 7 a n d 1 9 5 9. Particularly the last-mentioned year showed an extremely high figure. Moderately high totals were also recorded in 1943, 1949

and 1955. In the other years only some flocks or single birds were recorded. See also pp. 130—131.

The ringing figures agree very well with the observation results. The highest totals were obtained in 1957 and 1959. In 1955 and 1956 the situation is less obvious. The comparatively high observation figure in 1956 was not correlated with an equally high figure of ringed birds. Moreover, most of the birds were in this year trapped in the first half of September, *i.e.* before true migratory movements have usually started. Presumably, therefore, these birds belonged to the local breeding population, and hence the relatively high annual total does not prove any large-scale movement. The ringing figure in 1955, for example, is equally high as 1956 and much higher than in the preceding years. There was a peak in early October, as was to be expected if migratory movements are involved. For the evaluation of the ringing figures it should be kept in mind that the Great Tit is a numerous breeding bird in the area surrounding the observation and ringing places. Thus a certain proportion of the ringed birds are derived from the locally breeding stock. With regard to the discussion presented above (p. 92) it seems justified to conclude that the lacking correspondence may indicate that the extent of the movement was underestimated in 1955 whilst in 1956 the movement was probably not so important as indicated at a first glance on the observation figures. Further evidence bearing on this question will be presented in later connections.

The Blue Tit, like the Great Tit, occurs in strongly fluctuating numbers at Falsterbo. Judging from the observation figures the movements of 1949, 1957 and 1959 were of particularly large extent, whilst moderately high numbers were also recorded in 1952 and 1955. The ringing figures agree very well with these findings but point to the fact that the 1955 movement was probably of relatively larger extent than indicated by the observation figures. The same was found for the Great Tit, and the fact that both species showed observation figures below "expectation" may indicate that unfavourable wind conditions caused a deviation of the passage on the critical days.

From the available data it is possible to make some interspecific comparisons. It then appears that the Great Tit and the Blue Tit have usually occurred in large numbers in the same years, although

there are certain discrepancies. In 1957 and 1959 both attained peak totals; probably the same applies to 1955. On the other hand there was a certain movement of Great Tits in 1956, without counterpart in the Blue Tit, whilst the reverse was the case in 1952. From earlier years, when the observation figures are not possible to verify by ringing results, there are indications of simultaneous movement of both species in 1949 and of the Great Tit only in 1943 and 1950 (probably not of very large extent). The relation between the numbers of Great and Blue Tit is very variable. Thus the 1957 movement was dominated by Blue Tits and the 1959 movement by Great Tits. The agreement, thus, is not complete, but there is an undeniable tendency to synchronized large-scale movements in these two species. This feature became more prominent in the late 1950's, when the years of 1957 and 1959 were marked by unparalleled movements in both of them.

The Coal Tit reached a peak in 1953 when no other tit species occurred in appreciable quantities. There were smaller peaks in 1956 and 1957. In the latter year it coincided with large-scale movements in the Great and Blue Tits, but in the former year the other tit species exhibited only weak migratory tendencies. Thus it seems to be justified to conclude that the Coal Tit moves completely independently of the other species.

The position of the Longtailed Tit is yet uncertain. It has in fact occurred chiefly in years when the Great Tit and the Blue Tit have also been on the move. But this first impression needs to be modified for certain reasons. In the first place, we know that the origin of the Longtailed Tit movement in 1959 was quite different from that of the Great and Blue Tits (p. 117). In the second place, the Great Tit movement in 1956 probably was over-represented in the observation figures, and that year probably should be counted with the non-movement years for this species. I feel very reluctant to maintain, on the basis of available data, that the movements of the Longtailed Tit are in fact synchronous with those of the Great and Blue Tits.

In the table of the ringing figures from Falsterbo (Tab. 26) there are a few data that call for comment. The disproportionately high figures in November 1957 were caused by the fact that the ringers moved part of the trapping equipment into the gardens of the small towns of Falsterbo and Skanör and succeeded in trapping a large

proportion of the resident birds which had settled down for the winter. We are not permitted to conclude that there was any movement going on in that month. In 1960 the local stock of Great Tits almost certainly was not augmented by any influx from outside the area. Yet a fairly high figure was obtained, chiefly due to successful trapping in October, when as in 1957 a number of traps were moved into the gardens of the small communities. Mr. J. BANSTORP (*in litt.*) who was in charge of the ringing activities in the period in question confirms that according to his opinion no appreciable movements of tits were going on.

To conclude this section the following summarizing remarks may be presented:

1) The Great Tit, which is a numerous breeding bird in the area, is almost every year recorded on migrational flight. In some years the local stock is increased by large quantities of birds arriving from elsewhere. These large-scale movements are generally synchronized with those of the following species, although certain discrepancies occur.

2) The Blue Tit, which also belongs to the locally breeding fauna, occupies a nearly identical position as the preceding species, and its movements are, as mentioned above, largely synchronized with those of that species.

3) The Coal Tit is completely absent in some years but occurs in fluctuating numbers in other years. The intervals are irregular, and the movements are not synchronized with those of any other tit. The species probably does not breed regularly on the Falsterbo peninsula.

4) The Marsh Tit is absent as a breeding bird on the Falsterbo peninsula but occurs abundantly only approx. 30 km farther to the northeast. It is almost completely absent at Falsterbo, where only very few observations have been made.

5) The Willow Tit almost never comes as far as to Falsterbo from its nearest breeding places, which are situated approx. 60 km from the area. (It is not until still further away that the species begins to become numerous.)

6) The Crested Tit may breed locally, at least in some years. Nevertheless it is almost never recorded on actual migration flight

and has never been trapped. It very seldom leaves the pine areas. The distances to the nearest breeding places and to the area where the species begins to become numerous are approximately the same as in the preceding species.

7) The Longtailed Tit does not breed locally. It occurs very irregularly on passage migration at Falsterbo, and the movements tend to be late and of short duration. The tendency to simultaneousness between the movements of the Longtailed Tit and those of the Great and Blue Tits cannot be considered to be proven.

II. *Migration periods*

In the present paragraph the evidence concerning the migration periods of the Great, Blue and Coal Tits will be presented, together with some notes on the Longtailed Tit.

As is apparent from Tab. 27, the migration of the Great Tit is concentrated to the time space from the last third of September (earlier records are exceptional) to the end of October. This is confirmed by the ringing figures (Tab. 28). Omitting the years when only a few birds were counted, we find that the peak in the visible migration has fallen in the first third of October in three years (1950,

Tab. 27. Time course of the passage of the Great Tit at Falsterbo bird station.

Year	September			October			Total
Decade	I	II	III	I	II	III	
1949	—	—	194	51	157[1])	·	402
1950	—	—	—	242	30	16[2])	288
1952	—	—	—	2	—	—	2
1953	—	—	—	13	1	5	19
1954	—	4	—	—	—	—	4
1955	—	—	—	114	7	22	143
1956	—	—	—	56	25	1.372	1.453
1957	—	—	6	39	824	21	890
1958	—	—	2	2	—	—	4
1959	—	—	248	6.712	263	312	7.535

[1]) up to and including 17.10.
[2]) up to and including 29.10.

Tab. 28. Time distribution of Great Tits ringed at Falsterbo bird station.

Year	August			September			October			Total
Decade	I	II	III	I	II	III	I	II	III	
1954	2	2	2	1	—	—	6	2	—	15
1955	8	1	11	2	3	5	18	3	3	54
1956	6	1	8	14	12	3	1	5	3	53
1957	2	11	4	2	1	7	10	31	33	101
1958	2	4	3	—	—	—	4	1	7	21
1959	2	1	6	3	13	3	21	31	13	93
1960	—	—	—	2	—	1	6	—	54	63
Total:	22	20	34	24	29	19	66	73	113	400

Note: The high number of Great Tits trapped in October/III 1960 was caused by special efforts by the ringers.

1955 and 1959), in the second third once (1957) and in the last third once (1956). The situation in 1949 is unclear due to the early termination of the observation activities. The low figure in the first third of October in this year might have been caused by a period of unfavourable weather. Other explanations may also be relevant for such a period of low migration in the middle of the season. The difference in the time course of the 1955 and 1957 movements is also reflected in the ringing figures, whilst the ringing peak in 1959 fell somewhat later than that of the visible migration. As pointed out above (p. 96) the 1956 movement is not reflected at all in the ringing figures. The fact that the ringing total of this year was fairly high was chiefly caused by successful trapping in early September. The high ringing figure of October 1960 was, as explained above, caused by special efforts on the part of the ringers.

The Blue Tit is on the whole slightly earlier than the Great Tit (Tabs. 29 and 30). Disregarding those years when less than 100 birds were counted, we find that the peak fell in the last third of September once (1952), in the first third of October twice (1955, 1959), in the second third of October once (1957) and in the last third of October once (1953, a fairly low figure, to which not too much importance should be attached). The position in 1949 is uncertain, due to the early termination of the studies. The ringing results largely confirm the findings yielded by the observation activities. They

Tab. 29. Time course of the passage of the Blue Tit at Falsterbo bird station.

Year	September			October			Total
Decade	I	II	III	I	II	III	
1949	—	—	15	238	860[1])	·	1.113
1950	—	—	—	86	10	2[2])	98
1952	—	20	255	180	—	—	455
1953	—	—	—	1	32	121	154
1954	—	7	—	2	—	—	9
1955	—	—	3	558	51	87	699
1956	—	6	—	4	90	2	102
1957	—	—	168	687	3.093	1.664	5.612
1958	—	—	—	—	—	7	7
1959	—	5	717	2.364	312	175	3.573

[1]) = up to and including 17.10.
[2]) = up to and including 29.10.

Tab. 30. Time distribution of Blue Tits ringed at Falsterbo bird station.

Year	August			September			October			Total
Decade	I	II	III	I	II	III	I	II	III	
1954	—	1	—	1	—	1	—	—	3	6
1955	4	1	—	3	2	1	62	13	4	90
1956	—	—	3	1	3	4	8	2	—	21
1957	1	2	—	—	3	64	45	208	201	524
1958	—	—	—	—	—	—	1	3	9	13
1959	—	—	—	5	15	6	41	28	7	102
1960	—	—	1	—	—	1	1	—	4	7
Total:	5	4	4	10	23	77	158	254	228	763

point to the 1957 movement as being rather later than the other large movements. The material presented in Tabs. 25 to 26 demonstrates that little movement is going on in November. The same applies to the Great Tit.

As far as the Coal Tit is concerned the material is much less complete for ringing of this species has been on the whole unsuccessful in most years. The observation figures are presented in Tab. 31. They show that in each of the three years with appreciable Coal Tit movement, the peak period was different, falling as early as in

Tab. 31. Time course of the passage of the Coal Tit at Falsterbo bird station.

Year	August			September			October			Total
Decade	I	II	III	I	II	III	I	II	III	
1949	—	—	—	35	28	3	—	—[1]	·	66
1950	—	—	—	—	—	—	—	—	—[2]	—
1952	—	—	—	—	6	21	—	—	—	27
1953	—	—	—	—	15	15.624	2.195	594	—	18.439
1954	—	—	—	—	2	—	—	—	—	2
1955	—	—	—	—	—	—	—	—	—	—
1956	—	—	—	8	—	—	1.217	311	436	1.972
1957	—	—	20	254	21	147	4	6	—	452
1958	—	—	—	—	—	—	—	—	—	—
1959	—	—	—	—	—	5	2	—	—	7

[1]) = up to and including 17.10.
[2]) = up to and including 29.10.

the first third of September in 1957 and as late as the first third of October in 1956. This species is the only tit to have been recorded on migration flight in August. In 1956 there was still a considerable movement in the last third of October.

About the Longtailed Tit we have still less data. It may only be pointed out again that it is later than any of the three preceding species and that it usually passes through the area very rapidly. However, it seems certain that only a small fraction of the movements usually fall after the end of October.

Thus, the Great, Blue and Coal Tits all have variable migration periods. For the first-mentioned two species, however, this property is not more pronounced than in many other species (*cf.* cases described by LENNERSTEDT 1958: 321 *et seq.* and ULFSTRAND 1959 a: 155 *et seq.*). In the Coal Tit the variability seems to be exceptionally pronounced, as far as present evidence goes. The reasons for interspecific differences in degree of variability of the migration periods are largely unknown. Sometimes there is reason to believe that a delay is "artificial", *i.e.* caused by deviation of the migration beyond the viewing range of the observation site during the initial phases. When the environmental conditions change and the stream of migrating birds becomes relocated to over the observation site, the figures falsely indicate a delay. This does not seem to apply to tits, and

particularly not to the Coal Tit, the variations of which are much too great. It is often assumed that annual variations in the timing of various proximate releasing factors are responsible for the changes in migration period (*e.g.* NISBET 1957: 23 *et seq.*; *cf.* LENNERSTEDT *op. cit.*). Another possibility is that different populations are involved. As an average the Coal Tit is the earliest species on the move, followed by the Blue Tit and somewhat later again by the Great Tit. As far as the evidence goes, the Longtailed Tit seems to be the last of all.

III. *Concentration of visible migration to peak days*

It may be of interest to examine whether the observations of tits on visible migration are concentrated to a few single days or whether they are spread over a great many days. The data relating to this question in the Great, Blue and Coal Tits have been condensed in Tabs. 32 to 34.

Of all Great Tits counted on migration in a given season 37 to 94 % have come on the one best day. The average concentration to the best day amounts to 60 %. Combining the daily figures for the two best days, the corresponding percentage rises to 78 % and for the three best days to 87,5 %.

Tab. 32. Degree of concentration of the visible migration of the Great Tit to one, two and three best days of season at Falsterbo bird station.

Year	Highest daily figure	Two highest daily figures	Three highest daily figures	Annual total
1949	169 42,1 %	299 74,4 %	347 86,3 %	402
1950	126 43,7 %	192 66,7 %	222 77,2 %	288
1955	96 67,1 %	118 82,6 %	135 94,4 %	143
1956	1.370 94,2 %	1.399 96,2 %	1.422 97,8 %	1.453
1957	327 36,9 %	568 63,7 %	723 81,2 %	890
1959	5.826 77,4 %	6.369 84,5 %	6.636 88,1 %	7.535
Average:	60,2 %	78,0 %	87,5 %	

Tab. 33. Degree of concentration of the visible migration of the Blue Tit to one, two and three best days of season at Falsterbo bird station.

Year	Highest daily figure	Two highest daily figures	Three highest daily figures	Annual total
1949	530 47,6 %	685 61,5 %	830 74,5 %	1.113
1952	170 37,4 %	328 72,1 %	424 93,2 %	455
1953	115 74,6 %	128 83,2 %	138 89,6 %	154
1955	253 36,2 %	483 69,2 %	570 81,6 %	699
1957	1.327 23,5 %	2.496 44,4 %	3.516 62,4 %	5.612
1959	1.333 36,3 %	1.819 51,0 %	2.138 60,0 %	3.573
Average:	42,6 %	63,6 %	76,9 %	

Tab. 34. Degree of concentration of the visible migration of the Coal Tit to one, two and three best days of season at Falsterbo bird station.

Year	Highest daily figure	Two highest daily figures	Three highest daily figures	Annual total
1953	8.041 43,6 %	10.388 56,5 %	12.377 67,4 %	18.439
1956	467 23,7 %	877 44,5 %	1.233 62,5 %	1.972
1957	147 32,6 %	247 54,6 %	321 71,0 %	452
Average:	33,3 %	51,9 %	67,0 %	

In the Blue Tit the degree of concentration is less extreme, amounting to 43 % for the best day, 64 % for the best two days and 77 % for the three best days. Only three seasons have provided sufficient data for the Coal Tit. Judging from this less extensive material, however, the degree of concentration to peak days is still less pronounced in this species, being 33 % for the best day, 52 % for the two best days, and 67 % for the three best days.

Tab. 35. Degree of concentration of the visible migration of selected passerine species to one, two and three best days of season at Falsterbo bird station expressed as percentage of annual total. Figures are based on the period 1.8. to 31.10. (except 1950, when to 29.10.) and are averages for the years 1950 to 1956, inclusively (no material available for 1951).

Species	Highest daily figure	Two highest daily figures	Three highest daily figures	Annual total
Alauda arvensis	25,7	40,8	52,1	830
Lullula arborea	30,7	50,7	61,3	8.950
Hirundo rustica	21,5	34,3	43,1	25.400
Corvus monedula	25,5	44,0	57,2	22.200
Turdus iliacus	82,0	92,1	94,9	1.550
Anthus trivialis	29,9	48,5	60,8	27.800
Anthus pratensis	27,6	44,3	57,2	12.200
Motacilla alba	29,7	43,8	52,8	1.800
Motacilla flava	17,4	27,5	35,9	22.900
Carduelis spinus	25,8	41,1	51,9	12.800
Carduelis cannabina ..	24,3	41,2	53,5	49.300
Fringilla spp.	36,5	55,2	65,5	444.000
Emberiza citrinella	37,2	52,1	63,6	2.330
Emberiza schoeniclus ..	33,3	47,8	57,0	185

To put these figures in relief, Tab. 35 has been prepared, giving corresponding data for a number of passerine species other than tits. Even the Coal Tit is comparatively strictly concentrated to a few peak days, although there are a few species in Tab. 35 showing about the same high degree of concentration. The Blue and Great Tits show much stronger concentration to peak days than is common among passerines. In Tab. 35, however there is one species showing a much stronger concentration than even the Great Tit, *viz.* the Redwing (*Turdus iliacus*). This species is known to be chiefly a nocturnally migrating bird.

The conclusion to be drawn from these data is that the tits are exceptionally particular regarding the choice of days for migration (*cf.* RUDEBECK 1950: 53, 74). This applies particularly to the Great Tit, less so to the Blue Tit and still less to the Coal Tit, although also this species shows a higher concentration to peak days than most passerine birds. This was found already in a preliminary survey by the present author (ULFSTRAND 1957: 199—200).

Finally it may be pointed out that once again the Great Tit movement of 1956 stands out in comparison with all other years. In 1956 almost the whole annual total was accounted for by a single day's passage (26 October). If this year is excluded, the average concentration to best day of the season in the Great Tit falls to 53,5 %. This figure, however, is still high enough to point to the Great Tit as an unusually particular bird in its choice of migration days.

IV. *Tit migration in process*

The following notes on the behaviour of migrating tits and similar questions are based on the author's own observations, chiefly at Falsterbo. The behaviour of the Great, Blue and Coal Tits is so closely similar that the following description is valid for all three species, when there is no statement to the opposite effect.

The diurnal migration of tits may proceed in two rather different ways. First, they may move along through trees and bushes, keeping to a fairly defined direction although often being led astray from it temporarily by some micro-guidingline or "leading point" (GEYR VON SCHWEPPENBURG 1949, MALMBERG 1955: 161), *i.e.* some topographic feature attractive to the birds. They demonstrate a strong reluctance to move out over open areas, following tree and bush covered areas as long as possible. When reaching a corner of a grove, from which they have to depart over open ground, if they shall not have to abandon the direction completely, they gather in the tree tops of the outermost trees, often showing extreme agitation. They call excitedly, and brief song fragments are frequently heard. Sometimes some birds start singing their full song. The general excitation is also expressed by hot pursuits and frequent threat displays. Finally the birds depart, one by one or at most a few together, so that the flock becomes extended. Usually the birds make for the nearest visible tree clump or shrubbery, provided this goal does not carry them too much out of direction.

When moving from tree to tree in a grove or forest, they may feed on their way, although the feeding is rather casual, sometimes giving an impression of "nervousness". The individuals keep relatively close together, although no two birds stay in intimate proximity for any considerable period. There is a clear distinction between such tit

flocks and those that merely roam through the woods on foraging trips in winter.

Even a gap of less than 100 metres may give rise to much confusion and hesitation in a tit flock. After having departed from the trees, they often turn back, fly in circles, rise and fall and sometimes return to the trees from which they started. As mentioned above, they make for the nearest possible clump of trees, but they do not necessarily perch into each such area. It is merely as if they wanted to be close to some shelter, to use an anthropomorphic expression.

There is no sharp borderline between this kind of migratory proceeding and the second type, the true migratory flight. In this case the birds gather some height, usually after long hesitation, and fly off, much less dependent on minor topographical features than when moving as described above. The flight is rather rapid, calling is infrequent after the birds have really got under way and the flock is more compact, not so extended in the flight direction as when the birds have just started flying over a short open space. Only on rare occasions have I seen tits fly at such a height that it was not easy to determine them (ULFSTRAND 1959 b: 46—47).

The hesitation shown when approaching an open area is of course much increased when encountering the open sea at Falsterbo. It is common that a small Coal Tit flock will make repeated attempts for a whole day to depart from the light-house garden, which is the southwesternmost clump of trees in Scandinavia, but in vain. Presumably some flocks repeat their attempts for many days on end. The factor causing the abrupt return is sometimes the sudden appearance of a Sparrow Hawk (*Accipiter nisus*) or other bird of prey. The behaviour of tits on such occasions gives an extremely helpless and ineffective impression.

The extreme reluctance of tits to move over open areas may lead to considerable concentrations in wooded areas narrowing off towards the southwest. In one case I have seen up to 200 birds concentrated within a small area comprised of a few pines. As tits freely mix interspecifically, such concentrations are often composed of more than one species. It may be mentioned that Longtailed Tits almost always travel in pure flocks. Coal Tits may join flocks of Great and Blue Tits, but usually such combinations are soon disrupted. At the encounter of some topographical obstacle, such as an extensive open field, one species or the other is more reluctant to leave and then

the flock is split in fragments, often resulting in two more or less pure flocks.

This description has been made rather detailed, since little information concerning the behaviour of migrating tits is available. GAUSS (1959) published an account of the habits of migrating Coal Tits in the Alps, and his descriptions contain many similarities to the pattern outlined above. Finally, it may be mentioned that the great hesitation shown by tits at the encounter of the open sea is nothing qualitatively characteristic of these birds, but is on the contrary shared with many other species, belonging to all orders. However, it is more conspicuous in tits than in almost any other passerine birds that the author has had the opportunity to study. This adherence to tree-covered areas makes tits extremely dependent on guiding-lines.

D. The autumn migration of tits at Ottenby bird station

The annual fluctuations of the tit migration at Ottenby are apparent from Tabs. 36 and 37. At a first glance on Tab. 36 one is struck by the fact that at Ottenby as at Falsterbo, the Marsh, Willow and Crested Tits are absent from the observation data, *i.e.* they have never been recorded on migration flight at Ottenby bird station in spite of 10 years' daily observations. The Crested Tit has never been ringed there, whilst two Marsh Tits and one Willow Tit had been trapped. These facts confirm that these species rarely if ever undertake long-distance movements (p. 98).

The large-scale movement of the Coal Tit in 1953, apparent in the material from Falsterbo, was also strongly reflected in the Ottenby data. In 1956 and 1957 there were smaller peaks at Falsterbo and of these the former was reflected at Ottenby but not the latter. Of the Longtailed Tit movements recorded at Falsterbo those of 1956 and 1957 were also conspicuous at Ottenby but not that of 1959 (*cf.* p. 117). On the other hand, there was a movement at Ottenby in 1954, which is not apparent at Falsterbo. The Great and Blue Tits occur annually, or almost so, on migration at Ottenby, as at Falsterbo. The figures of the former species are rather even, and clear evidence for movements is somewhat difficult to extract. The ringing figures indicate some movement in 1948, 1949 and possibly in 1956, 1957 and 1959. It may be concluded that the numbers passing through the area in the latter three years were higher than in 1958 and 1960, for example, although there can be no question about mass movements.

Tab. 36. Annual totals of tits counted on visible migration at Ottenby bird station.

Year	Period	Great Tit	Blue Tit	Coal Tit	Marsh Tit	Willow Tit	Crested Tit	Longtailed Tit
1947	15.6.–14.11.	–	–	–	–	–	–	–
1948	2.6.–30.10.	149	127	8	–	–	–	20
1949	1.6.–31.10.	294	791	–	–	–	–	–
1950	29.5.–31.10.	55	62	–	–	–	–	7
1951	1.6.–31.10.	13	32	–	–	–	–	–
1952	1.6.–31.10.	17	520	2	–	–	–	6
1953	1.6.–31.10.	3	22	290	–	–	–	–
1954	1.6.–31.10.	23	82	–	–	–	–	17
1955	1.6.–29.10.	24	270	–	–	–	–	–
1956	1.6.–31.10.	5	–	–	–	–	–	–

Sources of information: the annual reports of Ottenby bird station, published *seriatim* in Vår Fågelvärld.

Tab. 37. Annual totals of tits trapped and ringed at Ottenby bird station.

Year	Period	Great Tit	Blue Tit	Coal Tit	Marsh Tit	Willow Tit	Crested Tit	Longtailed Tit
1948	1.8.–30.10.	107	51	5	–	–	–	10
1949	1.6.–31.10.	98	200	11	1	1	–	8
1950	1.5.–31.10.	20	24	–	–	–	–	7
1951	1.8.–31.10.	9	7	–	–	–	–	–
1952	1.8.–31.10.	33	103	6	–	–	–	–
1953	1.8.–31.10.	14	28	313	–	–	–	–
1954	1.8.–31.10.	20	26	–	–	–	–	57
1955	1.8.–29.10.	27	47	–	–	–	–	–
1956	1.8.–31.10.	57	26	19	–	–	–	113
1957	1.8.–2.11.	61	67	1	1	–	–	182
1958	1.8.–2.11.	13	7	2	–	–	–	–
1959	1.8.–31.10.	59	115	3	–	–	–	–
1960	1.8.–31.10.	28	12	.	.	.	.	.

Sources of information: From 1948 to 1950, annual reports of Ottenby bird station (Vår Fågelvärld, *seriatim*); for later years ringing diaries of Ottenby bird station, from which data were extracted by Miss Anna Tolstoy.

It may be suggested that at least in these three years, and perhaps also in 1948 and 1949, the birds recorded at Ottenby were chiefly made up by the population of the island of Öland. At least the data collected at Ottenby does not allow the conclusion that the birds have arrived from far away. The correspondence between the movements at Ottenby and Falsterbo is moderately good.

For the Blue Tit there is evidence for movements at Ottenby in 1949, 1952, and 1959, with smaller figures for 1948, 1955 and 1957. Except in 1949, the migration can hardly be classified as a mass movement, and it may be suggested again that the recruiting area was of rather restricted extent. The correspondence between Ottenby and Falsterbo is fairly complete.

E. Nocturnal migration in tits

Many passerine birds perform their migratory flight in the day as well as in the night. Yet another large category only exceptionally moves by day-time but almost exclusively in the night. The number of passerine species being completely restricted to diurnal migration is, on the other hand, relatively low. There are conditions under which normally nocturnal migrants may suddenly and for a brief period change their rhythm and migrate in the day. Some such situations have been discussed by M. MARKGREN (1955) and LENNERSTEDT (1958: 308—321).

For the study of nocturnal migration one is largely reduced to employing indirect methods. Telescope studies of translunar passage and particularly radar observations offer important new devices for this study but have the common disadvantage that the birds observed cannot be determined specifically. Therefore, for many problems one has to study the resting birds and from their occurrence deduce on their nocturnal movements, or study the birds killed at light-houses and light-ships. Only in the latter case it is possible to prove that the birds have in fact been undertaking migrational flight in the night.

A rich source of knowledge concerning the nocturnal migration of North European birds are the reports of birds killed at Danish lights, compiled by HANSEN (1954) for the period 1887 to 1939, inclusively. In Sweden there have been attempts to utilize the same source of information, and some results were published by OTTERLIND & WINGSTRAND (1945) and ENEMAR (1951, 1957 b).

HANSEN (*op. cit.*: 294) reports a total of 38 Great Tits killed at the lights in Denmark. They were derived from 35 different nights. One was killed in the last third of January, two in the last third of March, whilst the remainder was killed in the autumn months. The peak very markedly falls in the middle and last thirds of October. The earliest autumn casualities are from the last third of September, the latest from middle November. The agreement with the findings at Falsterbo is very good.

The Swedish material contains only six records of Great Tits, all from Utklippan to the south of the southeastern corner of the province of Blekinge. Two are from March, one from late October and three from November. It may be mentioned that the Great Tit has only on rare occasions been killed at the light on Heligoland, so that BUB (1941: 138) draws the conclusion that the species is almost exclusively a diurnal migrant.

Very few Blue and Coal Tits have ever been recovered at the lights. HANSEN (*op. cit.*) lists 9 Blue Tits and 4 Coal Tits. One specimen of the latter species was found in spring, all the others in autumn. The Blue Tit records are concentrated to the middle and last thirds of October, whilst the three Coal Tits were found one each in September, October and November.

The Swedish material contains two Coal Tits, one from the autumn of 1946 and one from the following spring. No Blue Tits were found.

For comparison it may be mentioned that the Danish material contains nearly 5.000 Robins (*Erithacus rubecula*), over 1.300 Goldcrests and over 200 Wrens (*Troglodytes troglodytes*). On the other hand only 8 Treecreepers were found.

It is of course to be expected that different species are differently likely to strike the lights and be killed, depending on migration periods, flight altitude, concentration to guiding-lines, flock size and many other things. However, the three tit species seem to be so similar with regard to most of these aspects that the material justifies the suggestion that the Great Tit is more inclined to nocturnal migration than the other two species. But at the same time it seems also to be necessary to draw the conclusion that a l l t i t s p e c i e s a r e p r i m a r i l y d i u r n a l m i g r a n t s.

Finally it may be mentioned that the Goldcrest is an almost purely nocturnal migrant, although abortive migration attempts by a few specimens have occasionally been recorded at Falsterbo, and perhaps

elsewhere. Very large quantities are involved in the movements, as apparent both from the high number of Goldcrests killed at the Danish lights, and from the incredible numbers sometimes found resting at suitable localities. The Treecreeper has, as far as I am aware, never been recorded at Falsterbo on diurnal migration flight, but in October 1956 I saw on two occasions a single Treecreeper join migrating flocks of Longtailed Tits, departing from a pine grove out over several hundred metres' open ground in the interior of Skåne. The fact that it is very scarce also in the material collected at the lights seems to indicate that only a very small proportion of the Scandinavian population leaves this area.

F. Ringing recoveries

I. *The bird station recoveries*

The number of recoveries yielded by the ringing activities of the Swedish bird stations is still very low. Yet there are a few details from those results worth mentioning. The recoveries are listed in Tab. 38.

Judging from the recoveries a considerable proportion of the Great and Blue Tits that have moved down to the observatories turn back in the same autumn north- and eastwards. This is illustrated by Nos. 4, 6, 8 and 14 in Tab. 38. These recoveries were made too early to be referred to "spring migration". A similar pattern was shown to exist in the Jay (*Garrulus glandarius*) by ENEMAR (1957 a: 34—35), when this species undertook a large-scale movement in 1955. According to the ringing recoveries many Jays returned to the interior of Skåne already in the same autumn. Seven birds were found, mainly in western Skåne, in the winter of 1955 to 1956 and three more in the spring of 1956. Four birds, on the other hand, were recovered in Denmark (Zealand). As pointed out by ENEMAR, no conclusion should be drawn concerning the proportion of Jays continuing their journey, respectively turning back. Yet, for this species as well as for the tits, the narrow stretch of open sea between Falsterbo and Zealand seems to be a difficult barrier. The reactions of tits when encountering the sea was described above (p. 107). A few Great and Blue Tits have been retrapped at the bird stations in autumns following the one during which they were ringed. This is the case with Nos. 2, 5, 7, 11, 12, and 13. No. 11 was also trapped in the intervening spring, which

Tab. 38. Recoveries of Great and Blue Tits ringed at Ottenby and Falsterbo bird stations. From the annual reports of the stations, published *seriatim* in Vår Fågelvärld.

No.	Ring number	Place	Date	Place and date of recovery
			Great Tit	
1	ZO 5134	Ottenby	12.10.1947	Köping, Öland (75 km N), 0.1.1948
2	ZO 5446	»	28.10.1947	Ottenby, 28.10.1948
3	ZOB 1508	»	17.10.1949	Själland (Zealand), Denmark, 29.11.1949
4	S 14815	»	20.10.1953	Gårdby, Öland (47 km NNE), acc. to letter mailed 9.1.1954
5	223743	Falsterbo	4.8.1955	Falsterbo, 28.11.1955
6	113860	»	26.9.1955	Ljunghusen (8 km ENE), 7.1.1956
7	112434	»	15.9.1955	Falsterbo, 30.8.1956
8	113170	»	23.8.1955	Falsterbo, 7.1.1956
9	208747	Ottenby	10.8.1957	Ottenby, 13.4.1958
10	134203	»	2.11.1957	Ottenby, 26.2.1959
11	213001	»	17.8.1958	Ottenby, 14.5.1959 and 18.10.1959
			Blue Tit	
12	ZOD 4873	Ottenby	7.10.1950	Ottenby, 7.10.1951
13	223770	Falsterbo	8.8.1955	Falsterbo, 30.8.1956
14	ZG 526	»	29.9.1952	Near Trelleborg (32 km E), 28.10.1952
15	ZAH 9434	»	9.10.1952	Karlshamn, Blekinge (150 km NE), 19.11.1953
16	131806	»	23.10.1956	Järrestad (ca 70 km ENE), 22.11.1957

indicates that it belonged to the local breeding population. In the other cases this is not certain. It seems likely that at least they did not breed in the immediate vicinity of the bird stations, for in that case many more retrappings would have occurred and not only one recapture in the migration season of a following year. It is a remarkable coincidence that several of these recaptures (Nos. 2, 7, 12 and 13) were made at nearly the same time in the different years, in two cases even on the very same day. Probably they have been nesting

at a distance of perhaps a few km and have got into the traps only during the period of migratory restlessness.

Finally, it may be worth mentioning that the only really distant recovery so far yielded by the bird station ringings is of a Great Tit, ringed at Ottenby in the middle of October 1949 and recovered on Zealand (Denmark) six weeks later. It is noteworthy that this happened in the only year when a really large-scale Great Tit movement was recorded at Ottenby and very marked also at Falsterbo. It is of course impossible to elaborate on this single recovery.

II. *Recoveries from the ringing activity of national schemes*

Ringing was taken up by the Gothenburg Natural History Museum and the National Museum of Natural History in Stockholm in the 1910's. A survey of the recoveries of tits has been published by RENDAHL (1959), who included all recoveries made up to and including 1956, in some cases also 1957 and 1958. RENDAHL also included recoveries from the Norwegian and Finnish ringing schemes and published complete lists of recoveries obtained from a distance of more than 10 km from the ringing place. Thanks to these full lists it is possible to examine critically his conclusions and also utilize the material for further purposes. This will be the subject of the present section.

Of Great Tits, ringed as young in the nest or immediately after having left the nest, 503 recoveries in later winters have been obtained. Of these 79 (= 15,7 %) were from distances over 10 km from the ringing place. Restricting our attention to those birds that were found in the first winter after their birth, it is found that 14,2 % of the young leave their birth-area in their first autumn. For the second to eighth winters, the corresponding figure is 20,5 %. This certainly does not prove an increased mobility in adult Great Tits. The difference is instead caused by the fact that some of the Great Tits that have moved away from their birth-place in their first autumn have not returned exactly to their breeding-area but stopped somewhere else. If they are recovered at their new breeding-place in some later winter, this may incorrectly be interpreted as migration in adult stage. This case history is strongly suggested by RENDAHL's (*op. cit.*: 367–368) statement that "im zweiten bis achten Winter sind die . . . Funde ziemlich gleichmässig in alle Himmelsrichtungen verteilt". This

is in contrast to the winter recoveries from the first winter which are concentrated in the S to W quadrant.

Since RENDAHL does not publish the annual ringing totals, it is impossible to analyse the material with a view at elucidating if there are different proportions of migrant vs. resident young Great Tits in different years. However, in another way it was possible to tackle this problem. Using the lists of "distant recoveries" (*i.e.* from a distance of more than 10 km from the ringing place), we may compute the average distance travelled in different years. There are 10 records from years known to have been characterized by heavy Great Tit movements at Falsterbo, *viz.* 1949, 1955 and 1957, and 10 from years with little movement noticeable at Falsterbo, *viz.* 1950, 1952, 1953, 1954, and 1956. The average for the first 10 recoveries amounts to 85 km, for the latter to 168 km, *i.e.* a difference of 100 %. Standard errors of the mean are ± 25,5 and ± 42,9, respectively. This indicates that the average distance travelled is greater in some years than in others but not whether differently large proportions of the population are involved.

Recoveries from winters later than the first must not be used for similar comparisons. The position of the bird after approx. 18 months is the result of too many movements.

Recoveries of Great Tits ringed as adults show that approx. 97 % of them remain close to the ringing place for the remainder of their life. It does not matter whether all recoveries are used or only those from later winters. The very small number of Great Tits that had undertaken long-range movements had all but three moved northwards (ENE—WNW). Since some of the "adult" Great Tits ringed in winter are probably young of the year, these movements are probably return migration following first autumn departures. Thus, it may be stated that the adult Great Tit in Sweden is an almost completely stationary bird.

There is little evidence for movements in the winter months. A bird from Nordmaling near Umeå on the Bothnian Gulf had moved 48 km in 43 days, starting from 10 December.

According to RENDAHL (*op.cit.*: 372) long-range movements are much commoner among North Swedish Great Tits than in the South Swedish population. As the ringing figures for each year are not given, it is impossible to check this statement that way. However,

if the birds that have undertaken long-range movements are divided in a northern and a southern group, using RENDAHL's demarcation line, it is found that the average distance travelled is closely similar (97 and 104 km, respectively).

As briefly mentioned above, the recoveries "nach allen Himmelsrichtungen" in the second to eighth winters are probably caused by "Umsiedlung", not by irregular movements in adult birds. It follows that the figure given by RENDAHL (*op.cit.*: 375) for "Umsiedlung" should be somewhat increased.

The recoveries yielded by the Norwegian ringing activities do not present any novel aspects on Great Tit movements. These birds tend to move in a more strictly southerly direction, which may be explained by the geographical position of the country in combination with the strict dependency of Great Tits on guiding-lines. HAFTORN (1950) has shown that Great Tits occur in autumn at various places lying far to the west but has no record of birds departing out over the open sea. Some Norwegian Great Tits move southeastwards and winter in the Middle Swedish plains. There is a remarkable record of a Norwegian Great Tit recovered on 1 April of the year following ringing at Rothenburg, Germany. RENDAHL suspects that there has been some mistake in the diaries of the ringer, and this is possible, although by no means necessary. The distance covered by this bird, approx. 750 km, has been surpassed by some intra-Swedish movements.

The Finnish records do not add any novel aspects. No record from abroad of a Finnish Great Tit has so far been obtained.

The following figures may be of interest: Of all Great Tits ringed as young and recovered in later winters (between September and April, incl.), 84,3 % in Sweden have occurred within 10 km of the birthplace, whilst the corresponding figures are for Norway 82,3 % and for Finland 91,8 %. This seems to indicate that the Finnish Great Tits are at least as stationary as the Scandinavian populations, which is slightly surprising with regard to the more severe winter climate of the former country. However, the Finnish material is not very extensive, and further data are necessary before detailed conclusions may be permitted.

According to the data presented by RENDAHL (*op.cit.*) the Blue Tit shows a stronger inclination of long-range movements than the Great Tit. Thus, only 65,4 % of the Blue Tits ringed as young were later found to have remained within the immediate surroundings of their

birth-place in their first winter. That means that 34,6 % had departed, which is more than twice the corresponding figure for the Great Tit (p. 114). A further difference is that the directions chosen by young Blue Tits are more variable and exhibit a distinct inclination towards the north and northwest. Particularly impressive are two recoveries of Blue Tits ringed in the province of Småland and found in the following winter in southeastern Norway. Evidence for overseas migration is provided by a bird that had travelled from Skåne to Jutland (Denmark).

The scanty Norwegian material does not require any comments, except that the movements are directed towards the northeast more commonly than those in Sweden. This may be an effect of the guiding-lines. No distant recoveries of Finnish Blue Tits are listed by RENDAHL.

For all other tit species the recoveries are very few. Two interesting recoveries of Coal Tits have been made, *viz.* one bird ringed as young in the province of Gästrikland, central Sweden, on 17 June 1943 and recovered on 10 September in the same year at Kemi in northern Finland, after a journey of more than 700 km to the NNE. As long as this record stands alone, it is not justified to attach any particular importance to it, but it is very remarkable indeed. The other recovery is of a Finnish bird, ringed at Björneborg in SW Finland, that was recovered in September 1956 on the islands of Åland between Finland and Sweden. It will be recalled that in 1956 there was an important movement of Coal Tits through southern Sweden (p. 95), and the above recovery indicates that at least part of the birds originated from east of the Baltic. The bird in question had travelled approx. 160 km towards the SW.

Proportionately, and absolutely, very small numbers of recoveries have been obtained of the Marsh, Willow and Crested Tits. All are from the immediate vicinity of the ringing place. Not a single recovery of a Longtailed Tit has so far been obtained. However, in late October 1959 a Longtailed Tit trapped at Falsterbo bird station was found to carry a U. S. S. R. ring. The bird had been ringed a fortnight earlier at Kaliningrad in Poland. This recovery proves that at least part of the birds involved in the 1959 movement originated from the southeastern corner of the Baltic, but it is very likely that the movement had its roots still farther to the east (ULFSTRAND in preparation).

G. Some data on recent Great and Blue Tit movements in NW Europe

It became known long ago that considerable movements of Great and Blue Tits were undertaken in Central Europe, particularly in Germany (DROST 1932, DROST & SCHÜZ 1933). Annual fluctuations were, however, scarcely discussed. GÄTKE (1895: 412) noted that tits appeared on Heligoland in annually fluctuating numbers, and BUB (1941) made a good case for the assumption that the numbers occurring on that island had undergone a longterm gradual decrease.

In connection with a detailed study of the 1957 tit movement, CRAMP, PETTET & SHARROCK (1960: 114—117) presented a useful review of recent Great and Blue Tit mass movements in northwestern Europe. These authors produced evidence showing that large influxes into Great Britain had occurred in 1949 and also, although in much lesser scale, in 1954. Then there was an enormous influx in 1957, which affected nearly the whole of the British Isles and probably extended even to the eastern parts of Ireland. CRAMP *et al.* (*op.cit.*: 104—105) compiled an informative map of the geographical extent of the 1957 movement, using both observations and ringing recoveries. It is very clear that the movement covered only the northwestern part of the continent, north of the Middle German mountains. Several ring recoveries demonstrate a strong tendency to return movement, and the fact that a bird was recovered as far east as in the Lithuanian S. S. R. shows that part of the population had a surprisingly easterly origin. From our point of view it is most interesting that CRAMP *et al.* were unable to secure any evidence of tit movements north of southernmost Sweden, and quote a letter from G. SVÄRDSON where it is suggested that Southern Sweden was in fact the northernmost limit of the populations involved in the mass movement. It is also interesting that from Esthonia, which is ornithologically kept under much closer control than most other East European areas, information was received to the effect that Coal Tits but not Great nor Blue Tits were on the move. It may be mentioned that a guess was hazarded by MATHIASSON (1960: 110) that the 1956 Great Tit movement at Falsterbo likewise was made up of birds from the southernmost part of Sweden only.

The huge 1957 movement has been documented also by RINGLEBEN (1958) and VAUK (1959), and its reflection at the Swedish bird stations was described in Chapter 7: C. VAUK found on Heligo-

land that 95 of 114 trapped Blue Tits were birds of the year, whilst only 21 of 59 Great Tits were juveniles. This finding is of interest with regard to the findings above of the adult Great Tits of Sweden as almost completely stationary (p. 115). A higher proportion of Great than Blue Tits settled down on Heligoland to spend the winter.

Recent studies on the bird migration in two high Alpine passes in Switzerland have revealed the existence of strong movements of Great and Blue Tits (GODEL & CROUSAZ 1958). In 1957 there was a marked rise in the numbers passing through this area. As shown by CRAMP *et al.* (*op. cit.*) this south European movement system seems to be separate from that of northwest Europe. Possibly however, the movements in the two systems are synchronous. The winter-quarters of the Great Tits passing through Switzerland have been demonstrated to consist of southeastern France as far south as the Mediterranean. The opinion that the movements in Southern Europe are synchronized with those in northwest Europe is supported by the facts that little migration was recorded in Switzerland in 1958 (VUILLEUMIER 1959: 70) but very heavy passage in 1959 (GLUTZ VON BLOTZHEIM 1960). In 1957 GODEL & CROUSAZ (*op. cit.*: 108) found that 90 to 95 % of the migrating tits were birds of the year.

Enquiries to British and German ornithologists have shown that very little Great and Blue Tit movement was recorded in 1958.

For 1959 the evidence is somewhat contradictory. As described above, the movement of Great Tits in particular was in that year higher than ever before at Falsterbo. The British network of bird observatories noted a certain influx of Continental tits but numbers were low (Report from Bird Observatories 1960: 97—147). Mr. S. CRAMP (*in litt.*) confirms that the influx into the British Isles was of relatively slight extent. Dr. H. RINGLEBEN (*in litt.*) found little evidence for tit movements in NW Germany in spite of considerable field-work, and Prof. Dr. H. SCHILDMACHER (*in litt.*) has kindly offered detailed information concerning the situation on the island of Rügen, where again tit movements were of insignificant extent. The same applies to Mecklenburg (Mr. H. DOST *in litt.*, *via* Prof. Dr. SCHILDMACHER).

Mr. S. CRAMP (*in litt.*) is of the opinion that the 1959 movement was "smaller than 1957 in this country, but larger in central Europe". Since CRAMP is preparing a detailed account of the 1959 movement we need not go into details here. The same author has generously

provided information (*in litt.*) showing that almost no Great or Blue Tit influx was noticed in the British Isles in 1960.

All the above information seems to show that in 1957 the Great and Blue Tit movements in the whole of northwestern Europe were of an unprecedented scale and that very considerable movements were also going on in 1949 and 1959. Smaller movements probably of more local extent occurred in some other years.

8. The ecological background of the movements of the Great and Blue Tits in Southern Sweden

In Chapters 3 to 7 various types of evidence bearing on the non-breeding ecology of tits, in part also of the Goldcrest and Treecreeper, were presented and discussed. The Great and Blue Tits have been in the centre of interest throughout, although their ecology has been put in relief through repeated comparisons with other species, particularly the Marsh and Coal Tits. Now it is necessary to try to coordinate the various kinds of evidence in order to throw light on the problem outlined in the Introduction, *viz.* the ecological background of the migratory movements in the Great and Blue Tits.

The most basic type of information concerns the food choice and food situation for different species in different years (summarized in Chapter 3: E for the species inhabiting deciduous woods). It was found that the Great Tit based its entire food economy of beech mast, when this was available (p. 27). Also the Marsh Tit and Coal Tit were found to be much attracted to this food source, the latter species only more temporarily, the former in a degree comparable to the Great Tit. The Marsh Tit, moreover, not only fed extensively on mast when present but also deposited large stores which could be exploited to some extent also in the winter following the one during which they were deposited (p. 37). The Blue Tit also utilized beech mast but not to the extent shown by the Great and Marsh Tits. Yet there are reasons to believe that mast was a positive factor for the Blue Tit also as an easily accessible and highly nutritive reserve supply (p. 32). The Marsh Tit largely remained a vegetarian in the absence of beech mast, whilst the Great Tit (to a large extent) and the Blue Tit (almost entirely) turned to animal food supplies. Neither of

these species were found to store food. The Great Tit was recorded to find and consume one year old beech mast on the ground, but there were no indications that this source of food was of quantitative significance for the species (p. 27). Also some cases of robbing stores prepared by the Marsh Tit were observed, but again this activity did not seem to play an important rôle (p. 28).

It is rather generally supposed that ecological segregation is an adaptation to food scarcity (p. 56), *i. e.* its development in a given habitat indicates that the species are at least temporarily facing shortage and that the populations are at least partly regulated by food scarcity. This being accepted, the fact that ecological segregation was well developed, although not complete, in the absence of beech mast may be used as an indication that tits feeding in deciduous woods in winter are sometimes threatened by food shortage and that they have as a defence evolved segregation with regard to food resources drawn upon, thereby improving the food situation (Chapter 3: F). When beech mast is available, segregation is largely given up, as found also by other investigators, indicating that this food is utilizable by several species without provoking competitive relationships between the species involved (p. 58). It may be mentioned in passing that many species besides the tits were feeding on beech mast.

Many more tits were found to inhabit the beech and mixed woods when mast was available than when it was not (Chapter 5). In other words, the mast very much improved the carrying capacity of these habitats. This was found to apply both to the Öved (p. 78) and Bökeberg (p. 43) woods. The population of Marsh Tits did not fluctuate in anything like the proportions shown by the Great and Blue Tits (p. 79). This difference is certainly caused by the higher mobility of the last two species, which brings large quantities of birds in contact with the beech woods during the autumn movements.

It was possible to generalize from these findings thanks to the information yielded by the Winter Bird Census (Chapter 6). It was shown that the southernmost of the five districts, into which Southern and Middle Sweden was divided, was characterized by large and violent changes in population density to the effect that t h e d e n s i t y w a s v e r y m u c h h i g h e r i n b e e c h m a s t w i n t e r s t h a n i n t h o s e t h a t h a d n o t m a s t c r o p. Such fluctuations were found in the Great and Blue Tits but n o t in the Marsh

Tit, as was to be expected on the basis of the local investigation. It is very interesting that the district lying immediately north of the southernmost one showed changes in the opposite direction. In this paper fluctuations in species other than the Great, Blue and Marsh Tits are not analysed.

The migratory movements recorded at the Swedish bird observatories were described in Chapter 7, where information concerning the ringing recoveries and movements in other parts of Europe was also presented. In the present connection the interest is mainly focussed on the annual fluctuations of the Great and Blue Tits, the Marsh Tit being almost completely absent from the observatories. It was found that there is a clear tendency to synchronous fluctuations in the former two species, particularly in the really large-scale movements, and the conclusion seems inevitable that some common factor is involved. It was also found that the Great Tit passage at Ottenby is of moderate extent, and it is suggested that at least for the Great Tit mainly birds from the island of Öland are involved in the passage over Ottenby (p. 110). The Coal and Longtailed Tits were found to be poorly or not at all synchronized with the Great and Blue Tits, although the position in the Longtailed Tit is somewhat uncertain (p. 97). The increased tendency to Great Tit movements in certain years was possible to demonstrate also in the material of ringing recoveries published by RENDAHL (1959). Regional differences were not possible to demonstrate in that material (pp. 115—116).

In many other species characterized by large-scale annual fluctuations in the migratory habits, it has been found that some food factor is involved (see discussion in SCHÜZ 1952: 152—161). The food studies performed by the present author demonstrated that if any food factor may exert an influence on the migratory movements of the Great and Blue Tits, it has to be beech mast. Therefore it is necessary to examine if any correlation exists between beech mast crop and tit movements, as recorded at the bird stations. The annual fluctuations in the fruiting of beech are set forth in Fig. 7, based on data in TIRÉN (1948 to 1950) and FALL (1951 to 1960). It is apparent that 1949, 1955, 1957 and 1959 were marked by particularly poor crops. A glance on the material presented in Chapter 7: C I is sufficient to reveal that a very close correlation exists. Among the four years with poor mast crop, the three years

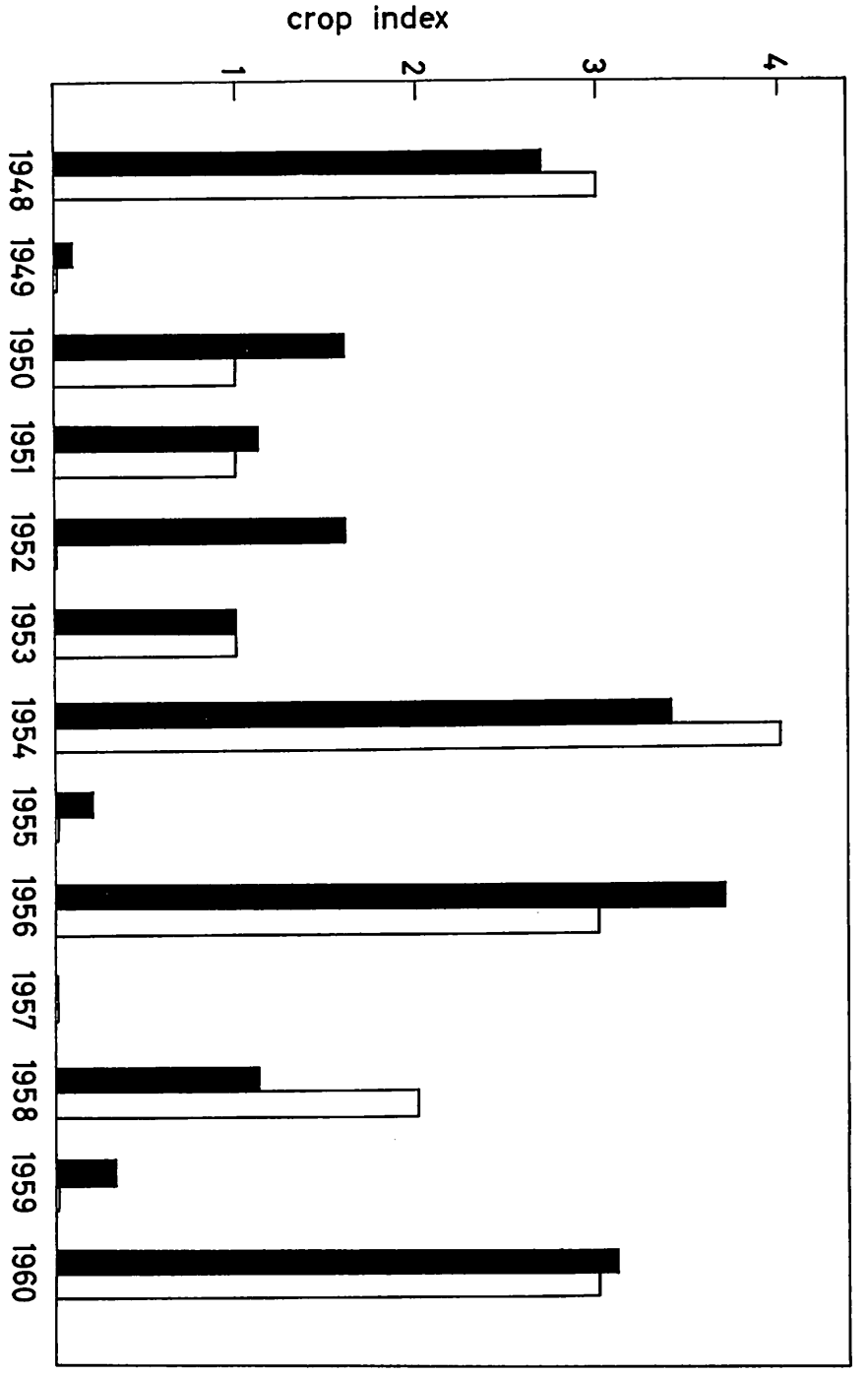

Fig. 7. The beech mast crop in 1948 to 1960. Black = average for the whole beech wood district of Southern Sweden, white = the province of Skåne except its NW part. Based on data in TIRÉN (1948 to 1950) and FALL (1951 to 1960).

with really big movements are included, and for the fourth year (1955) it was concluded that the passage probably was much underestimated at the Falsterbo bird station (p. 96). On the other hand, Great and Blue Tits were almost absent in such years as 1952, 1954, 1958 and 1960, when the crop was of considerable size. It may be pointed out that the relatively low overall crop index in 1958 was caused by failure in the more northerly and unimportant beech districts (*cf.* LINDQUIST 1931), whilst the crop in the more southerly and more extensive beech areas was fairly rich.

The information presented in Chapters 5 and 6, however, makes it probable that the populations involved in the movements are by no means only those which breed in the beech mast areas of Southern Sweden. In beech mast years there seems to be a large scale influx of Great and Blue Tits in the beech woods, as demonstrated by the Winter Bird Census data (Tabs. 22 to 24). In mast-less years, the birds inhabiting the beech woods seem to abandon these areas to some extent. The movements obviously involve birds from an extensive part of Sweden, north of the main beech wood area. It seems possible that increased movements are noticeable over a large part of Fenno-Scandia in the same years (p. 131). From these facts it is inevitable to draw the conclusion that absence of beech mast as such cannot be made responsible for the initiation of the movements but that some other factor must serve as proximately releasing stimulus.

Further confirmation of the opinion that populations north of the beech wood district are involved is found in the undeniable simultaneousness between the movements at Ottenby and those at Falsterbo (p. 110).

Fortunately an extensive and careful study on the breeding biology and population dynamics of the Great Tit exists, *viz.* that by KLUIJVER (1951). For the present discussion the most important result obtained by KLUIJVER is the demonstration of the correlation between population density and migratory tendencies (see also KALELA 1954, LACK 1954 and works quoted by him). With regard to the exceptionally solid foundations of KLUIJVER's results, it seems to be a justified generalization to assume that

the same mechanism is in operation also in Swedish tit populations. There are no investigations from Sweden concerning the population dynamics of the Great and Blue Tits. Nor is it possible to look for some meteorological or other environmental factor that might be used as an indication of breeding success, for the annual fluctuations of the autumn tit populations are influenced by a great number of factors in a highly intricate pattern, as abundantly demonstrated by KLUIJVER (*op. cit.*). The Winter Bird Census results do not argue against the possibility of an overall increase in the Great and Blue Tit populations over the last three or four years, which have, moreover, all been marked by fairly mild winters, but more cannot be said at the moment (pp. 87—88).

The self-regulation of population density also takes the expression that the attractivity of a restricted habitat decreases after a certain degree of "saturation" (KLUIJVER 1951, LACK 1952, KLUIJVER & TINBERGEN 1953: 285). The density at which saturation is reached seems to vary strongly with food supply, at least during the non-breeding season, as demonstrated by the influence of beech mast on the "carrying capacity" of the beech woods in Southern Sweden.

Accepting that KLUIJVER's findings may be transferred to the populations inhabiting this country, we are able to present the theory that Great and Blue Tit movements are started as a response to increased population density but that the extent of the wanderings is strongly influenced by the food situation encountered on the way. If the migratory tendency is strong, many Great and Blue Tits from Scandinavia extend their travels as far as to the provinces of Skåne, Blekinge and Halland, where a large proportion of them become concentrated in the beech woods. In Skåne the concentration to the central parts is reinforced by the great dependency of the birds on micro-guiding lines and detailed topography (Chapter 7: C IV) during their movements. If a favourable food situation is met with in the form of a rich beech mast supply, many or all of the birds get "caught" in the beech woods. If no mast is available, they have to continue and are then recorded at Falsterbo and at other places as undertaking a mass movement. This hypothesis concerning the significance of beech mast also takes into consideration

the exceptions from the general rule of correlation between failing mast crop and strong migration. Thus, the fact that no great movement may accompany a situation of complete mast crop failure may easily be explained with reference to the possibility of a low population density in the recruiting area. For example, the poor mast crop of 1955 was, as far as the evidence goes, not accompanied by a really large-scale tit movement, although its extent is likely to have been underestimated at Falsterbo (p. 96). It may be suggested that this may be correlated with the "desert summer" of 1955 which possibly had a negative effect on woodland passerine birds. On the other hand, if the migratory tendency is very strong and exceptionally many birds gradually accumulate in the beech woods, the density may cause a sudden and late "spilling over" even though a rich beech mast crop is available. Such a situation may have occurred in 1956, the movement then being very late (p. 99) and of very brief duration (p. 106) but yet rich in individuals.

The intricate interplay of different factors at the initial phases of a large-scale exodus exposed itself during the field studies, devoted chiefly to the feeding habits, at Öved in October 1959. At the same time as a large movement was recorded at Falsterbo (Tabs. 27 to 28), the Great Tits suddenly abandoned beech as a feeding station (p. 25 and Tab. 2), their food seeking intensity rose to its midwinter value (p. 67 and Tab. 15) and there was an increase in the frequency of calling (p. 63 and Tab. 15) and of aggressive encounters (p. 70 and Tab. 15), both the latter phenomena indicating "excitement". During the same month a sharp decrease in the local population of Great Tits occurred (pp. 76—78 and Fig. 6), and it may be assumed that at the same time the movements leading up to the large-scale redistribution of the South Swedish populations apparent in the Winter Bird Census material (Chapter 6: B) were also performed. The interrelationships between these different phenomena are difficult to disentangle. All of them, however, seem to be correlated with a change for the worse in feeding possibilities, caused by the absence of beech mast, the shortening duration of day light and the influx of birds from areas north of the beech district.

In short: due to its climatical and — more directly — vegetational characteristics, the beech wood areas in southernmost Sweden are suitable for large numbers of Great Tits as a wintering area, accom-

modating the "surplus" of the population that is pressed out on migration. The suitability of the area is, however, subject to great annual variations, depending on the fruiting of beech.

The picture of the migration of the Great and Blue Tits emerging from the various types of evidence is one of a complicated and flexible pattern, where partial migration and irruptive components are mixed. Great differences seem to exist in different populations. CRAMP *et al.* (1960: 185) argued that the movements of the Great and Blue Tits in northwestern Europe be classed as irruptive. This term has been much abused, and its ecological and adaptive significance has therefore been very differently appraised by different workers. For recent views, see the discussion in for example RUDEBECK (1950), SCHÜZ (1952), LACK (1954) and SVÄRDSON (1957). If this term is to retain any meaning at all, there is need for a restriction of its field of use and for a definition. It seems to be considered by most or all recent students in this field that f o o d is always involved in a direct way (*cf.* BERNDT & DANCKER (1960: 106) for the Jay (*Garrulus glandarius*)). The food conditions met with on the way largely determine the extent and the timing of the journeys, although high population density as such may act as a proximate releasing factor. The best demonstration of the influence of population density on the migratory habits is KLUIJVER's (1951) study on the Great Tit. For many species the food factor may exert its influence from the beginning, *i.e.* already in or near the breeding-areas of the participating populations. That seems to be the usual case with many of the "classical" irruption species, such as Nutcracker (*Nucifraga c. caryocatactes* & *N. c. macrorhynchus*), Great Spotted Woodpecker (*Dendrocopos major*), Pine Grosbeak (*Pinicola enucleator*) and Crossbills (*Loxia spp.*), just to select a few. All these species seem to be more or less stationary in those years, when the food situation is satisfactory. However, more observations are needed. It is of interest to find that G. MARKGREN & LUNDBERG (1959: 196) believe that the Pine Grosbeak under special circumstances also moves without regard to the food supply, in fact will pass over areas where food is plentiful. Compare the comment below on the Waxwing! In other cases the food factor does not come into action until the birds have travelled a more or less considerable distance. This seems to be the case in the Brambling (GRANVIK 1916, 1917, LACK 1954), possibly also in the Fieldfare (*Turdus pilaris*), Siskin (*Carduelis spinus*), Redpoll (*Carduelis flammea*) and a few

others. The Great and Blue Tits seem to belong to this group also, and therefore it is entirely justifiable to classify these species as irruptive migrants. The last six species are partially or wholly migratory in all years.

Also in the Waxwing (*Bombycilla garrulus*) commonly cited as an extreme "irruption bird", part of the population seems to move annually, the food factor playing no significant rôle (SIIVONEN 1941). Another part, on the contrary, is extremely dependent on the food situation, which exerts a strong influence of the course of the movement in time and space (*cf.* HANSSON & WALLIN 1958). Here, as usually, it is impossible to draw sharp limits.

It should not be forgotten that the population dynamics also contribute to characterizing a true irruptive migrant. The irruption species often seem to fluctuate violently with regard to the distribution and population density. This is known in a few cases but only suspected in many more. The exceptionally large fluctuations in the populations of some irruptive migrants was stressed by SCHÜZ (*op. cit.*) in suggesting the alternative term "*Gradationsvögel*".

The Great and Blue Tits seem to differ from many irruption species with regard to the fact that only a relatively small part of the population is involved in the movement. A considerable proportion of the population remains in the breeding-area, and these species thus are morphic (HUXLEY 1955) with respect to the migration habits. Such morphism is usually considered to be an adaptation to strongly fluctuating environmental conditions (HUXLEY 1942; for morphism in migration habits see particularly LACK 1943/44, 1948). Climatical conditions have usually been held responsible for the perpetuation of migratory morphism, and this in my opinion is almost certainly true for most cases. A typical example of a partial migrant is the Swedish population of the Goldcrest, which is known to depart from our coasts in huge quantities but may nevertheless be found in midwinter over most of its breeding-range. It does not seem so obvious, however, that the partial migration in the Great and Blue Tits may be explained simply as a response to variable climatical conditions. It is true that there is a cline in the migratory status of Great Tit populations, starting with the completely stationary birds of Southwestern Europe and the British Isles, and reaching the opposite extreme, that of obligatory migration, for example in the Ural district of the U.S.S.R. (GROTE 1919: 374, 1937),

indicating adaptation to climatical conditions. However, the number of young Great Tits departing from their birth-area is remarkably constant over much of Europe, as far as present evidence goes: Switzerland (PLATTNER & SUTTER 1946/47), Germany (DROST 1932) and Fennoscandia (RENDAHL 1959; see Chapter 7: F). In this connection it is important to keep in mind the fact that migratory undertakings should never be interpreted as "race suicides" or, in general, as some kind of "sacrifice", as has sometimes been attempted. I fully agree with the views expressed by LACK (1951, 1954), SVÄRDSON (1953) and WALLGREN (1956), for example, that migratory habits are adaptations evolved by natural selection, and that they are constantly being subjected to selective pressure (*cf.* RUDEBECK 1950, 1956). Tits are, as KALELA (1958: 26) rightly points out, basically stationary birds, and migratory undertakings conferring selective disadvantages would almost certainly be given up in a relatively short time.

Rather I would make the suggestion that the productivity of some Great Tit populations is so great that the habitats regularly get overcrowded in autumn by young birds, and this overcrowding, linked with food scarcity, will release the migratory tendency, particularly in those individuals which will have greatest difficulties in obtaining space and food (*cf.* KALELA 1954). For these individuals departure provides a chance of finding a less crowded habitat where to spend the winter and sometimes also where to settle down to breed. Consequently their chances of survival improve, if they move. This does not mean that their chances of survival, absolutely speaking, are high. On the contrary, all evidence goes to show that tits have an extremely high annual turnover, *i.e.* a very great proportion of the population dies between two breeding seasons (*e.g.* KLUIJVER 1951). It is also known that young birds are somewhat more likely to succumb than older individuals per unit time (LACK 1946, 1954 for survey, SNOW 1956 for the Blue Tit) and that the turnover is proportional to the productivity which varies regionally (SNOW *op.cit.* for the Blue Tit). It would appear that the productivity is so high that local mortality factors which in some areas may be able to regulate the numbers of tits in a given area (GIBB 1956: 428) do not keep step and therefore there is a perpetual tendency to population increase. The density having reached a certain threshold, the chances for survival suddenly deteriorate for the socially and physically inferior birds (*cf.* LACK, GIBB & OWEN 1957), which are then unable to secure a territory and

probably find it difficult to obtain food at a satisfactory rate. Departure from the crowded area, hence, is the only way out, although the chances of survival may rise only slightly.

It may be suggested that the recurrent population increases supposed or known to occur in the classical irruption birds may have the same simple background: lack of agreement between local mortality factors and reproductive potential.

The morphic migration habits and the irruptive tendencies, combined with the physiological ability to withstand the climatical strains of northern climates and the capacity to exploit various food sources in an efficient way, seem to grant the flexibility which obviously is an extremely valuable adaptation for all birds wintering in temperate areas charcterized by violent annual fluctuations in both climate and food supply.

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Postscript

In the autumn of 1961 the largest passage of Great and Blue Tits ever recorded took place at Falsterbo bird observatory. Unfortunately, regular observations were not carried out as in previous years, but thanks to reports from the ringers, particularly Mr. A. GUNNARSSON and from several visitors, particularly Mr. H. BEHMANN, Hildesheim, Germany, as well as a number of days' observations of my own, it is possible to state that numbers by far exceeded those recorded in any previous autumn. As many as approx. 10.000 individuals of each of the two species were counted in one single day (12 October), and thousands were on the move on several other days in middle October. A few Coal Tits were also present, but numbers were relatively low.

The movement of the Great and Blue Tits began already in middle September and had not finished completely around 1 November, when the ringers concluded their activities. However, numbers had then fallen very considerably, and perhaps the birds present at that time merely were making abortive attempts at migration. Probably the culmination occurred around 10 to 15 October. Mr. GUNNARSSON trapped approx. 200 tits and points out (*in litt.*) that as he received very few retrappings, the movement was obviously relatively direct. Thus, the high figures were not influenced by large numbers of birds turning back and being counted twice or more.

Own observations showed that the beech woods in central Skåne were virtually devoid of mast in the autumn of 1961. Thus, this is a further instance of correlation between strong movements in the Great and Blue Tits and absence of beech mast (pp. 122—124).

Census work in the Öved wood in late December 1961 and early January 1962 showed that the Great Tit population amounted to approx. 15 individuals and that the Blue Tits were somewhat more numerous. These figures agree extremely well with those obtained in the winter of 1959/60, when no beech mast was available (*cf.* p. 78).

The tit movements over the Åland archipelago in the Baltic have been described and discussed by LINKOLA (1961) in a recent paper. LINKOLA's observations on the island of Signilskär cover almost exactly the same period as the studies at Falsterbo bird station, *i. e.* 1949 to 1959. By far the largest movement in this period was recorded in 1959, whilst smaller movements were established in 1949 and 1955. The evidence concerning the directions of the migrating birds is of a rather conflicting nature. Thus, most of birds were seen to move east to southeast, but ringing returns were obtained from WSW to SSW (as well as one 14 km to the east of the ringing place). There was a distinct return passage in the spring of 1960. The above data refer to the Great Tit. The Blue Tit was also most numerous in 1959, whilst the Coal Tit moved in large numbers in 1956, when one recovery of this species was received from Germany.

LINKOLA's data thus confirm the opinion that the Great and Blue Tits recorded at Falsterbo as well as those wintering in Skåne in years with a rich mast crop probably originate from relatively distant areas, although it is likely that the influx from over the Baltic is of rather small extent.

A ringing recovery, kindly communicated by Mr. S. ÖSTERLÖF (*in litt.*), shows that also the 1961 movement was in part made up of birds from the east side of the Baltic. Thus, one Great Tit that was picked up dead at the extreme northern point of Gotland in the Baltic on 27 November had been ringed in the Latvian SSR (57° 01′ N. lat., 24° 18′ E. long.) on 4 August 1961. Another bird, ringed in the Åland archipelago in the autumn of 1959, was found dead on the Swedish east coast in July 1960.

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Svensk sammanfattning: **Om talgoxens *(Parus major)* och blåmesens *(Parus caeruleus)* ekologi utanför häckningstiden samt deras flyttningsrörelser i södra Sverige. Med jämförande undersökningar över besläktade arter.**

1. *Inledning*

Den undersökning, som härmed presenteras, påbörjades i förhoppningen att kunna lämna ett bidrag till förklaringen av de gåtfulla flyttningsrörelser, som fastställts hos talgoxen och blåmesen. Dessa arter uppträder i starkt växlande antal vid våra sydsvenska fågelstationer, samtidigt som de i betydande antal övervintrar över hela sina utbredningsområden inom vårt land. Svartmesens (*Parus ater*) flyttningsrörelser, å andra sidan, har befunnits vara korrelerade med felslagen granfröskörd. Olika avsnitt av ekologin blev föremål för undersökning: näringsvanor under vinterhalvåret, födosöksintensiteten, det allmänna beteendet, populationsförändringar inom valda provytor i Skåne, annuella och regionala differenser i populationstätheten över större områden i Sydsverige. Till grund för skildringen av flyttningsrörelserna lades det material, som under en lång följd av år insamlats vid Falsterbo fågelstation.

2. *Beskrivning av undersökningsområdena*

Huvuddelen av förf:s eget fältarbete utfördes i det inre av Skåne. En blandskog nära Öved vid Vombsjön ca 30 km E Lund visade sig väl lämpad för fältstudier över näringsvanorna. Denna skog (fig. 1 och 2 a) består av bok, ek, al, tall och gran med tillskott av enstaka askar, björkar och almar. Undervegetationen består av ett buskskikt av bl. a. hylle och björnbär. Området står i kontakt med andra skogspartier, varför mesarna har goda möjligheter att passera ut ur och in i området. Några hus finns ej i detta skogsområde.

Dessutom företogs jämförande studier dels i Bökeberg (fig. 2 b), en ren bokskog av måttlig ålder, dels i Vombs fure (fig. 2 c), ett rent tallbestånd.

3. *Näringsvanorna hos mesar, trädkrypare och kungsfågel*

I avsnitten 3 A och B framlägges en översikt över tidigare arbeten av samma inriktning som det föreliggande, resp. över faunornas uppgifter om de studerade arternas näringsekologi. Av svensk litteratur visade sig NILSSON (1858) ge bäst upplysning. I 3 B refereras dessutom vissa utländska specialundersökningar över mesarnas näringsval, nämligen HARTLEY (1953), GIBB (1954 a) och BETTS (1955).

I avsnitt 3 C lämnas en redogörelse för undersökningsmetodiken. Det har icke ansetts nödvändigt att komplettera undersökningen med maginnehållsanalyser, utan en rent observationell metod har använts. Längs dag för dag identiska marschrouter registreras näringsstationerna för de aktuella arterna, dvs. man bokförde platser i terrängen, där fåglarna iakttages syssla med näringssök. Så ofta som möjligt antecknas naturligtvis vad de äter, men detta är icke alltid möjligt att urskilja. Det var dock nästan alltid möjligt att avgöra, om en viss fågel var på sök efter vegetabilisk eller animalisk föda. Klassifikationen av näringsstationerna växlade på olika provytor, såsom framgår av tabellmaterialet.

För att alla iakttagelser skulle bli likvärda utfördes de i form av upprepade standardobservationer (GIBB 1954 a: 513—514). Varje fågel observeras under 5—10 sek., varefter man antecknar dess näringsstation, beteende- och aktivitetstyp, relation till andra fåglar (om den ingick i en flock etc.) och andra data av intresse. Iakttagelser av fåglar, som var tydligt störda av observatörens närvaro, lämnades utan avseende. Det aktgavs på att varje individ endast noterades en gång, och allt fältarbete utfördes på förmiddagen. Dagar med ogynnsamt väder undveks.

Den mest betydande svårigheten var, att åtskilliga arter transporterar födopartiklar från det ställe, där de påträffats, till ett annat för att konsumera dem. I samband därmed står problemet med näringshamstringen (HAFTORN 1954, 1956 a, b, c, 1959 och andra arbeten). Eftersom transporterna oftast utföres med stora, relativt lätt identifierbara partiklar, har det bedömts sannolikt, att denna vana inte introducerar något större fel i registreringarna, och vad beträffar hamstringen gäller, att fågeln i hamstringsögonblicket visserligen icke utnyttjar en näringsstation utan förbereder en, så att en observation av hamstring kan sägas vara likvärd med en observation av näringssök i inskränkt bemärkelse.

Avsnitt D framlägger primärmaterialet rörande de studerade arternas näringsvanor i Öved, Bökeberg resp. Vomb. Skildringen är uppdelad på de olika arterna. Talgoxen (tab. 2) livnärde sig huvudsakligen av bokollon hösten 1958 och den påföljande vintern. Av alla besök i bok gällde 90 % utnyttjandet av ollonen. F. ö. var buskvegetationen en starkt frekventerad näringsstation, liksom marken, där bl. a. nedfallna bokollon men också diverse animalisk näring eftersöktes. Påföljande vinter saknades bokollon så gott som fullständigt. Frekvensen av näringsstationer i bok sjönk starkt, och de inom området övervintrande talgoxarna livnärde sig huvudsakligen av animalisk föda. Hösten 1960 utgjorde ånyo bokollonskörden den huvudsakliga födan för talgoxen. Några gånger iakttogs talgoxar vintern 1959/60 utnyttja kvarliggande bokollon efter föregående säsongs rika skörd. Några fall av näringsparasitism hos arten kunde fastställas: det gällde röverier riktade mot entitans hamstringsförråd. Vissa iakttagelser tyder på att detta beteende utvecklats från en attack riktad mot fågeln, medan denna ännu bär den näringspartikel, som skall hamstras.

Blåmesen (tab. 3) visade sig långt mindre intresserad av bokollonen. I alla lägen utgjordes denna arts stapelföda av lägre djur, men av allt att döma spelade ollonen en viktig roll som lättillgänglig reservföda. Av de olika trädslagen visade blåmesen en tydlig preferens för eken, något som också fastställts vid utländska undersökningar. Med hänsyn till den sekundära betydelse, som bokollonen hade för blåmesen, är det naturligt, att differenserna mellan artens näringsvanor i närvaro, resp. frånvaro av bokollon, blev väsentligt mindre genomgripande än hos talgoxen.

Svartmesen (tab. 4) visade sig som väntat huvudsakligen knuten till barrträden. Icke så få fåglar noterades dock i bokarna, där ollonen utgjorde den huvudsakliga attraktionen.

Entitan (*Parus palustris*; tab. 5) visade sig utnyttja bokollonen i nästan samma utsträckning som talgoxen. En hel del ollon konsumerades ej genast utan hamstrades. Särskilt favoriserad som hamstringsplats var eken. Som sekundära näringskällor tjänstgjorde t. ex. hyllebär och framför allt diverse örters frön, främst *Galeopsis*. Under vintern 1959/60, då inga bokollon fanns att tillgå, kom örtfrön att spela en dominerande roll. I någon utsträckning kunde också entitorna nyttja fjolårsollon, som de anträffade på hamstringsplatser uppe i träden. I ett ringa antal fall kunde fastställas, att entitan hamstrade föda i marken eller i stubbar etc. på ringa höjd över marken. Sammanfattningsvis kan om entitan sägas, att den i alla lägen visade tydlig preferens för vegetabilisk föda, alltså även under den vintersäsong, då bokollonskörden slagit fel.

Trädkryparen (*Certhia familiaris;* tab. 6) är som bekant i sitt näringssök inskränkt till trädens stammar och de största, mer eller mindre vertikala grenarna. Artens näringsstationer fördelade sig icke slumpvis över de tillgängliga trädarterna, utan oregelbundna fluktuationer förekom, vilkas bakgrund ej är efterforskad.

Kungsfågeln (*Regulus regulus;* tab. 7) visade sig som väntat vara knuten till barrträden, på hösten i lika mån till tall och gran, mot vårkanten alltmera övergående till gran. Kungsfågeln betraktas allmänt som rent insektivor, och något tecken som tydde på motsatsen framkom ej. Temporära preferenser för lövträd registrerades, och på en annan lokal, en lund bestående enbart av ek och al med undervegetation främst av hassel, kunde förf. fastställa att en flock om fyra kungsfåglar tillbringade hela tiden jan.—april 1960. Arten synes sålunda vara kapabel att effektivt söka näring även i ren lövskog och detta t. o. m. under svåra vinterförhållanden.

I Bökeberg (tab. 8) gjordes jämförande iakttagelser, som i allt väsentligt bestyrkte de i Öved framkomna rönen. Vid förekomst av ollon utgjorde dessa en dominerande del av talgoxens föda, och då de saknades, visade denna art sig företrädesvis ställd på animalisk näring. Även blåmesen iakttogs i en hög procent av alla fall vara sysselsatt med utnyttjande av bokollonen, ehuru i vissa fall det möjligen var insekter i eller på boknötterna, som eftersöktes. Bortsett från ollonen var blåmesen av allt att döma rent insektivor på denna lokal. I jan. 1959 befanns åtskilliga svartmesar nyttja bokollonen som föda. De gjorde raider in från i omgivningen befintliga grandungar, dit de återvände efter en ollonmåltid. Då inga ollon fanns, undveks den rena bokskogen av svartmesen. Entitan visade stark förkärlek för bokollonen, i vilkas frånvaro dieten var huvudsakligen animalisk. Lokalen var nämligen fattig på annan vegetabilisk föda.

I Vombs fure (tab. 9) befanns talgoxen inta ett mycket begränsat spektrum av näringsstationer, med tyngdpunkten på primärgrenarna nära stammen. Talgoxarna

genomsökte också anhopningar av kvistar och barr som fastnat i klykorna samt gamla bon av ekorre, ringduva etc. Blåmesen var mycket fåtalig i denna rena tallskog och anträffades huvudsakligen på genomresa. Svartmesen var däremot rätt talrik och sökte sin föda i grenverkets perifera delar. Tofsmesen (*Parus cristatus*) intog en position mellan talgoxens och svartmesens näringsstationer, medan entitan liksom blåmesen endast var en tillfällig gäst. Trädkryparen vistades självfallet på stammarna, medan kungsfågeln, ytterst talrik på platsen, höll till i samma zon som svartmesen.

I avsnitt E genomföres en jämförelse mellan de arter, som har sin tyngdpunkt i lövskogen, nämligen talgoxen, blåmesen och entitan. Med utgångspunkt från de värden som meddelats i tabellerna och i de artvisa redogörelserna har bokollonens totala betydelse för de tre arterna beräknats, varvid följande approximativa resultat nåtts: för talgoxen var 50 % av alla näringsstationer riktade på utnyttjandet av ollonen, medan motsvarande siffra för blåmesen var 15 % och för entitan 35 %. Dessa siffror hänför sig till midvintern 1958/59. En liknande kalkyl har gjorts för hösten 1960 med följande resultat: talgoxen 65 %, blåmesen 20 %, entitan 40 %, alltså samma rangordning men överlag något högre siffror.

I tab. 10—11 jämföres näringsvanorna i Öved resp. Bökeberg under närvaro, resp. frånvaro av bokollon. Talgoxen, blåmesen och entitan utnyttjade företrädesvis olika näringskällor vid frånvaro av bokollon, och även vid närvaro av sådana hade de klart markerade skiljaktigheter beträffande sina sekundära näringskällor.

Dessa problem ventileras ytterligare i avsnittet F. Först och främst kan det framhållas, att de tre arterna är ekologiskt segregerade vid frånvaro av bokollon, något som antyder att knapphet på föda vintertid är en viktig populationsreglerande faktor (Lack 1954). Vid närvaro av bokollon reduceras segregationen, i det att alla arterna samfällt nyttjar denna näringskälla. Vad beträffar barrskogen antyder de gjorda undersökningarna, att den ekologiska segregationen där är mycket starkt utpräglad (jfr tab. 9). Detsamma har på basis av ett mycket större datamaterial också påvisats av Haftorn (1956 c). Likheterna mellan dennes och förf:s resultat illustreras i fig. 3. Det verkar sannolikt, att denna utpräglade segregation hänger samman med hamstringen: en nödvändig förutsättning för detta beteendes biologiska lönsamhet är att arternas näringsstationer är relativt distinkta, så att en given arts förråd inte tullas av andra arter och så att medlemmarna av den egna arten har största möjlighet att effektivt exploatera de kollektivt samlade förråden.

4. *Näringssökintensiteten och förekomsten av aggressiva beteenden*

Inledningsvis (avsnitt A) framhålles, att det må antagas, att näringssökintensiteten approximativt avspeglar födotillgången, så att mycket intensivt näringssök indikerar födoknapphet. Vidare har det i litteraturen hävdats, att aggressivitet, betingad av »konkurrens» om näringen, är en betydelsefull faktor i vinterns näringsförhållanden för ett antal fågelarter.

I avsnitt B diskuteras klassificeringen av olika aktivitetstyper. För föreliggande syfte ansågs det tillfyllest att endast skilja på kategorierna: näringssök, flykt, interspecifik aggressivitet, intraspecifik aggressivitet, sång och direkt sexuella beteenden, övriga aktivitetstyper. Data insamlades i form av standardobservationer.

Det erinras i avsnitt C om att man av fysikaliska grunder har rätt att vänta att en liten organism intar mer föda i procent av kroppsvikten än en större och att därför en mindre art kan förväntas uppvisa det mest intensiva näringssöket. Så har också visat sig vara fallet i flera utländska undersökningar och kunde här än en gång bekräftas (tab. 12). I denna tabell jämföres dels resultaten från vintrarna 1958/59 och 1959/60 i Öved, dels de siffror som publicerats av GIBB (1954 a). I något fall, t. ex. kungsfågeln, torde differenserna böra förklaras genom artens svårtillgänglighet för aktivitetsstudier. Vad beträffar entitan kan man möjligen gissa på en mindre hamstringsaktivitet i det brittiska undersökningsområdet. Mest påfallande är dock överensstämmelserna. Alla dessa data har sammanfattats i fig. 4.

De säsongmässiga förändringarna i näringssökintensiteten illustreras i fig. 5, som baserar sig på tab. 15—20. Här framgår en väntad intensitetstopp vid midvintertid. En särskild undersökning gick ut på att fastställa, om närvaron av bokollon påverkade näringssökintensiteten (tab. 14). Så visade sig vara fallet hos talgoxen, som tydligen hade lättare att tillfredsställa näringsbehovet i ett område med bokollon än i ett jämförbart område utan denna näringskälla. De genomresande svartmesarna dröjde i bokskogen, varför denna art fick en högre intensitetssiffra här än i ollonfri lövskog. Mot denna bakgrund kan det synas oväntat, att midvinterintensiteten hos talgoxe var ungefär densamma vid ollontillgång som utan (fig. 5). Detta torde bero på att näringsbehovet var stort på morgnarna efter de långa vinternätterna, så att intensiteten under alla omständigheter hölls hög. Entitans hamstringsvana kommer arten att få en långt utdragen period av intensivt näringssök.

De aggressiva beteendena skildras i avsnitt D. Direkta slagsmål var mycket sällsynta och registrerades endast åtta gånger: fyra mellan kungsfåglar vintertid och fyra mellan blåmesar i april. Oftare sågs diverse hotattityder. De säsongmässiga frekvensfluktuationerna framgår av tab. 15—20. Slutsatsen av undersökningarna blir, att inom det aktuella undersökningsområdet mesarna näppeligen förlorade resp. vann nämnvärda kvantiteter föda genom våld och hot. Inga märkbara skillnader mellan ollonvintrar och ollonfri vinter kunde fastställas.

5. *Säsongmässiga och annuella populationsfluktuationer i Öved*

Givetvis bedömdes det som primärt viktigt att undersöka populationsfluktuationerna inom undersökningsområdet. Detta skedde medelst enkla linjetaxeringar (avsnitt B), någon annan metod föreligger knappast för fågelpopulationer utanför häckningstiden. Det verkar sannolikt att denna enkla teknik är bättre lämpad för vinterinventeringar än för bestämningar av häckfågelpopulationer (jfr ENEMAR 1959).

I avsnitt C framlägges de nådda resultaten, som illustreras i fig. 6. Vad talgoxen beträffar var populationen under den ollonfria vintern endast ca 1/3 av den, som registrerades de båda ollonvintrarna. Siffrorna för dessa senare överensstämmer rätt väl inbördes. Materialet indikerar en första utvandring under sommaren, eftersom septemberpopulationen är långt mindre än vårpopulationen plus ungarna. Hösten 1959 skedde en oerhörd minskning i oktober, samtidigt med att talgoxesträck fastställdes vid Falsterbo fågelstation, och denna utvandring synes representera det »äkta sträcket». Möjligen indikeras också en tredje utvandring, nämligen i midvintern, och

det bör därvid ha varit frågan om den inflyttning till hus och samhällen, som regelmässigt sker vid bistrare väder.

Blåmesens fluktuationer löper nära parallellt med talgoxens. Entitan däremot uppvisar mycket stabilare siffror. Det förtjänar att nämnas, att bevis för återkomst till lokalen av talgoxe under våren erhölls samt att häckpopulationen av denna art efter den stora utvandringen 1959 hade sjunkit markant. Övriga arter synes inte tarva kommentarer.

6. *Annuella och regionala differenser i populationstätheten hos talgoxe, blåmes och entita*

I avsnitt A diskuteras avsaknaden av data rörande vinterfågelfaunan i Sverige och skildras organisationen av »Vinterfågelinventeringen», en samfälld undersökning, i vilken årligen hundratals fältornitologer medverkar. Vinterfågelinventeringens för- och nackdelar diskuteras något, även om en noggrannare utvärdering av siffermaterialets tillförlitlighet får anstå. För regionala jämförelser uppdelades södra och mellersta Sverige i fem distrikt, enligt vad som framgår av text å p. 82.

I avsnitt B redogöres för inventeringsresultaten, som sammanfattas i tab. 22—24. I tab. 21 lämnas dessutom en översikt över de olika distriktens skogliga egenskaper. För talgoxens del fastställdes i distrikt I en måttlig nedgång från 1958/59 till 1959/60 och en mycket stark ökning i populationstätheten, hela tiden mätt som antal fåglar observerade per 10 timmar fältarbete, från 1959/60 till 1960/61. Högsta tätheterna rapporterades därvid från bokskogsbiotoper i Skåne och Blekinge. Distrikt II avviker markant från denna bild. Här skedde en svag ökning (sannolikt att bedöma som status quo) i första fallet och en avsevärd nedgång i andra fallet. I distrikt III är de annuella fluktuationerna relativt odeciderade. För distrikt IV fastställdes ökning i första fallet och status quo i andra fallet. Det stora och heterogena distrikt V har inte lämnat ett acceptabelt material.

Den väsentliga skiljelinjen går mellan distrikt I (Skåne, Halland och Blekinge) å ena sidan och de övriga distrikten å den andra. Minskningen inom distrikt I mellan de båda första vintrarna saknar motsvarighet och likaså ökningen mellan de båda senare. Totalantalet inräknade talgoxar uppgår till 9.000—14.000 ex. per säsong.

Blåmesen visar i distrikt I en utveckling, som löper parallellt med talgoxens, och den huvudsakliga skillnaden är, att ökningen, som noterades 1960/61, var av ännu oerhördare omfattning (över 200 %). De högsta täthetsvärdena erhölls i bokskogsytor. Övriga distrikt skiljer sig markant från distrikt I, liksom hos talgoxen. Detaljerna framgår av tabellerna. Totalt har mellan 1.800 och 3.500 blåmesar årligen inräknats.

Entitan visar en nästan otrolig stabilitet i distrikt I, och även totalvärdet för hela landet är mycket likartat vid de tre tillfällena. De nordligare distrikten, där entitan uppnår relativt låga värden, visar fluktuationer, vars signifikans dock nedsättes av de små siffrorna. Entitans stabilitet i distrikt I är ett viktigt stöd för realiteten bakom talgoxens och blåmesens fluktuationer: ifall de senare betingas av t. ex. ändrat »biotopval» hos medarbetarna i Vinterfågelinventeringen, borde också entitan, som förekommer i samma biotoper som de båda andra arterna, ha uppvisat fluktuationer i samma riktning.

7. *Höstflyttningsrörelser hos mesar i södra Sverige, speciellt vid Falsterbo*

Efter en kort översikt över det vid de svenska fågelstationerna insamlade materialet tages detta i avsnitt B upp till kritisk bedömning. Metoderna vid Falsterbo såväl som vid Ottenby har bestått i observationer av dagsträcket från en vald punkt samt ringmärkning av rastande exemplar. Observationstekniken lider av den svagheten, vad beträffar känsligheten för annuella fluktuationer, att en mindre temporär och lokal sträckvägsomläggning kan leda till en falsk bild av fluktuationerna. Ringmärkningsverksamheten är mindre påverkad av denna felkälla. Här är det i stället ändringar i utrustning, personal etc. som kan orsaka svårutredda felmöjligheter. Sammanfattningsvis kan man påstå, att om båda metoderna visar på stark rörelse i bestånden, är detta säkerligen riktigt, och om båda visar på ringa rörelse, är detta sannolikt också korrekt. Svårt blir det när skiljaktiga indikationer föreligger. Det synes motiverat att tillmäta en hög ringmärkningssiffra stor beviskraft, även om få fåglar noterats på sträck. Hög sträcksiffra korresponderande med låg ringmärkningssiffra är en svårtolkad situation, som får upptagas till skärskådan i varje enskilt fall.

I avsnitt C framlägges materialet rörande mesarnas flyttningsuppträdande vid Falsterbo fågelstation. Årssummorna för sträckande resp. ringmärkta fåglar återfinnes i tab. 25—26. Entita, tofsmes och talltita (*Parus montanus*) saknas så gott som fullständigt. Stjärtmesen (*Aegithalos caudatus*) och svartmesen förekommer vissa år, den senare ibland i mycket stort antal. Talgoxen och blåmesen förekommer praktiskt taget varje år men i starkt växlande myckenheter och inbördes dominans. Dessa bägge senare är överlag synkrona, även om överensstämmelsen ej är alldeles komplett, medan de inte är synkrona med vare sig stjärt- eller svartmes och dessa senare ej heller inbördes. För talgoxens och blåmesens del är beläggen otvetydiga utom åren 1955 och 1956. I olika sammanhang kan emellertid indicier anföras, som visar, att rörelsernas omfattning sannolikt blev underskattade det förra och överskattade det senare året.

Såsom framgår av tab. 27—31 är sträckperioderna underkastade starka annuella variationer, dock ej av exceptionell omfattning utom möjligen hos svartmesen. Stjärtmesen synes i allmänhet vara på färde senast, svartmesen tidigast, medan talgoxe och blåmes intar mellanställningar.

I tab. 32—34 har de sträckande mesarnas koncentration till säsongens en, två och tre bästa dagar beräknats. I genomsnitt kommer 60 % av hela säsongens talgoxsumma på en dag, de två bästa dagarna svarar för 78 % och de tre bästa för 87,5 %. Motsvarande siffror är för blåmesen 43 %, 64 % och 77 % samt för svartmesen 33 %, 52 % och 67 %. Dessa siffror bör jämföras med dem i tab. 35, där motsvarande data lämnas för en serie andra tättingar. Endast rödvingetrasten (*Turdus iliacus*) av alla de valda arterna kommer upp i så höga värden som mesarna, och detta är ju som bekant övervägande en nattflyttare. Slutsatsen blir, att mesarna, och särskilt talgoxen, ställer särdeles svåruppfyllbara krav på omvärlden för att dagsträck över havet skall realiseras.

Efter en skildring av mesflyttningens förlopp i naturen, vari särskilt påpekas deras extrema beroende av ledlinjer och -punkter, följer en översikt över mesarnas sträckförhållanden vid Ottenby fågelstation (tab. 36—37). Likheterna med Falsterbo är betydande, men många intressanta skillnader kan också fastställas. Två av de tre

svartmesflyttningar som noterats vid Falsterbo registrerades vid Ottenby, och samma var fallet med stjärtmesen, för vilken art Ottenby dessutom hade en säsong med rörelse som saknar motsvarighet i Falsterbo. För talgoxen är siffrorna rätt jämna med antydan till toppar särskilt 1948 och 1949 men möjligen också 1956, 1957 och 1959. Det synes knappast vara frågan om massträck, utom möjligen 1949, utan de utsträckande fåglarnas rekryteringsområde kan mycket väl ha varit inskränkt till Öland. Samma är i stort sett förhållandet hos blåmesen, där toppar nåddes 1949, 1952 och 1959 samt i mindre mån 1948, 1955 och 1957. Även hos blåmesen synes 1949 ha varit det mest markanta vandringsåret vid Ottenby.

I avsnitt E framlägges en del data angående nattsträck hos mesar. Materialet består huvudsakligen av rapporter angående fyrfallna fåglar. Mycket få mesar har fallit, vilket antyder, att nattsträck icke är en vanlig företeelse hos dessa arter.

Återfynd av ringmärkta mesar är än så länge fåtaliga vad beträffar våra fågelstationers resultat (avsnitt F). De få som finns har sammanställts i tab. 38. Åtskilliga exemplar har av allt att döma vänt tillbaka efter ett eller flera sträckförsök, havet har alltså för dem varit en oöverkomlig barriär (jfr ENEMAR 1957 a). En talgoxe märkt vid Ottenby återfanns på Själland. Det är ett intressant sammanträffande att detta skedde just 1949 (jfr ovan).

De av Göteborgs Naturhistoriska Museum och Naturhistoriska Riksmuseet i Stockholm rapporterade återfynden har sammanfattats och diskuterats av RENDAHL (1959), till vars arbete hänvisas för alla detaljer. RENDAHL inkluderade också norskt och finskt material i sin studie. I Sverige förflyttar sig 15,7 % av talgoxårsungarna mer än 10 km från födelseplatsen, medan äldre fåglar av allt att döma är nästan fullkomligt stationära. Återfynden från år, då vandringsrörelser fastställts vid Falsterbo fågelstation, ligger i genomsnitt dubbelt så långt från märkplatsen som andra år. Till skillnad från RENDAHL kan förf. inte finna några tecken som tyder på att nordsvenska talgoxar i genomsnitt företar längre resor än de sydsvenska populationerna. De norska och finska talgoxårsungarna visar ungefär samma proportion kvarstannare contra flyttare som de svenska.

Blåmesen visar i RENDAHLS material större rörlighet. Icke mindre än 34,6 % av årsungarna flyttar mera än 10 km från märkplatsen. En märklig tendens till NW-riktat sträck låter sig fastställa.

Övriga mesarter har lämnat få eller inga återfynd, och de som finns belägger deras extrema fasthållande vid födelseorten. Några fjärrfynd av svartmes föreligger dock.

I avsnitt G ges en kort översikt över vandringsrörelser hos talgoxe och blåmes i NW Europa utanför Sverige. I detta sammanhang är en uppsats av CRAMP, PETTET & SHARROCK (1960) särskilt värdefull. I Storbritannien har ankomst av talgoxe och blåmes från kontinenten fastställts 1949, 1954 (i ringa skala) samt 1957. Dessutom har brevledes och på andra sätt erhållits uppgifter om en betydande mesvandring 1959. Vandringsrörelsen 1957 stod i centrum för de nämnda författarnas studie. Återfynd av ringmärkta fåglar erhölls så långt bort som i Litauiska Sovjetrepubliken, men inga tecken tydde på att populationer från Mellan- och Nordsverige var inblandade. Ett möjligen separat system av flyttande mesar har konstaterats i Schweiz. Dessa mesars vinterkvarter utgöres av franska medelhavskusten.

8. *Den ekologiska bakgrunden till de sydsvenska talgoxarnas och blåmesarnas flyttningsrörelser*

Grundläggande för bedömningen av flyttningsrörelsernas ekologiska bakgrund är kännedom om näringsvarorna. Det viktigaste rönet från denna del av ifrågavarande undersökning var, att talgoxen och entitan samt — ehuru i mindre utsträckning — blåmesen intensivt exploaterade bokollonskörden, när sådan förelåg. Entitan hamstrade dessutom stora mängder bokollon. Vid frånvaro av bokollon fortsatte entitan att leva på huvudsakligen vegetabilisk kost, medan områdets talgoxar och blåmesar i stor utsträckning var hänvisade till animalisk föda. Bokskogarna hyste mycket större talgox- och blåmespopulationer, när ollonen var talrika, än annars. Detta kunde påvisas i förf:s egna områden och kunde dessutom utsträckas till att gälla det svenska bokskogsdistriktet överlag tack vare Vinterfågelinventeringen. Entitan visade ej motsvarande fluktuationer.

Vidare har det kunnat visas, att talgoxens och blåmesens flyttningsrörelser i allmänhet är synkrona, medan de saknar synkronitet med övriga mesars rörelser.

Hos många arter har man funnit, att stora annuella fluktuationer i flyttningens förlopp i rum och tid betingas av motsvarande fluktuationer i någon näringsfaktor (översikt hos SCHÜZ 1952). Om någon sådan faktor skall kunna tänkas ligga bakom fluktuationerna hos talgoxe och blåmes, måste det enligt de resultat, som nåtts i denna studie, vara bokollonen. De annuella variationerna i bokollonskörden illustreras av fig. 7. Det är påfallande att 1949, 1955, 1957 och 1959 utmärktes av särskilt dålig, nästan helt utebliven skörd. Av dessa är 1949 samt 1957 och 1959 påvisade som exceptionellt starka flyttningssäsonger, medan det framlagts indicier på att 1955 års vandring av olika skäl blev underskattad vid Falsterbo fågelstation. Å andra sidan saknades flyttande talgoxar och blåmesar så gott som fullständigt 1952, 1954, 1958 och 1960, då skörden var mer eller mindre god. Det rätt låga skördeindexet för 1958 betingas av de nordligare och mindre omfattande svenska bokskogsdistrikten, medan i de skånska bokskogarna, som kvantitativt dominerar, skörden var mycket god.

De data, som framlagts i kap. 5 C och 6 B, visar emellertid, att icke endast bokskogarnas mespopulationer är inbegripna. Under bokollonår ökas vinterpopulationen genom tillströmning norrifrån, dessutom säkerligen genom minskad utvandring av de lokala mesarna. Under ollonfria år tömmes skogarna däremot på mesar i stor utsträckning: dels synes de norrifrån kommande mesarna inte slå sig ned, dels utvandrar lokalpopulationerna. Följaktligen kan ollonskörden i och för sig inte göras ansvarig för utlösningen av vandringsrörelserna.

Dessbättre finns en ypperlig studie av talgoxens populationsekologi från Holland (KLUIJVER 1951). Denna undersökning har invändningsfritt ådagalagt sambandet mellan ökande populationstäthet och ökande vandringstendens. Följaktligen har vi rätt att förmoda, att även i Sverige startas vandringsrörelserna som ett svar på ökad populationstäthet. Vandringarnas förlopp i tid och rum blir däremot beroende av näringssituationen under vägen (jfr SVÄRDSON 1957). Om en rik bokollonskörd föreligger i bokskogsdistrikten, fångas de vandrande mesarna i stor omfattning upp här, men om sådan skörd ej finnes, vandrar de vidare och registreras då vid Falsterbo

fågelstation på utsträck. Variationer på temat kan givetvis förekomma. Talgoxsträcket 1956 kom sent och passerade mycket hastigt, samtidigt som det fanns en tämligen rik ollonskörd. Möjligen har tillströmningen till bokskogarna blivit så stor, att i sent skede mättnadspunkten överskridits, vilket resulterat i en abrupt vandringsrörelse.

Talgoxens och blåmesens vandringsrörelser synes således följa ett komplext mönster. De är utan tvivel i n v a s i o n s a r t a d e (för diskussion av invasionsbegreppet se bl. a. RUDEBECK 1950, SCHÜZ 1952, LACK 1954 och SVÄRDSON 1957). Härmed bör förstås, att deras förlopp är underkastat näringssituationernas variationer i tid och rum på ett mera direkt sätt än vad som är fallet med icke-invasionsartade flyttningar. Hos somliga arter gör sig detta födans inflytande på sträcket märkbart ända från starten i häckningsområdet, medan hos andra arter sträcket till en början synes löpa årsvisst och regelbundet och först på ett senare stadium bli avhängigt av någon näringsfaktor. Det sistnämnda synes vara fallet hos talgoxe och blåmes, då bokollon inte spelar någon avgörande roll vid starten av flyttningen utan endast för det senare förloppet.

Talgoxen och blåmesen avviker från de flesta »klassiska» invasionsarterna genom att endast en ringa del av populationen deltar i flyttningarna. De är alltså p a r t i e l l a f l y t t f å g l a r, m. a. o. populationen är polymorf med avseende på flyttningsvanorna. I många fall anses starkt varierande klimatiska faktorer vara den selektiva bakgrunden för bibehållande av polymorfismen i flyttningsvanorna, men så synes knappast vara fallet hos de studerade arterna. Snarast synes populationernas tendens till produktionsöverskott vara den betingande faktorn, i kombination med näringsbrist. Särskilt hos socialt underlägsna exemplar torde utvandring till andra lokaler erbjuda något ökad möjlighet att överleva vid allt för stor populationstäthet. Möjligen kan en bristande kongruens mellan lokala mortalitetsfaktorer och reproduktionspotentialen vara en förklaringsgrund värd att pröva även för mera »typiska invasionsfåglar».

Flyttningsvanornas polymorfa fördelning i populationen, invasionstendenserna och — givetvis — den fysiologiska motståndskraften mot låga temperaturer jämte förmågan att effektivt exploatera varierande näringskällor synes i kombination erbjuda underlaget för den flexibilitet, som uppenbarligen är en ytterst värdefull egenskap hos fåglar, som övervintrar i tempererade regioner karakteriserade av kraftiga annuella fluktuationer med avseende på både klimatet och näringstillgången.

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