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MORTALITY AND DISPERSAL IN SUMMER AND ITS CONSEQUENCES FOR THE DENSITY OF GREAT TITS *PARUS MAJOR* AT THE ONSET OF AUTUMN

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1. INTRODUCTION

1.1. THE PROBLEM

Many studies on the ecology of bird populations have been centered on the problem of the density dependence of the key parameters of population dynamics: survival, dispersal and reproduction. Agonistic behaviour (manifested in rank order and/or territory occupancy) has often been considered to influence dispersal, breeding density and even population size (Kalela 1954, Wynne Edwards 1962, Lack 1966, Fretwell *et al.* 1970, Brown 1969, Klomp 1972). However, the way in which population fluctuations in one habitat and the characteristic level come about is usually not clarified (Brown 1969, Davies 1978a, Klomp 1972, Watson & Moss 1970). In many of the reviews on this subject the Great Tit *Parus major* L. is presented as an example, because the species has been studied extensively.

Several authors (Van Balen 1973, Dhondt 1971, Kluyver 1971) have shown that the levels of breeding density are characteristic for the type of habitat while in each habitat the breeding density fluctuates from year to year. The density level in oakwoods is several times the level in pinewoods, while the level for mixed forests is between the two. The year to year fluctuations in breeding density are fairly well synchronized over large geographical areas in north-western Europe (Perrins 1965, Lack 1966, Berndt & Hensz 1967). Peaks are found after winters with a high beechmast crop while lows are found after years without a beechmast crop (Van Balen 1980, Drent 1983, Perrins 1966). The extent of additional feeding by humans during winter also appeared to affect in a positive way the size of the breeding populations (Van Balen 1980, Dhondt 1971, Drent 1983, Von Haartman 1971, 1973). In the past Kluyver and Lack have presented deviating views on the way in which, particularly the characteristic level of the fluctuations had evolved. Both authors agree that the critical factor causing these characteristic levels is the local-survival of juveniles outside the breeding season. Kluyver (1951, 1953, 1956, 1971) stated that the number of young Great Tits in particular would mainly be affected by the density of adults and juveniles in summer, causing varying proportions of young to disperse, mainly in September, because of intraspecific strife as a result of territory-occupancy. In contrast Lack's (1954, 1958, 1964, 1966) hypothesis was that the number of Great Tits would depend mainly on mortality due to starvation (shortage of food) particularly within one month after fledging. Territorial behaviour then operates only as a local spacing-out mechanism after the density-dependent mortality has occurred. In the international debate bordering on this controversy (see the review by Chitty 1967), dispersal in the post-fledging period as shown by Dhondt (1979) and Goodbody (1952) was overlooked as a factor influencing local density. The central issues, therefore, are to decide how and when mortality and dispersal come about and how agonistic behaviour affects these parameters.

In an effort to help to close the gaps so clearly underlined by Chitty (1967) a study of the key parameters of population dynamics in the Great Tit was undertaken in 1968 at the instigation of H. N. Kluyver, H. Wolda and G. P. Baerends. In this study special attention was paid to agonistic behaviour (manifested in rank order and territory occupancy) and dispersal and the significance of these for the individual birds and the population as a whole in a proximate way.

In another paper (Drent 1983) I have analysed the territorial behaviour of the Great Tit and its consequences for breeding density. In line with Kluyver's suggestion, territorial behaviour in autumn (but also in winter and spring) sets a limit to the density of territories. The males that are unsuccessful in acquiring a territory in autumn sometimes manege to fill a vacancy that occurs later, but the majority either die or emigrate (Drent 1983). The upper limit is influenced by the density of both the adult and the juvenile males (candidates) present in the area of study. Differences in the density of autumn territories between years, and between habitats can be explained as resulting from the number of adult and juvenile males interacting at that time.

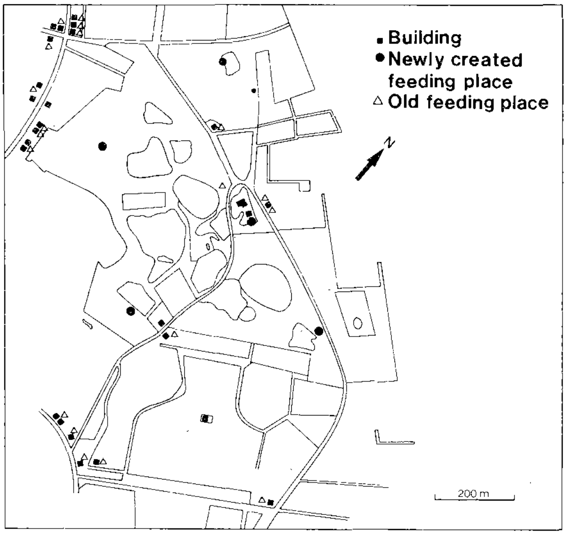

Fig. 1. Map of the Vosbergen Estate.

It is the aim of the present paper to detect mechanisms that are important in determining density for both adults and juveniles at the onset of autumn (1 September).

2. AREAS AND METHODS

2.1. AREAS OF STUDY

The study was conducted between 1968—1971 in a mixed wood (37 ha) on the estate Vosbergen near Groningen (Fig. 1). Part of the wood (indicated in the tables and figures by V.E.) is divided into forest plots separated by avenues of tall trees, and part is open woodland. Each forest plot is dominated by one or two tree species, particularly *Betula* sp., *Fagus sylvatica*, *Larix* sp., *Pinus sylvestris*, *Quercus robur*, and *Quercus rubra*. The open woodland contains small groups, rows and avenues of tall trees of the same species distributed between agricultural land, lawns and buildings. Most of the forest plots are smaller than 1 hectare (mean ± 0.5 ha). The numerous avenues of tall trees consist of oaks with some beeches. The nest boxes are so distributed over the area that 92 per cent of them are within 25 m of oaks. There were only a few nestboxes present prior to 1968 (Table 3). After the 1968 breeding season a large surplus of nestboxes were distributed, regularly over all the wooded areas on and around the estate. Throughout the year and particularly in winter artificial feeding stations were present near farms, houses and buildings in and around the wood. Every point in the study area was not more than 175 m away from a feeding station. In years with a good beechmast crop each point was not more than 100 m away from a seed-bearing beech tree. On the west the wood borders on a village with many gardens and a park, with only a few oaks. On the other sides the wood is adjacent to other woods, a few of which are rich in oaks, and agricultural land with avenues, hedgerows and farmhouses with gardens, containing few oaks.

During the breeding-season of 1970 additional standard observations were carried out on an adjacent area of 23 ha (called Park), consisting of a park of about 10 ha and adjacent gardens. The most common tree species here are *Pinus sylvestris* and several exotic species. Only 5 per cent of this area was covered with oaks and beeches, isolated old trees or small groups of young trees scattered over the area.

From 1975 onwards the study was continued on a 75 ha section of the area of study by the population ecology research group of the Institute for Ecological Research, in the National Park De Hoge Veluwe near Arnhem (Fig. 2, see also Van Balen 1980), here indicated as Hoge Veluwe

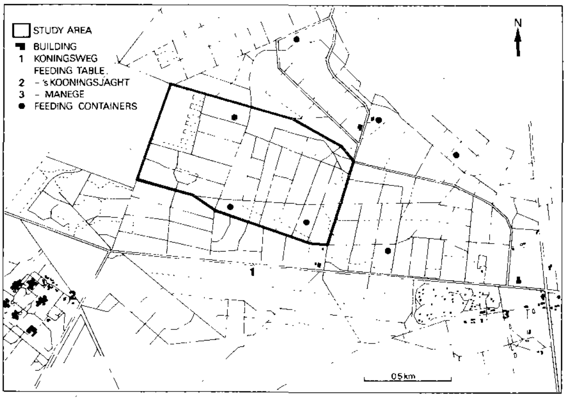

Fig. 2. Map of the Hoge Veluwe area.

(H.V. in the tables and figures). The area is covered by a mosaic of plots of coniferous and deciduous forest. From previous experiences it could be concluded that this is a relatively poor habitat for Great Tits. Each plot covers about 1 ha, and is dominated by one occasionally two tree species. The most common tree species are *Pinus sylvestris*, *Larix* sp., *Pseudotsuga menziesii*, *Quercus robur*, *Quercus rubra*, *Betula* sp., and *Fagus sylvatica*. Compared with the Vosbergen Estate the proportion of oaks and beeches is smaller while that of pines and birches is larger (Table 1). Moreover, most of the oaks on the Hoge Veluwe are smaller and less well developed than those at Vosbergen. In contrast to the Vosbergen Estate the oaks are concentrated in large plots. Thus 33 per cent of the nestboxes did not have oaks within a 50 m distance. There are also a smal number of large beeches scattered over the area. In the direct surroundings of the study area beech trees are more numerous, but these are distributed unevenly in groups and rows (see Van Balen 1980: Fig. 5). In the years with a good beechmast crop each spot in the area was not more than 600 m from a seedbearing beech. In the 1974/1975 and 1975/1976 seasons, seed food (sunflower and hemp seeds) was provided at two spots, one container per spot. Other artificial feeding sites were present in the adjacent forest on the north and east and near buildings on the north, the south-east and south-west side of the area of study. These feeding sites were present from 1967 onwards. Every point of the area of study was within 600 m of an artificial feeding site. In April 1976 the seed containers were removed, this meant that the nearest source of artificial food (near houses) was 150—3000 m away. Since 1959 a surplus of nestboxes has been present, regularly distributed over the area of study. The area of study borders on the west on heathland, the south on woodland without nestboxes and a limited number of natural holes (see Van Balen *et al.* 1982), and on the remaining sides by woodland with a surplus of nestboxes. The structure and composition of the surrounding woodland is similar.

2.2. METHODS

On Vosbergen Estate and the Hoge Veluwe the (territorial) behaviour and its effects on survival and dispersal are being studied within the context of a study of the population ecology of the species.

For the behavioural study it is necessary that the individuals can be recognized, and their presence, status, the characteristics of the territories, reproductive success and the causes of disappearance (emigration, death) are assessed. In order to obtain this information standard observations and measurements were carried out very frequently throughout the year. Capture-recapture campaigns with mistnets were carried out at least twice a week. From October to March the nestboxes were inspected for roosting birds twice a month. Between April and July nestbox inspections were carried out weekly to assess the reproductive parameters. All Great Tits and their young were ringed with a numbered aluminium ring. Each full-grown Great Tit was aged and sexed (see Dhondt 1970). Additionally, they were provided with an individual code of colour-rings. The nestlings received a code of colour-rings characteristic for their brood. When they were recaught after fledging the brood-code was replaced by an individual code of colour rings.

Table 1. The composition of the forest in percentage surface covered by different tree-species. Vosbergen Estate (V.E.): 37 ha, Hoge Veluwe (H.V.): 75 ha

	V.E.	H.V.
Broad-leaved trees		
Oaks	39.9	18.1
Beeches	10.2	0.4
Other species	9.8	23.6
Coniferous trees		
Larches	5.4	10.5
Pinus spec.	16.1	34.3
Other species	18.6	13.1

On the 15th day of life the young were weighed and sexed (see Dhondt 1970). It is not possible to sex Great Tits reliably till after the post-juvenile moult in late summer. Recoveries after the post-juvenile moult showed that between 10—20 per cent of the young were incorrectly sexed in the nest. To eliminate these errors a correction was made for each sexe separately. For this correction a parameter for recovery rate per sexe was introduced, assuming that this parameter was independent of correctness of sexing in the nest.

Field observations on the presence and the behaviour of individual birds were carried out during routine walks that covered the whole area of study. These walks were held throughout the year, but most frequently between 1 September and 1 May. Consequently there is accurate knowledge of the presence of individual birds in the area of study, particularly from 1 September onwards, usually with an error of less than half a month. During these walks territories were mapped by plotting on a map the observed border disputes and the responses to models and playback of recorded song. Information on the fate of individuals that had disappeared was obtained by frequent searches for remains of Great Tits. Particular attention was paid to feathers left by predators, raptor pellets and fox droppings.

In a strip of up to 500 m around the area of study efforts were occasionally made to detect emigrants. In winter regular captures and observations of marked individuals were carried out at feeding stations in the surrounding of the area of study. Moreover, where possible, roosting and breeding birds were captured in nestboxes. Shortly before the start of the breeding season a search was made in the surrounding 200—300 m, for the territory owners originating from the area of study. These observations were more accurate for males than for females. Recoveries from outside the area of observation revealed the fate of a few emigrants. In spite of great efforts to trace all emigrants, the actual number will be higher. Firstly, because most of the observations occurred within a restricted area while from the few recoveries outside this area, it is clear that a number of individuals, particularly nonterritorial birds, ranged over a much larger area than that covered by the study. Secondly, using our methods there is often an interval of several months between the date of departure from the study area and the first opportunity to detect emigration. So a number of emigrants could have died or dispersed further before detection. Thirdly, emigrants with non-territorial status could easily be overlooked.

Methods specific for the problem studied will described under the appropriate heading.

3. BREEDING DENSITY

At the start of the breeding season the mean density of males was higher on the Vosbergen Estate than on the Hoge Veluwe (Table 2). They corresponded with the levels for the same type of habitats (Van Balen 1973, Dhondt 1971, Kluyver 1971).

In most years a number of males (pairs) did not possess a territory in the area of study (Dhondt *et al.* 1983, Drent 1978, Eyckerman 1974). These males (guest males) were either non-territorial or possessed a territory at some distance from the area of study. They behave inconspicuously and are tolerated on the territories by the host males. The hosts, selected by the guest pairs, start breeding relatively early in the season. The guest pairs lagged behind more than a week (Drent 1978, Dhondt *et al.* 1983, Eyckerman 1974) which probably increases their chances of being accepted in the host territories.

The annual density of territorial and guest males in both areas, greatly differed from year to year. The highest densities of territorial males were found after winters with a rich beechmast crop, intermediate densities after winters with an artificial supply of seed food, while the lowest densities were found after winters without one of these seed sources. (Table 2: for H.V.: $\chi^2 = 33.7050$, d.f. 2, $P < 0.0005$.) After winters with a seed food stock the breeding densities were higher on the Vosbergen Estate than on the Hoge Veluwe (Table 2). More guest males were present after winters with a rich beechmast crop than in other years, being a higher proportion of the total number of males present (Table 2: H.V. data: $\chi^2 = 11.1406$, d.f. 1, $P < 0.001$). On the Hoge Veluwe this difference could have been higher, because in the years after a rich beechmast crop several late-immigrating potential guest pairs (minimum 0.8 and 0.5 per 10 ha in 1975 and in 1977, respectively), were unable to find a vacant nestbox in the strips of wood just inside the area of study, and hence emigrated again within a day or two. The large majority of the guest males and females were first year birds (over all years: n = 102, 84 per cent). All non-territorial guest males (n = 28) were in their first year.

In many years a varying number of males remained unmated (Table 2), whereas in one year (H.V. 1976) there were two bigamous females. The unmated males did not in any way attempt to reproduce whereas the two bigamous females reproduce successfully without much help from the local territorial male. Females choose their

Table 2. Density (number/10 ha) of different categories of males in 1968—1971 (Vosbergen Estate) and 1974—1979 (Hoge Veluwe) B: rich beechmast crop in winter; F: seed-food supply (in containers) from September to April

Year	Feeding conditions in preceding winters		Density of			% guest males	Density of		% unmated males
			all males	territorial males	guest males		mated males	unmated males	
1968	—	F	11.1	11.1	0	0	10.8	0.3	2
1969	—	F	10.8	10.5	0.3	3	10.3	0.5	5
1970	—	F	12.2	11.6	0.5	4	11.9	0.3	2
1971	B	F	16.4	13.8	2.7	16	14.3	2.2	13
1974	—	F	6.3	6.0	0.3[1]	4[1]	6.3	?	?
1975	B	F	11.1	8.5	2.5	23	10.1	0.9	8
1976	—	F	6.5	6.1	0.4	6	6.5	0.0	0
1977	B	—	10.9	9.1	1.9	17	10.8	0.1	1
1978	—	—	5.3	4.8	0.5	10	5.1	0.3	5
1979	—	—	4.0	3.7	0.3	7	4.0	0.0	0

[1] The data were calculated from nest-box inspections, captures and observations after the breeding season.

males with a strong preference for territorial males. On average only 3.1 per cent of the territorial males, in contrast to 21.1 per cent of the guest males, remained unmated during the breeding season; this difference is significant (Fisher test: To = 5.3575, Pd(To) < 0.0001). Since all guest males with a known territory outside the study area were paired, the proportion of unmated males among the non-territorial guest males is particularly high.

As has been mentioned on the Vosbergen Estate the number of nestboxes was greatly increased after the 1968 breeding season. this increase was not followed by an increase in the number of territorial males (Table 2) or in the number of breeding pairs (Table 3). The proportion of pairs with a known nest-site did not change (Table 3). However, after a surplus of nestboxes was provided the proportion of pairs which nested in nestboxes increased markedly. Thus in contrast to some other studies (see Van Balen *et al.* 1982) the number of nest-sites in this mature, relatively unmanaged wood did not limit the density of breeding pairs.

4. REPRODUCTION

4.1. DENSITY OF FLEDGLINGS

In both areas of study all pairs, irrespective of their territorial status, made a reproductive attempt. Unlike the results obtained by Eyckerman (1974) and Dhondt *et al.* (1983) territorial and guest pairs did not differ in the mean number of first brood fledglings per pair in any of the years (Drent 1978). The difference in result between the studies is not surprising because as the inter-nestbox distance in this study was greater than the critical inter-nest distance which is 30 m (Dhondt *et al.* 1983).

The exact number of fledglings of pairs nesting in sites other than nestboxes is unknown. In order to calculate the total density of fledglings, it was assumed that the number of fledglings per pair was the same for both categories of pairs. This probably means that it is an overestimate of the real fledgling density, as the nesting success in natural nestsites is lower than in nestboxes (Van Balen *et al.* 1978). On the Hoge Veluwe in contrast to the Vosbergen Estate only very few pairs (at most 1 per cent) built nests outside the boxes.

On the Vosbergen Estate more young were fledged per unit of area than on the Hoge Veluwe. This also applied when production figures are compared at the same density (Fig. 3). This difference is mainly caused by a difference in the loss between laying and fledging (V.E. 15—25 per cent, H.V. 38—67 per cent of the eggs). This difference in nesting success between the two areas was in accordance with the data from the literature for these types of habitats (*e.g.* Van Balen 1973, Dhondt 1970). There was a great difference in the areas of study with regard to the loss of complete clutches, due to desiccation because of defective egg shells, and starvation of young.

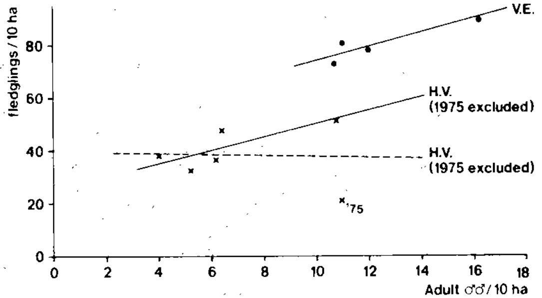

Fig. 3. The relation between the density of adult males and the density of fledglings in two areas: dots: Vosbergen Estate (1968—1971); crosses: Hoge Veluwe (1974—1979). Fledglings = first and second broods. V.E. $r = +0.9256$ $0.10 > P > 0.05$; H.V., 1975 excluded, $r = +0.7615$, $P > 0.05$; 1975 included, $r = -0.0797$, $P > 0.05$.

Table 3. The distribution of first brood breeding attempts over nestboxes and other sites on the Vosbergen Estate. Other sites: tree holes, holes in buildings, etc.

Year	No. of boxes	No. of breeding pairs	Percentage in		
			nestboxes	other sites	unknown
1968	15	40	28	65	8
1969	200	38	82	16	3
1970	200	44	89	5	7
1971	200	53	91	2	8

On the Hoge Veluwe study the 1975 breeding season was exceptional, extremely high losses were recorded for all stages of the reproductive cycle, 38 per cent of the breeding pairs failed to produce at least one fledgling (in other years less than 15 per cent) and 54 per cent of the nestlings died, probably from starvation, compared to less than 30 per cent in other years. This exceptionally low reproductive success in 1975 was associated with a prolonged period of very wet and cold weather before and during the first part of the breeding season.

Several authors (*e.g.* Van Balen 1973, Dhondt 1970, Kluyver 1951, Lack 1966, Perrins 1965) have shown the existence of negative density dependent effects of density of breeding birds on the number of fledglings per pair. Dhondt (1970) nevertheless showed that for different habitas, within the observed range of breeding densities, the number of fledglings per unit of area increased with density. In his study on the Hoge Veluwe Van Balen (pers. comm.) found a similar phenomenon. Our study also showed that, considering 1975 on the Hoge Veluwe exceptional, the number of fledglings per unit area tended to increase with the density of males (Fig. 3), but the regression coefficients were not significant.

4.2. SEX-RATIO OF FLEDGLINGS

Since only males occupy a territory the number of fledged young males will be particularly important for a study on the relationship between territorial behaviour and population dynamics. It is often assumed that the sex-ratio at hatching is about 1 : 1. Dhondt (1970) found that the sex-ratio on the 15th day after hatching deviated from the 1 : 1 ratio in favour of the males when mortality in the nest was high. In the present study some suggestion of this phenomenon was only found in 1975 on the Hoge Veluwe. The sex-ratio (males/females) in that year tended to be higher in first broods with a high nestling mortality than in first broods with a low mortality (1.1 *v.* 0.9, $\chi^2 = 2.832$, $0.10 > P > 0.05$). Dhondt (1970) found that the mortality in the nest increased with the density of the breeding pairs. These results indicate that the sex-ratio of the fledglings changes in favour of males as the breeding density increases. In both areas of study, however, a tendency towards the opposite effect was found. Combining the data of both areas the sex-ratio of the fledglings decreased as the density of the adult males increased, thus in favour of females (Fig. 4). A similar decrease in the sex-ratio with density in favour of males was found when only the fledglings of brood with no nestling mortality were used ($r = -0.8703$, $P < 0.05$). In view of this result Dhondt's data (Dhondt 1970, Tables 3.3 and 3.27) were re-analysed. The analysis shows that the proportion of males among the fledglings was not only positively correlated to the nestling mortality ($r = +0.5694$, v. = 19, $P > 0.01$) but also negatively correlated to the breeding density ($r = -0.4811$, v. = 19, $P < 0.05$). The multiple correlation coefficient between the proportion of males (dependent variable) and the density of breeding pairs and nestling mortality (independent variables) is significant ($r = 0.6471$, $P < 0.01$). The data could be interpreted as follows: firstly, when density increases the proportion of males among the hatched young decreases. Secondly, after hatching nestling mortality is differential in favour of males and thereby changes the sex-ratio. In oakwood the nestling mortality is positively correlated with density. This nestling mortality is differential in favour of males. Both effects of density on the sex-ratio counteract each other in determining the sex-ratio of the fledglings.

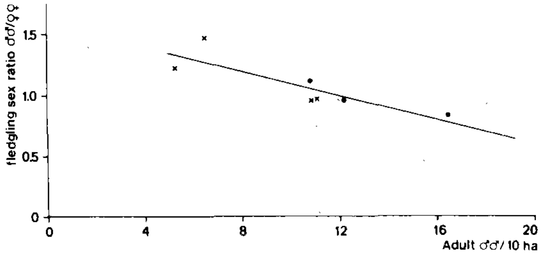

Fig. 4. The relationship between the density of adult males and the sex-ratio (♂♂/♀♀) among the fledglings. Dots: Vosbergen Estate (1969—1971); crosses: Hoge Veluwe (1975—1978). $r = -0.8582$, $P < 0.05$; Spearman rank correlation Ro = 108, P = 0.01.

The mean level of breeding density of the various habitats differ markedly; the habitats with the lowest mean density (those that are poor in oaks) usually have the highest proportion of eggs which do not result in fledglings usually be-

Table 4. The proportion of males among the fledglings in relation to: the tree species composition of the area, the mean breeding density (number/10 ha) and the nest mortality (egg and nestling losses, only nests with at least one fledgling were used)

Area	Tree species composition[2]				mean breeding density	mortality in the nest (%)	proportion of male fledgings (%)
	oaks	beeches	other brood leaves	conifers			
Citadel Park[1]			3		3.2	48.7	54.4
Hoge Veluwe	1		1	2	8.4	35.0	51.7
Hutsepot[1]		3	1	1	9.5	24.6	47.6
"C.O.O."[1]	1			3	11.0	31.7	50.1
Vosbergen Estate	2	1	1	1	13.1	20.1	47.3
Maalte Park[1]	2	1	1		14.7	31.3	46.9
Zevergem[1]	3	1			17.4	24.9	46.4

[1] Data from Dhondt 1970: his chapter 1—4 and Tables 3.3, 3.19 and 3.26.

[2] 1 = 5—25 per cent, 2 = 25—50 per cent and 3 = more than 50 per cent of the trees.

cause of nestling mortality (*c.f.* Van Balen 1973, Dhondt 1970). As a result of this one would expect the proportion of males among the fledglings to decrease as the level of density increases. Data in this aspect were available for 7 habitats: 5 from Dhondt's study (1970) and 2 from the present study (Table 4). The correlation between the proportion of males and the mean breeding density was negative and significant ($r = -0{,}9050$, $P < 0.01$) while between the proportion of males and nestling mortality was positive and also significant ($r = +0.8944$, $P < 0.01$). The multiple correlation coefficient between these dependent and two independent variables is also high ($r = 0.9576$, $P < 0.01$). The influence of both independent variables is significant (student's t-distribution one-tailed $tx_1 = 2.3725$, and $tx_2 = 2.1706$ both $P < 0.05$) and 92 per cent of the variation in the proportion of males in the different habitats can be ascribed to one of two factors namely the mean breeding density and the nestling mortality.

5. SUMMER SURVIVAL OF ADULTS

The local density of adult birds in early September was known accurately (Table 5). Almost all adult males (and females) were present in the breeding season and had territorial status. Only rarely were some guest birds or recent adult immigrants present. From these data the local survival rate between breeding time and 1 September could be calculated. The local survival of both sexes was high in both areas of study, and survival in males was slightly higher than in females in all years (Table 6). When the data of all years were combined, the difference was significant (V.E.: 70.6 *v* 56.2, $\chi^2 = 5.5542$, $P < 0.025$ and H.V.: 79.1 *v* 60.4, $\chi^2 = 24.5552$, $P < 0.001$). Most of the guest pairs emigrated from the area of study soon after their young were fledged or at the end of the breeding attempt (Drent 1978). Consequently their local survival rate was very low and differed greatly from that of the local territory owners, who seldom emigrated. Rarily a territory owner and his mate shifted his territory to adjacent areas of the forest. In contrast to territorial males, females which had lost their territorial mate, left the territory ground and sometimes the area of study in their search to another territorial mate. Consequently local survival is in males, and to a lesser extend in females a close approximation of real survival.

In each of the two areas the survival of territory owners did not differ between the years (♂♂ V.E.: $\chi^2 = 0.4295$, $P > 0.75$, and H.V.: $\chi^2 = 2.5384$, $P > 0.50$; ♀♀ V.E.: $\chi^2 = 0.5442$, $P > 0.75$, and H.V.: $\chi^2 = 5.1086$, $P > 0.25$). There was no indication of a negative correlation of adult survival with the density of adults, the density of juveniles and the average number of juveniles per pair when breeding ended. The combination of the almost total disappearance of the guest males and the low numbers of adult emigrants, means that any difference between the years in the density of territorial breeding birds influenced the comparable figures for September (*c.f.* Table 2, 5).

The survival of territorial birds on the Vosbergen Estate was slightly lower than on the Hoge Veluwe (Table 6: ♂♂: $\chi^2 = 24.4384$, $P < 0.001$, and ♀♀: $\chi^2 = 14.2285$, $P < 0.05$). This was because the effect of human activities in the former area was greater. The loss of adults occurred mainly directly after the nestling period, when the parents roamed with their brood. During this period predation by domestic cats and fatal accidents around buildings and on roads, caused the death of some adults. However, in spite of this difference between the areas in survival of territorial birds the total September density of all adult males and females and that of adult males who were territory owners at beginning of the breeding season still reflects the differences in breeding density between the areas. After winters with an artificial supply of seed only the density on September 1st was higher on the Vosbergen Estate (1968, 1969, 1970) than on the Hoge Veluwe (1974 and 1976, Table 5).

Van Balen (1980) found on the Hoge Veluwe a negative correlation between the number of breeding birds and their survival until the following breeding season. A tendency to a similar negative effect is apparent in the present data. In the two years during which the breeding density was high (1975 and 1977) the local survival was significantly lower than in other years ($\chi^2 = 4.5167$, $P < 0.05$) As has been shown in years when the breeding density is high the proportion of guest males is also relatively high (Table 2), but most of these males and their mates left the area after breeding which results in a very low local survival rate of this category (Table 6). Therefore the relationship between breeding density and subsequent survival of the territory owners was studied in detail. During the two years that the breeding density was high the local survival rate was not lower than that in the other years (Table 6: $\chi^2 = 0.2785$, $P > 0.05$). Hence the correlation between breeding density and subsequent local survival rate is caused mainly by the emigration of guest pairs, that are particularly abundant in years with a high density. Observations in the direct surroundings of the area of study showed that there is no evidence that these emigrants suffer a higher mortality than the territory owners in the area of study.

Table 5. The density (number/10 ha) of different categories of adults on 1 September in 1968—1970 (Vosbergen Estate) and 1974—1978 (Hoge Veluwe)

Year	Density of males with different status in breeding season				Density of females
	all	territorial	guest	immigrants after breeding	
1968	8.1	8.1	0	0	6.5
1969	7.8	7.8	0	0	5.4
1970	8.1	8.1	0	0	7.0
1974	5.3	5.2	0	0.1	3.9
1975	7.7	7.6	0.1	0	5.3
1976	5.9	5.7	0	0.1	4.1
1977	8.8	8.5	0.1	0.1	6.8
1978	4.4	4.3	0.1	0	1.6[1]

[1] In 1978 part of the females (1.7/10 ha) had left the area as winter migrants (Drent 1979).

Table 6. The local survival rate (%) of different categories of adult males and females between the breeding season and 1 September. Data from the Vosbergen Estate (1968—1970) and the Hoge Veluwe (1974—1978)

Year	Males			Females	
	all	territorial	guest	all	mates of territorial males
1968	73.2	73.2	—	57.5	57.5
1969	72.5	74.4	0	52.7	54.1
1970	66.7	69.8	0	59.1	61.9
1974	83.0	86.7	0	61.7	64.4
1975	69.9	89.1	5.3	52.6	71.0
1976	87.8	93.5	0	63.6	78.3
1977	79.3	94.1	7.1	63.0	79.1
1978	82.5	88.9	25.0	65.8[1]	70.6[1]

[1] Corrected for winter migrants which had left the area temporarily before 1 September (Drent 1979).

6. DISPERSAL AND MORTALITY OF COMPLETE BROODS (FAMILY GROUPS)

6.1. INTRODUCTION

Each year a number of broods of both territorial and guest pairs disappeared completely shortly after fledging, whereas other broods escorted by their parents immigrated. In some cases the parents were observed without young within a few days after fledging, long before the young could fend for themselves. None of these young were later recovered or retrapped. This suggests that in these cases the complete broods succumbed. There was no difference between the weights on the 15th day of the young of broods who disappeared completely when compared with those of broods of which at least one young was recaptured (in each of the 6 years, $P > 0.05$). There were indications that bad weather during the first days after fledging caused the death of complete broods confirming earlier findings by Royama (1962) for the Great Tit and Smith (1967) for the Black-capped Chickadee *Parus atricapillus*. Further it is possible that in the first day(s) after fledging complete broods were predated by various corvids (Drent & De Goede, unpub. data).

In a number of other cases observations and recaptures had shown that broods left the area of study mostly already during the day of fledging. In these cases the parents disappeared temporarily from the area of study. During second broods, however, the females stayed and only the male was temporarily absent. Observations on marked broods have shown that directly after fledging the parents guided their young in a relatively fast and direct move with low foraging frequency to areas at a distance of up to two kilometres from the fledging site. However, at least 80 per cent of the broods moved between a negligible distance and one kilometre. In the next days the parents guided their young within a restricted area. For parents which had guided their young over considerable distance (several hundreds of metres) on the day of fledging, this foraging area was in section much smaller than the distance moved in the first day. This foraging area often did not at all fall in the foraging area of the parents during spring and breeding period.

The area to which a brood migrates is highly determined by the distribution of oak-patches in the region, and earlier (foraging) experiences gained by the parents, particularly the male, during the first two months after their own fledging. Almost without exception the broods of those parents whose fledgling foraging area was known, were located there (Table 7), regardless whether the brood had left or had passed through suitable foraging areas, (*e.g.* areas rich in oaks). Parents that had foraged in this period as juvenile in the area of study stayed there with their brood, whereas parents that foraged as juvenile elsewhere, brought their broods out of the area of study. If the members of a pair originated from different

Table 7. Comparison of the expected and the observed distribution of autochthonous broods in the dependent period within and outside the areas of study. Percentages of fledged broods in parentheses

Area	Year	Density (number/10 ha) of			Drop in density caused by emigrant broods		Percentage correct location	
		breeding pairs	broods fledged	broods observed	observed[1]	expected	all broods	emigrant broods
V.E.	1969	10.3	11.9			1.4 (11)		
V.E.	1970	11.9	12.7	11.9 (94)	1.6	1.6 (13)	97	83
V.E.	1971	14.3	12.2			1.9 (16)		
Park	1970	7.9	6.5	5.6 (86)	4.3	3.5—4.8 (53—73)	95	94
H.V.	1975	10.1	6.3			3.1 (49)		
H.V.	1976	6.5	9.6	8.5 (89)	0.8	0.9 (10)	97	83
H.V.	1977	10.8	9.1			1.5 (16)		
H.V.	1977[2]	10.4	9.7	9.0 (93)	1.9	2.2 (22)	96	86
H.V.	1978	5.1	5.2			2.3 (44)		
H.V.	1979	4.0	6.3			4.1 (66)		

[1] Boundary-broods (see text) omitted.

[2] In part of the Hoge Veluwe area regular observations on the location of broods were made.

areas the male almost always decided the move. these findings enable us to predict which broods can be expected to leave the area of study (Table 7). Most of the broods, whether resident or emigrant, were found in woodlots that were rich in oaks. In both areas and in all years (n = 6) all first broods spent more than 80 per cent of their foraging time in oaks. This was the case whether or not the fledging site was surrounded by oaks; for example in 1976 on the Hoge Veluwe the two categories of broods foraged 88 and 81 per cent of their time, respectively, in oaks ($\chi^2 = 0.6068$, $P > 0.25$, n.s.). Second broods foraged less frequently in oaks than first broods, but more frequently than can be expected for random foraging.

Some of the broods visited the neighbouring areas frequently, particularly if these were rich in oaks. If the outlying areas were more favourable than the area of study the young stayed after independence in the former area and became by definition emigrants.

After ten to twenty days the parents returned to the former territory without young. Observations have shown that almost invariably the young remained in the area to which they were guided by their parents.

In some years and areas, the quantitive effect of the disappearance and dispersal of broods on the density of broods roaming locally, were studied. Routine walks that covered the whole area of study including a surrounding strip of about 50 m were carried out almost daily. During each walk the broods were located and if possible identified by means of the coloured rings of the young and the parents. All autochthonous residents and some of the immigrant broods were identifiable. Simultaneously capture-recaptures with mistnets were made. All broods of which at least one young was captured were also observed several times. So it could reasonably be assumed that all unobserved autochthonous broods had vanished completely from the area within a few days after fledging, either because of mortality or emigration. Several of the observed broods lived partly inside and partly outside the area of study (boundary broods). These broods were counted half as resident and half as emigrant broods. Thus the locally fledged broods could be classified into resident broods and broods that had disappeared (Table 8). Part of the broods that had disappeared were identified outside the area of study, by observation or capture, but this gives only a minimum value for the emigration of broods. This minimum value (observed emigrants, Table 7), can be compared to the expected number of emigrant broods, based on the experiences of the male parents. The identities and the numbers of observed emigrant broods coincided very well with those which were expected.

The broods that disappeared (Table 7) could be divided into three categories: identified emigrant and boundary broods and those broods that had disappeared either by mortality or through unobserved dispersal (a, b and c in Fig. 5). Between 17 and 43 per cent of the broods that disappeared, *i.e.*, only 6 to 13 per cent of the fledged broods, were never observed again,

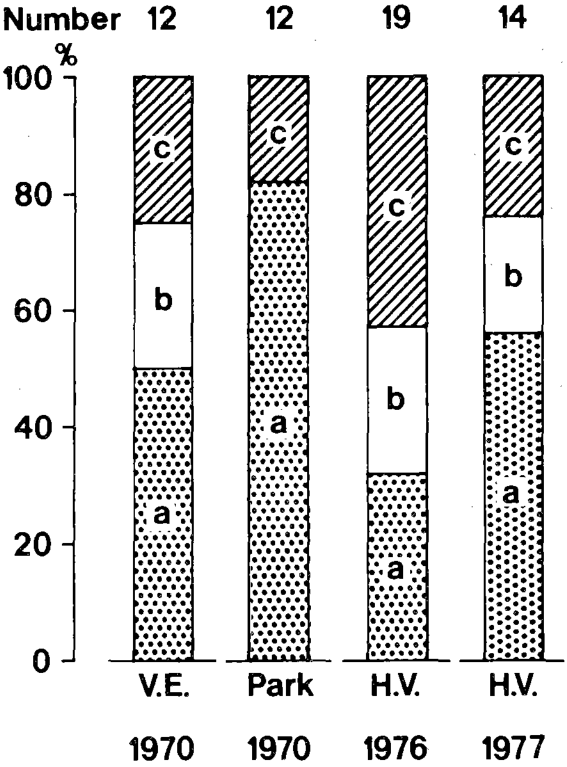

Fig. 5. Broods that disappeared from the area of study separated into three categories (see text). a) observed outside the area of study (emigrant broods). b) boundary broods. c) fate of broods unknown.

thus mortality of complete broods after fledging was rather an unimportant factor.

In spite of great efforts not all the immigrating broods could be colour-ringed for individual recognition. The frequency of observations of marked immigrant broods did not differ significantly from that of the resident autochthonous broods. Assuming that this was also the case for the unmarked immigrant broods, the density of immigrant broods could be calculated from the ratio of the numbers of observations of (marked and unmarked) immigrant and autochthonous broods and the known density of autochthonous broods. The results are summarized in Table 8 and will be commented on for each area of study separately.

6.2. THE VOSBERGEN ESTATE AND ITS SURROUNDING

On the Vosbergen Estate there was a high density of fledged broods in all years, whereas the density of expected emigrants was low (Table 7). Full data is only available for 1970 showing that most of the broods expected to emigrate were emigrants in reality and formed the majority of the identified emigrant broods. Only a few broods had disappeared, and many broods immigrated. Consequently the total density of broods that roamed the main area of study was high, nearly twice the density that fledged originally (Table 7, 8).

During the Vosbergen Estate study almost all observed broods, which roamed the area in June were first broods. Therefore, it is not surprising that the composition of the juveniles, that were captured in June 1970 was similar to the composition of the observed broods (53 per cent of the juveniles and 55 per cent of the broods were immigrants). The proportion of immigrants among the juveniles in June 1969 and 1971 is known and amounted to 55 and 52 per cent, respectively. Since the density of fledged broods and of expected emigrant broods was similar in the three years (Table 7), the number of immigrant broods can be expected to have been as high in 1969 and 1971 as it was in 1970. So during the whole Vosbergen Estate study the balance between immigration and emigration was strongly in favour of the immigrants, resulting in a sudden marked increase of broods in the area of study shortly after fledging.

Table 8. Density (numbers/10 ha) of different categories of broods in different areas in the dependent period just after the dispersal of broods. Percentages of total broods fledged in parentheses

Area	Year	Density		
		resident	immigrants	total
V.E.	1970	9.5 (75)	11.6	21.1
Park	1970	1.3 (20)	1.3	2.6
H.V.	1976	7.1 (74)	2.0	9.1
H.V.	1977	6.4 (65)	2.6	9.0

Almost all broods that left in the Vosbergen Estate were retrapped or observed in two nearby areas with many oaks. More than 75 per cent of the immigrant broods of which the fledging site in 1970 was known came from adjacent areas with few oaks. One such area, a park with many pinetrees and adjacent gardens, was only 100 m removed from the Vosbergen Estate, here emigration strongly exceeded immigration (Table 7, 8). The large scale emigration of broods was in accordance with expectation (Table 7), since most of the male parents had spent their own fledgling period elsewhere. The emigrated broods were almost all recovered in oak rich areas such as the Vosbergen Estate. In 1970 there had been a one way migration between the Park and the Vosbergen Estate. Incidental observations lead to the supposition that this probably occurs also in other years.

A similar phenomenon was found in 1970 between another adjacent area Oosterland and the Vosbergen Estate. This area consisted mainly of avenues and hedgerows with few oaks. From this area 9 (75%) of the marked broods moved to the Vosbergen Estate, whereas only one brood from the Vosbergen Estate roamed in an area overlapping both areas. In the Oosterland area the total density of roaming broods had also dropped notably to far below the fledging density.

6.3. THE HOGE VELUWE

On the Hoge Veluwe area the density of fledged broods showed large annual fluctuations (Table 7). Second broods were much more common than on the Vosbergen Estate. Nevertheless the density of fledged broods was lower due to the high number of pairs that failed to produce fledglings. In 1975 38 per cent of the breeding pairs had failed to produce any fledglings while second broods did not fledge at all. Consequently the density of broods was low in relation to the breeding density. In contrast, in 1976 and in 1979 a high proportion of the pairs produced two broods, resulting in a relative high density of family groups. The number and the proportion of expected emigrant broods also strongly differed between the years (Table 7). In 1975, 1978 and 1979 the expected proportion was considerably higher than in 1976 and 1977. For 1975 this was mainly due to the high density of guest pairs. Most of these pairs had arrived late in spring from a nearby area with few nest holes. In 1978 and 1979 many of the breeding males only entered the area of study in March. They had arrived as non-territorial males from nearby areas where survival in winter was high, due to artificial provision of food, and they were able to settle in the area of study because the winter mortality among the residents had been high (Van Balen 1980, Van Balen & Drent 1980, Drent 1979, 1983). By contrast, in 1976 and 1977, after winters when the survival rate was high in the area of study due to the large stock of seed food, most of the breeding males were present from the previous breeding season onwards.

In 1976 and 1977 only a few broods left the area of study (Table 7). These were mainly the broods that were expected to emigrate. The density of immigrant broods was low and did not fully compensate for the total loss of autochthonous broods (Table 8). Incidental observations and captures in 1975, 1978 and 1979 indicated strongly that the density of immigrant broods was not higher than that in 1976 and 1977 (2—3 broods per 10 ha). On the other hand, the paucity of local recaptures in these years indicates as was expected that more broods than in 1976 and 1977 had emigrated (Table 7). The balance between immigration and emigration here was evidently in favour of emigration.

The observations showed that on the Hoge Veluwe region dispersal did not take the form of a one way migration stream between the area of study and its surroundings.

Concluding: The distribution of the family groups after fledging is strongly determined by the occurrence of oaks. This is brought about by the tendency of the parents to bring their young to the area they themselves foraged as fledglings. Thus the origin of the breeding birds has to be incorporated in the prediction of distribution of family groups.

7. SUMMER SURVIVAL OF AUTOCHTHONOUS JUVENILES

In early September the density of autochthonous juveniles in the area of study, their identity and sex were known exactly. In both areas of study the more young that fledged the more were present in early September although only on the Hoge Veluwe area the number of data were sufficient to show this correlation (Fig. 6, H.V: $r = +0.9429$, 3, $P < 0.05$). This positive correlation was due particularly to males (♂♂ : $r = +0.9797$, $P < 0.05$; ♀♀ : $r = +0.7240$, $P > 0.10$).

Both the number of fledged males and females on the Vosbergen estate was about twice as high as on the Hoge Veluwe (Table 9). On the first of September, however, there were 6.3 times as much autochthonous females and 3.6 times as much autochthonous males on the Vosbergen Estate than on the Hoge Veluwe. These changes were due to the fact that the local survival rate for both sexes was markedly higher on the Vosbergen Estate than on the Hoge Veluwe (Table 10). In both areas the local survival rate of males was higher than for females, although

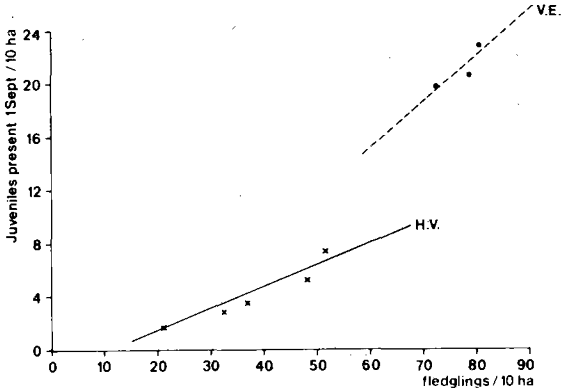

Fig. 6. The relationship between the density of fledglings and the density of these locally present on 1 September. Dots: Vosbergen Estate (1968—1970); $r = +0.8543$, $P > 0.05$; crosses: Hoge Veluwe (1974—1978); $r = +0.9429$, $P < 0.05$.

the difference was only significant for the Hoge Veluwe data (Table 10: $\chi^2 = 2.5031$, $P > 0.10$ and $\chi^2 = 18.8349$, $P < 0.0005$).

In chapter 6 it has been shown that a varying proportion of the fledged broods had left the Hoge Veluwe area shortly after fledging. To eliminate this effect, the local survival rate has been calculated separately for the young of broods that were expected to stay in the area (Table 10). The local survival rate of these young was again higher on the Vosbergen Estate than on the Hoge Veluwe (all young: $\chi^2 = 27.0011$, $P < 0.0005$; ♂♂: $\chi^2 = 8.8817$, $P < 0.0005$ and ♀♀: $\chi^2 = 25.3778$, $P < 0.0005$). For the Hoge Veluwe the annual differences in male survival between the years had now completely disappeared ($\chi^2 = 0.3573$, d.f. 3, $P > 0.90$). In contrast an annual difference in the female rate was observed: in 1975 and 1976 the local survival rate of females was lower than in 1977 and 1978 (Table 10: $\chi^2 = 9.1718$, d.f. 3, $P < 0.05$).

Reports of juveniles from outside the area of study showed that many juveniles of both emigrant and resident broods lived there at 1 September (Table 9). As argued the reported numbers of emigrants are minimum values. The young of the emigrant broods left the area directly after fledging, while those of resident broods left only after attaining independence about 2 to 3 weeks after fledging. The number of young males of emigrant broods was particularly high in years in which the initial density of the broods was high (Table 7, 9).

Table 9. The density (number/10 ha) of male and female autochthonous fledglings and the numbers of these present at 1 September in- and outside the area of study. The emigrants are categorized into whether they had belonged to broods expected to stay or to leave the area of study based on previous experience of adults (see text). Data from the Vosbergen Estate (1969-1970) and the Hoge Veluwe (1975-1978)

Year	Males				Females			
	fledged locally	present locally	drop in density caused by dispersal of		fleged locally	present locally	drop in density caused by dispersal of	
			broods (emigrants broods)	individuals of resident broods			broods (emigrants broods)	individually of resident broods
1969	38.2	10.9	1.3	3.8	34.9	8.7	1.2	6.1
1970	39.1	11.8	1.3	4.3	40.2	8.8	1.9	6.5
1975	10.4	1.2	1.7	1.5	10.7	0.5	0.7	0.5
1976	28.9	4.3	1.2	4.3	19.5	0.9	2.0	3.1
1977	25.6	4.8	1.0	3.8	26.6	2.7	1.3	5.3
1978	18.1	2.4	2.7	2.4	14.3	1.5	1.8	1.7

Table 10. The survival (%) of autochthonous fledglings until 1 September for the area of study (local survival) and for the region (min. total survival). The young are categorized as in Table 9. Data from the Vosbergen Estate (1968—1970) and the Hoge Veluwe (1974—1978)

Years	All young			Males			Females		
	local survival		total survival	local survival		total survival	local survival		total survival
	all broods	resident broods	resident broods	all broods	resident broods	resident broods	all broods	resident broods	resident broods
1968	28	28	40	—	—	—	—	—	—
1969	27	27	42	29	30	41	25	24	43
1970	26	27	43	30	32	44	23	24	42
mean difference[1]						11			19
1974	10	—	—	—	—	—	—	—	—
1975	8	14	33	12	20	47	5	8	19
1976	11	12	32	15	19	38	4	5	20
1977	14	16	37	19	21	38	10	11	35
1978	12	20	42	13	21	42	10	18	43
mean difference[1]						19			25

[1] The mean difference between local and total survival represent the mean proportion of emigrants from the area of study.

Not only the local survival rate but also a minimum value for the total survival rate of the young of resident broods could be calculated (Table 10). In both regions the minimum total survival rate is markedly higher than the local survival rate and also much higher than the figures reported in the literature (Dhondt 1970, 1979, Kluyver 1951, 1966, Webber 1975). The literature suggests that the cause of the departure of fledglings is crowding. However, our findings completely contradict this view, since at the Hoge Veluwe a higher proportion of fledglings of both sexes left as compared to the Vosbergen Estate. The figures also show that in both areas relatively fewer males than females emigrated.

On the Vosbergen Estate region there was no difference in total survival rates between years or sexes (Table 10: for all years $P < 0.75$). On the Hoge Veluwe region there was no annual difference in the total survival rate of the males (Table 10: $\chi^2 = 1.5170$, d.f. 3, $P > 0.50$), but for the females the annual differences were significant (Table 10: $\chi^2 = 16.3143$. d.f. 3, $P < 0.001$). The total survival rate differed significantly between the sexes in the first two years of this study (both $P < 0.05$), but not in 1977 and 1978 (both $P > 0.25$). In contrast to the local survival rate the total survival rate of males did not differ between the two areas (Table 10: $\chi^2 = 0.6545$, $P > 0.25$). This also applies to the Vosbergen Estate data for the females and for the females on the Hoge Veluwe in the last two years, but not during the first two years of the study (Table 10: $\chi^2 = 0.008$, $P > 0.975$ and $\chi^2 = 7.7812$, $P < 0.001$, respectively).

In general it can be stated that in early September at least 40 per cent of the fledglings were still alive. The real figure probably approaches 50 per cent because the extent of dispersal has been underestimated (section 2.2). The differences found in the local survival rate of fledged young between the two areas, between the years and between the sexes, can all except 1975 and 1976 of the Hoge Veluwe study be explained by dispersal. In these two years the mortality of the females was extremely high.

Table 11. The local survival rate (LS) and minimum survival rate (TS) up to the next month (% recaptured) of autochthonous young females caught in June, July and August 1976—1978, on the Hoge Veluwe

Year	June		July		August	
	LS	TS	LS	TS	LS	TS
1976	17	43	33	67	44	78
1977	38	62	38	72	38	62
1978	40	70	50	75	40	60

8. CHANGES IN SURVIVAL AND DISPERSAL WITH TIME

Since trapping was carried out frequently every year except 1968 on the Vosbergen Estate and 1975 on the Hoge Veluwe, most autochthonous juvenile Great Tits, that were locally alive on 1 September, had been captured at least twice during the preceding period. In 1968 capture was carried out frequently in only a few locations while in 1975 capture was hindered by unsuitable weather conditions.

In general, captures of juveniles within 10 days after fledging were rare. Those caught in June all had fledged 10 to 23 days previously. This is about the time that the young attain independence which is 14—20 days after fledging (Goodbody 1952, Hinde 1952, own obs.). For every juvenile that had been captured a record was kept as to whether it was still alive a month later and whether it was inside or outside the area of study.

The captures were supported by observations of colour-ringed individuals. The most accurate determinations of the presence of the tits was done for the juveniles caught in August, as the recordings were done more intensively after 1st September.

The local survival rate, the minimum total survival rate and the minimum emigration rate until the next month were calculated for each

Table 12. The percentage of autochthonous fledglings alive 15 days after fledging, of first broods from which at least one young was recovered locally. Calculation based on Lincoln index (see text). Data from the Vosbergen Estate (1969—1970) and the Hoge Veluwe (1976—1978)

Year	Percent alive	
	recaptured	calculated
1969	53	79
1970	60	73
1976	53	82
1977	51	67
1978	51	81

monthly cohort of captured autochthonous and immigrant juveniles of both sexes. To avoid any age dependent effects on survival and dispersal (Dhondt & Hublé 1968, Dhondt 1970, 1981, Webber 1975) the analysis was done for first brood young only, as the majority (64—100 per cent) of fledglings were in this group. Since it appeared that in nearly all cases the results did not differ significantly between autochthonous and immigrant young of the same sex (Test of Fisher, $P > 0.05$; for total survival rate, Table 13, see also Dhondt 1979), the two categories were combined except where otherwise stated.

In the monthly calculations the difference in the survival rate between birds from 1976 and those from 1977 and 1978 (Table 10) was only found in the survival rate from June to July (Table 11). In 1976 this survival rate was lower than in 1977 and 1978 (LS: $\chi^2 = 3.9133$, $P < 0.05$ and TS: $\chi^2 = 2.9558$, $P < 0.10$). No such differences were found for the survival rate from July to August and from August to September. Moreover the survival rate from June to July 1976 was lower than that from July to August and from August to September (Table 11; LS: $\chi^2 = 2.9861$, $P < 0.10$ and TS: $\chi^2 = 4.1419$, $P < 0.05$). As this did not apply to the other two years the survival rate of the cohort caught in June 1976 differed significantly from all other cohorts (Table 11; LS: 16.7 *v.* 40.2 ± 4.2[1]) per cent and TS: 43.3 *v.* 68.5 ± 5.2[1]) per cent). Considering June 1976 exceptional the data of all cohorts of autochthonous and immigrant juveniles did not differ significantly (LS: 40.2 ± 4.2[1]) *v.* 45.8 ± 7.0[1]) and TS: 68.5 ± 5.2[1]) *v.* 71.4 ± 6.1[1]) per cent, respectively). Monthly survival rates differed only between the autochthonous and immigrant females in the cohorts captured in June 1976 (LS: 16.7 *v.* 46.2 per cent, $\chi^2 = 4.1419$, $P < 0.05$ and TS: 43.3 *v.* 76.9 per cent, $\chi^2 = 4.1163$, $P < 0.05$).

We may conclude that the difference in survival of autochthonous females up to 1 September between years (Table 10), must have been due to events occurring somewhere in or before the period between the mean capture dates of the juveniles caught in June and July, that is between 17 and 35 days after fledging. From the life tables it appeared that the proportion of fledged young from first broods, that were caught or observed 15 days after fledging, amounted to more than 50 per cent, in all years (from Table 12: V.E. 57 per cent, H.V. 52 per cent, $\chi^2 = 2.9827$, $P > 0.05$). The number of juveniles alive around the 15th day (10—18) after fledging can be calculated by means of the standard Lincoln index. this shows that the survival rate until the 15th day after fledging is high and does not differ between the two areas (from Table 12: V.E.: 76 per cent, H.V.: 74 per cent, $\chi^2 = 0.3958$, $P > 0.50$). There were no significant differences between 1976, 1977 + 1978 in the Hoge Veluwe study. Also there was in 1976 no significant difference in the calculated survival rate for males and females (♂♂: 84, ♀♀: 79 per cent, $\chi^2 = 0.3918$, $P > 0.25$). So the relatively low survival rate in 1976 occurred after the 15th day of fledging, thus after attaining independence.

Table 13. The minimum total survival rate (%), until the next month, of autochthonous and immigrant juvenile males and females caught in June, July and August. Data combined for the Vosbergen Estate (1969—1970) and for the Hoge Veluwe (1976—1978) (in parentheses for 1977—1978)

Sex	Area	Status	Period of capture		
			June	July	August
♂♂	V.E.	Aut.	72	73	84
		Imm.	67	81	80
♂♂	H.V.	Aut.	69	75	71
		Imm.	68	70	75
♀♀	V.E.	Aut.	74	74	76
		Imm.	64	66	82
♀♀	H.V.	Aut.	55 (67) 1	73	67
		Imm.	74	63	79

[1] Difference between autochthonous and immigrant juveniles; chi-square: $P < 0.05$.

Except for the autochthonous females caught in June 1976, there was no significant difference in the monthly total survival rate between the months, between the two areas, between the sexes or between autochthonous and immigrant juveniles (Table 13). About 73 per cent of the juveniles survived until the next month, this is about 92.5 per cent per week. This weekly survival rate results in a rate until September (about 12 weeks) of nearly 40 per cent, which is

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[1]) 95 per cent confidence interval.

within the survival range found earlier (Table 10).

Emigration rate often differed strongly between areas and sexes. As stated earlier differences in the local survival rate could be ascribed to differences in the emigration rate. Since the trends in the dispersal rate did not significantly differ between the years in the same area the data were averaged over the years. Fig. 7 shows that the emigration rate of the juveniles caught in June did not differ between the sexes (in both areas $P > 0.75$), but markedly differed between the areas (♂♂: $\chi^2 = 8.9078$, $P < 0.005$; ♀♀: $\chi^2 = 6.7044$, $P < 0.01$). In both areas the emigration rate of the males for the successive cohorts decreased but only significantly so on the Hoge Veluwe (V.E.: $\chi^2 = 1.4923$, $P > 0.25$, and H.V.: $\chi^2 = 10.9333$, $P < 0.005$). This suggests that the males became gradually more sedentary. Consequently, the difference in emigration rate between the two areas decreased in time, becoming insignificant for the males caught in August (June cohorts: $\chi^2 = 8.9078$, $P < 0.005$, July cohorts, $\chi^2 = 8.5634$, $P < 0.005$; and August cohorts: $\chi^2 = 1.2136$, $P > 0.25$, respectively). On the Vosbergen Estate the emigration rate of the cohort of females increased significantly during the season (Fig. 7: $\chi^2 = 3.8854$, $P < 0.05$) whereas on the Hoge Veluwe it remained at the same high level. Consequently, as was the case for the males, the difference between the two areas in the emigration rate of females gradually disappeared becoming insignificantly for the July and August cohorts (Fig. 7: $\chi^2 = 6.7044$, $P < 0.01$; $\chi^2 = 2.337$, $P > 0.10$ and $\chi^2 = 0.2259$. $P > 0.50$, respectively). The dispersal rate of the females was ultimately high in both areas.

The increase of emigration-rate of females on the Hoge Veluwe corresponded with a decrease in foraging activities in oaks. As an example the juveniles foraged in June 1970 85 per cent of their time in oaks compared to 46 per cent in August. The figure for random foraging will be 41 per cent. This decrease in preference to forage in oakpatches was confirmed by where the emigrants were recovered. In 1970 64 per cent of the recovered emigrants, that had left the area of study during June and the first half of July, were found in areas abundant in oaks, compared to only 22 per cent ($\chi^2 = 4.9733$, $P < 0.05$) of those that had left between 15 July and 1 September whereas 25 per cent was expected on the basis of random dispersal.

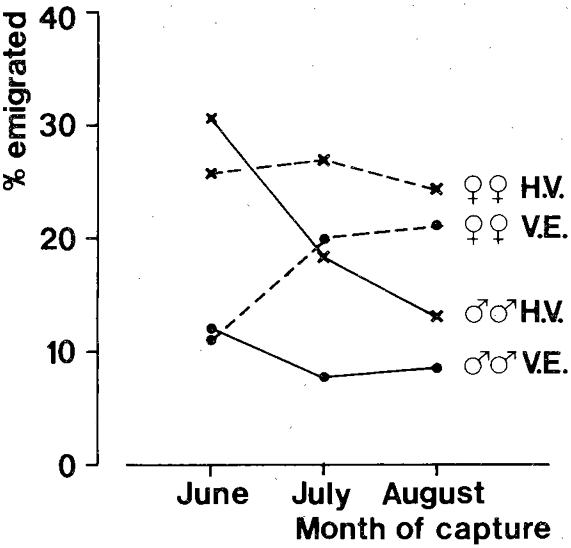

Fig. 7. The percentage of emigrant juvenile males (solid line) and females (broken line) alive one month after being captured in June, July and August. Dots: Vosbergen Estate (1969—1970); crosses: Hoge Veluwe (1976—1978).

In conclusion, it can be said that the difference in survival until 1 September between the two areas occurred in both sexes particularly in the first weeks after attaining independence. These two weeks will be referred to as "the critical period". The difference in dispersal between the sexes gradually builds up between June and September. The latter result confirmed the conclusions reached by Dhondt (1979) and Webber (1975).

9. FACTORS AFFECTING SURVIVAL AND DISPERSAL OF JUVENILES

9.1. DENSITY IN SUMMER

In the literature there is conflicting evidence to the extent on which the local survival rate is dependent on the density of adult and juvenile tits during the summer. In some studies the local survival rate of autochthonous juveniles until early winter or the next breeding season was negatively correlated with the summer densities (Dhondt 1971, Klomp 1980, Kluyver 1971), but in others no correlations were found (Van Balen

1980, Webber 1975). In the present study on the Vosbergen Estate, the area with the highest summer densities (Table 2, Table 9), local survival rate was greater (Table 10) and the emigration rate smaller than on the Hoge Veluwe (Fig. 7). On the Hoge Veluwe the annual summer densities of adults and juveniles of resident broods had varied greatly without a recognizable negative effect on survival rate or a positive one on dispersal. These data suggest that until 1 September the local survival rate, and dispersal rate from the area of study is dependent on area and not on density.

9.2. PROPORTION OF SECOND BROOD YOUNG

Several authors have mentioned that second-brood young have a lower local survival rate and a higher dispersal rate than first-brood young (*e.g.* Dhondt 1971, Kluyver 1954, 1971). From this it can be expected that any differences in the proportion of second-brood young between years will be reflected in differences in local survival rate and in dispersal rate of the fledglings. On the Vosbergen Estate the proportion of second-brood young was very low, less than 10 per cent. On the Hoge Veluwe the proportion of second-brood young varied from zero to 36 per cent. Although in a few years second-brood young tended to have a lower survival rate until 1 September than first-brood young the differences between the two categories were very small and almost always not significant. So it was not surprising that the correlations between the proportion of second-brood young and the local survival rate and dispersal rate until 1 September were not significant in both areas.

9.3. FLEDGING WEIGHT

9.3.1. Variations in fledging weight

Several authors (Dhondt 1970, Moss 1972, Perrins 1965, Webber 1975) have found that the recovery or survival rate increases with increasing body weight measured on the 15th after hatching, which is more or less equal to the fledging weight (Van Balen 1973, Gibb 1950). Since these authors could show that the fledging weight of the recovered residents did not differ from that of the recovered emigrants, they favoured the idea that mortality shortly after fledging depends on fledging weight.

In accordance with the literature (see Van Balen 1973) in the oak-rich Vosbergen Estate the fledged males and females of resident and emigrant broods were heavier than those in the moderately oak-rich Hoge Veluwe (Table 14: chi square test, in all cases $P < 0.001$). The two areas differed particularly in the proportion of young lighter than 16 g (V.E. *v.* H.V.; ♂♂: 0.7 *v.* 17.9 and ♀♀: 6.4 *v.* 22.2 per cent, $P < 0.001$). These differences between the two areas corresponds with the differences in local survival rate but the differences in dispersal rate was the reverse.

In both areas and in all years males were on average 0.8 g heavier than females (Table 14, *c.f.* Dhondt 1971).

On the Hoge Veluwe the annual mean fledging weight for 1976 was significantly lower than for other years (Table 14: chi square test, in all cases $P < 0.05$). This difference is also found for the fledging weight of the autochthonous juveniles that were recaptured in June but not for that of the immigrants (Table 15). In 1976, but

Table 14. Mean fledging weight (in g) of juvenile males and females of resident and emigrant broods (see text). Vosbergen Estate (1969—1970) and Hoge Veluwe (1975—1978)

Sex	Brood	Vosbergen Estate		Hoge Veluwe			
		1969	1970	1975	1976	1977	1978
♂♂	Resident	18.3	18.1	17.7	17.2[1]	17.7	17.8
	Emigrant	18.2	18.2	17.3	16.0	18.1	17.9
♀♀	Resident	17.4	17.2	16.9[1]	16.5[1]	17.1	17.2
	Emigrant	17.1	17.3	16.0	15.5	17.7	17.1

[1] Difference between resident and emigrant juveniles; chi-square: $P < 0.05$.

Table 15. Mean fledging weight (in g) of juveniles recaptured in June. Sexes, as well as autochthonous and immigrant Tits are separated. Data from the Hoge Veluwe

Sex	Origin	Year of capture		
		1976	1977	1978
♂♂	Autochthonous	17.4	17.5	18.2
	Immigrant	18.3	18.1	18.3
♀♀	Autochthonous	16.1	17.0	17.5
	Immigrant	17.9	17.2	17.1

Difference between years: Kruskall and Wallis test.
Aut. ♂♂ $H_0 = 5.0222, 0.05\ P < 0.10$
Imm. ♂♂ $H_0 = 0.4148$ n.s.
Aut. ♀♀ $H_0 = 9.7454\ P < 0.01$
Imm. ♀♀ $H_0 = 2.9610$ n.s.

not in 1977 and 1978, the difference between the fledging weights of autochthonous and immigrant juveniles was significant for both sexes (Wilcoxon, $P < 0.05$). For the females this difference corresponds with a difference in survival rate (Table 10).

In two of the six years (1975 and 1976) there was a significant difference between the fledging weights of the young of resident and emigrant broods, the first ones being heavier (Table 14). This difference was more pronounced for females than for males. In 1975 the difference between resident and emigrant broods coincided with an extremely high nestling mortality. The difference in mean fledging weight between young of resident and emigrant broods was mainly due to a difference between young of territorial pairs and those of guest pairs. However, the nestling mortality did not differ between the young of territorial pairs and those of guest pairs (54.8 *v.* 53.9 per cent, $\chi^2 = 0.0188$, $P > 0.75$). In 1976, a year with a normal nestling mortality (21 per cent) the difference in mean fledging weight between young of resident broods and those of emigrant broods coincided with the above mentioned low annual mean fledging weight in alle categories of young (Table 14). A more detailed analysis of this season is presented in 9.3.3. The data from 1975 and 1976 strongly suggest that, in years when it was difficult to provide the nestlings enough food resulting in a low survival rate after fledging (Table 10) the resident pairs were more successful in producing heavy young than the immigrant pairs. The immigrant pairs are guest pairs and territorial pairs arrived during winter and spring. They had often to be content with a section that was only infrequently foraged by the males that had settled earlier (Drent 1983), indicating that they bred in nestboxes surrounded by the worst foraging ground.

Since all young of emigrant pairs left the area shortly after fledging, these emigrants will have lower fledging weights than residents in those years. In order to allow for this phenomenon, a further analysis to the effects of fledging weight on survival and dispersal was made restricted to the juveniles of broods that remained in the area.

9.3.2. Annual mean fledging weight, survival and emigration after independence

When the data of both areas of study are combined the local survival rate until 1 September is positively correlated with the annual mean fledging weight (Fig. 8). Analysing this for first-brood young separately, the correlation was significant for both sexes (Fig. 9). For the males the correlation depends completely on the differences in local survival rate between the two areas. For the females, however, not only the differences in local survival rate between areas but also for the Hoge Veluwe separately the difference between years seemed to be of importance although the correlation is not significant ($r = 0.8656$, v. = 2, $P > 0.05$). In section 7 it was shown that the level of local survival rate depends both on mortality and especially

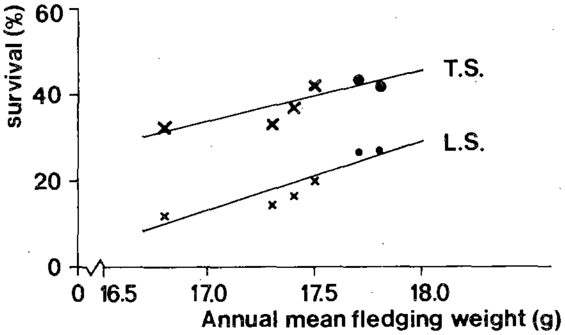

Fig. 8. The relation of local survival rate (L.S.) and total survival rate (T.S.) between fledging and 1 September with annual mean fledging-weight of resident broods. Dots: Vosbergen Estate (1969—1970); crosses: Hoge Veluwe (1975—1978). For local survival rate $r = 0.9441$, $P < 0.01$; for total survival rate $r = 0.8627$, $P < 0.05$.

on dispersal. The total survival rate is therefore used to eliminate the effect of dispersal as good as possible. For the two areas of study together there was as in local survival rate a positive correlation of total juvenile survival rate with annual mean fledging weight (Fig. 8). For the first brood males alone the correlation was very weak and not significant whereas for the females the positive correlation was significant (Fig. 9). The fact, that the fledging weight of males is correlated with the local survival rate, but not with the total survival rate, suggests that fledging weight should be negatively correlated with the dispersal rate. Only a weak tendency in the expected direction was found if the emigration rate was estimated as the number of young alive at 1 September outside the area of study divided by all young fledged (Fig. 10:a). Assuming the change to emigrate alike for all fledged individuals in a particular year, this estimation of emigration, depends on the survival rate. Therefore, the emigration rate was estimated as the number of young alive at 1 September outside the area of study divided by all young alive at that date. The correlation with this emigration rate proved to be significant (Fig. 10:b). For first brood females and males the same correlation was found (♂♂: $r = -0.8155$, ♀♀: $r = -0.8591$, both $P < 0.05$). However, part of this correlation is based on differences between the two areas. In the Vosbergen Estate region a lower proportion of the young alive at 1 September lived outside the area of study than on the Hoge Veluwe (♂♂: 26 *v*. 50, and ♀♀: 42 *v*. 62 per cent). For the Hoge Veluwe separately a negative correlation between emigration rate and annual mean fledging weight was also found ($r = -0.9597$, $P < 0.05$). This correlation for males and females separately was not significant and weaker for males than for females ($r = -0.2240$, and $r = -0.7542$, respectively, $P > 0.05$).

In conclusion we can say that since local survival rate is the result of survival and emigration, correlations between local survival and fledging weight have therefore to be corrected for emigration rate, to give a picture of the rela-

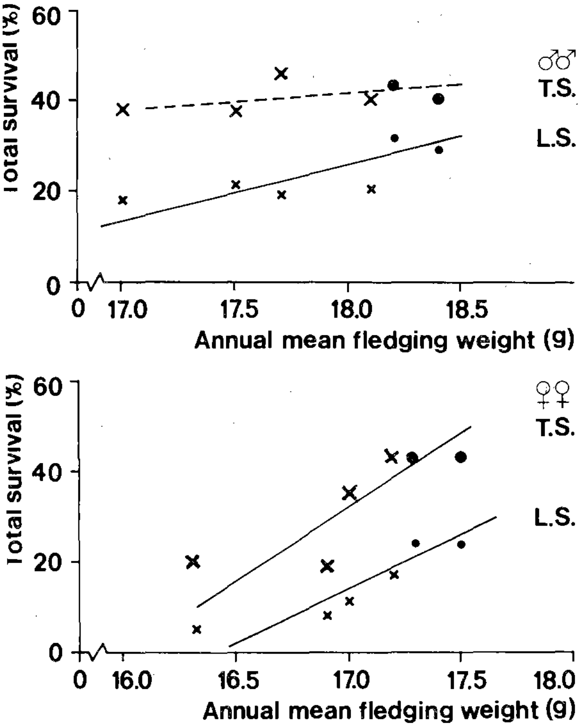

Fig. 9. The relation of local and total survival rate (L.S. and T.S.) with annual mean fledging weight of resident first-brood young for both sexes separately. Dots: Vosbergen Estate (1969—1970); crosses: Hoge Veluwe (1975—1978). ♂♂ L.S.: $r = +0.8519$, $P < 0.05$, T.S.: $r = +0.3612$, $P > 0.05$; ♀♀ L.S.: $r = +0.9088$, $P < 0.05$, T.S.: $r = +0.8711$, $P < 0.05$.

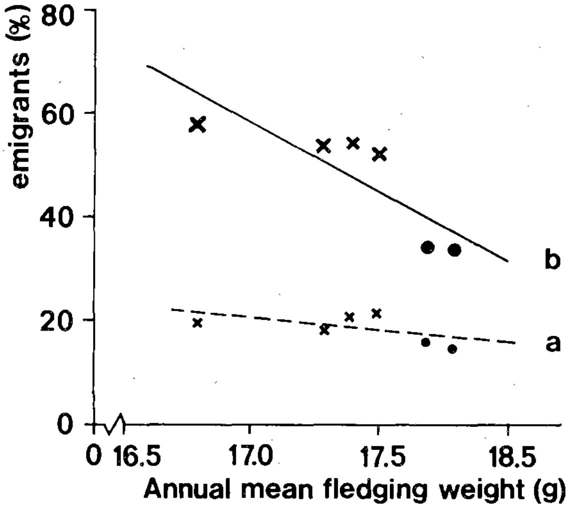

Fig. 10. The emigration rate (%) in relation to mean fledging weight. Emigration rate was estimated as: a. the number of young alive at 1 September outside the area of study divided by all fledglings of resident broods. b. the number of young alive at 1 September outside the area of study divided by all young of resident broods alive at that date. For a: $r = -0.5837$, $P > 0.05$; for b: $r = -0.8056$, $P < 0.05$.

tion between real survival and fledging weight. Taking this into account a positive relation of total survival with fledging weights exists for females only. The negative relation between emigration and fledging weight, corrected for survival, exists although mainly dependent on differences between areas.

9.3.3. Differential survival according to weight (1976 season)

The juveniles from resident broods can be divided in two categories: those that remained in the area (residents) and those that left the area (emigrants) after attaining independence. For all years the mean fledging weight of these two categories did not differ significantly (Wilcoxon in all cases, $P > 0.05$). This result confirmed the results obtained by Dhondt (1970) and Webber (1975). Consequently all recovered juveniles of the resident broods could be used for an analysis of the relationship between fledging weight and survival.

In order to study the relation between survival and weight, the mean fledging weights of nestlings from first broods, of juveniles recaptured in June and July and of those alive on 1 September are presented in Table 16. For all years except 1976 these four values are not significantly different indicating that there is no marked relation between survival chance and fledging weight in these years.

In the exceptional year 1976 the juveniles alive in September had a higher mean fledging weight than all first-brood fledglings. The mean weight of the fledglings was lower than in other years, but this was not the case for the juveniles alive in September. The differential survival rate in 1976 as indicated by the difference in weight between fledged individuals and those that survived, was more pronounced for the females than for the males, (Table 16: 1.2 *v.* 0.8 g). This meant that the difference in the mean weight between the sexes decreased from 0.7 at fledging to 0.3 for birds recaptured in September. This is remarkable as in all other years the difference between the sexes had remained about 0.8 g. Almost all juveniles caught in June 1976 were at that moment becoming independent. Their mean fledging weight was the same as for all fledglings (Table 16) indicating that during the period of dependence no selection by fledging weight had occurred. This was confirmed by daily counts of broods with individually marked young (see De Goede 1982). The juveniles, recaptured in July were significantly heavier at fledging than the sample of all fledglings but their fledgling weight did not differ from the birds alive in September (Table 16). Hence in 1976 between mid-June and mid-July, thus shortly after attaining independence, differential mortality of lighter young males and females had taken place. This coincided with the period in which the survival rate of autochthonous females in particular was fairly low. Particularly males below 16.0 g and females below 15.0 g disappeared during the critical period (1976: ♂♂: 73 *v.* 39 per cent, $\chi^2 = 7.0701$, $P < 0.01$, and ♀♀: 92 *v.* 59 per cent, $\chi^2 = 4.9226$, $P < 0.05$). In all other years a similar tendency was found, but it was not significant, probably

Table 16. The mean fledging weight (in g) of first-brood young of resident broods and the mean fledging weight of subsamples captured in June and July, and of those alive on 1 September. Data from the Vosbergen Estate (1968—1970) and the Hoge Veluwe (1975—1978)

Year	Males				Females			
	at fledging	captured in		alive in September	at fledging	captured in		alive in September
		June	July			June	July	
1968	18.2	—	—	18.2	17.5	—	—	17.5
1969	18.3	18.2	18.3	18.4	17.5	17.3	17.6	17.6
1970	18.1	18.2	18.3	18.3	17.3	17.4	17.5	17.5
1975	17.5	—	—	17.9	16.9	—	—	16.7
1976	17.0	17.3[2]	17.7	17.8[1]	16.3	16.1[1]	17.4	17.5[1]
1977	17.5	17.5	17.8	17.8	17.0	17.0	17.2	17.2
1978	18.1	18.2	18.2	18.1	17.2	17.3	17.4	17.4

[1] Comparison between the four subsamples of fledging weights/year, Kruskall and Wallis, $P < 0.05$.

[2] Comparison between subsamples of June and July, Wilcoxon, $P < 0.05$.

Table 17. The mean fledging weight (in g) and total survival rate to beyond the critical period (see text) of first brood young in relation to the date of weighing on the Hoge Veluwe 1976. For the analysis only broods of parents with at least one capture of a young of the first brood before independence are included

Weighing dates	N	First-brood young	
		mean fledging weight	total survival (%)
Till June 30th	51	15.6	27.4
After June 30th	78	17.3[1]	55.1[2]

[1] T = Wilcoxon: 5.6368, $P_DT_o = 0.0214$.
[2] $\chi^2 = 9.5479, P < 0.005$.

due to the low numbers of juveniles with fledging weights below the mentioned limits. These data confirm those found by Webber (1975).

When the survival data for 1976 were inspected in greater detail, it was evident that other factors than fledging weight also affected the survival rate. It appeared that for the young of those broods of which at least one young was recaptured locally during the period of dependence, the mean fledging weight and the survival rate were correlated with the time of fledging. The young of early first broods are lighter and have a lower survival rate than the young of first broods that have hatched later (Table 17).

It appeared that within broods, the young that weighed most had a better chance of survival (67 *v.* 33 per cent, $\chi^2 = 4.0000$, $P < 0.05$). This difference disappeared, however, when analysed for the sexes separately (♂♂: 64 *v.* 58, and ♀♀: 28 *v.* 33 per cent, both $P > 0.50$). Differences within broods are connected with sex rather than with fledging weight, but marked differences between broods seem to a large extent to be correlated with the fledging weight and date.

9.3.4. Mean fledging weight of the brood in relation to survival rate

The results presented in the preceding section prompted us to analyse the inter-brood differences in greater detail.

In 1976 in first broods of which at least one young was recaptured locally during the period of dependence, the intra brood variance in fledging weight was significantly smaller than the inter-brood variance (all young F 16.110 = 14.9032, $P < 0.001$; ♂♂: F 15.58 = 15.1515, $P < 0.001$, and ♀♀: F 14.34 = 8.0520, $P < 0.001$). Therefore the hypothesis was tested that the total survival rate to beyond the critical period was positively correlated with the average fledging weight of the brood. This correlation was confirmed (Fig. 11a). There is, however, a potential complication if only body weight is used as a measure of condition, because about 60 per cent of the variation in the average adult body weight is genetic (Van Noordwijk *et al.* 1980). Assuming that the mid-parent value (defined as the mean of the parental weights) for body weight is a useful measure for the body size of the parents and hence of the young (Garnett 1976, Van Noordwijk *et al.* 1980) the difference between the average fledging weight of the young and the mid-parent weight is used as an indication of the condition of the brood (condition index). The mid-parent values were calculated from weights measured in spring, particularly during the nestling stage. During this period the parents weight is at its lowest (Drent unpub. data), and therefore closest to their lean weight, corresponding to their size. Garnett (1981) has shown that only about 9 per cent of the variation in fledging weight is explained by the fat content that is often taken as a measure of condition. However, particularly in 1976 the mean fledging weight of the broods was often up to 20 per cent lower than the mid-parent value. Similar results were obtained by Van Noordwijk (pers. comm.), who compared the tarsus length of parents and offspring in 1977 in the Liesbos area. These results suggest that the index for condition not only indicates a deviation in fat content but, in extreme cases, also in either protein content and or body size. Important in this respect is that body size (as measured by weight or tarsus length) is definitively determined by the 15th day of life (Garnett 1981).

In the 1976 data the variation in the condition index between broods was considerably higher than the variation in the mid-parent values (coefficient of variation 2.40 *v.* 0.48). The correlation coefficient between survival and mid-parent weight was positive but not significant ($r = 0.3182$, v. = 16, $P > 0.05$, n.s.) while that

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9.3.4. Mean fledging weight of the brood in relation to survival rate

The results presented in the preceding section prompted us to analyse the inter-brood differences in greater detail.

In 1976 in first broods of which at least one young was recaptured locally during the period of dependence, the intra brood variance in fledging weight was significantly smaller than the inter-brood variance (all young F 16.110 = 14.9032, $P < 0.001$; ♂♂: F 15.58 = 15.1515, $P < 0.001$, and ♀♀: F 14.34 = 8.0520, $P < 0.001$). Therefore the hypothesis was tested that the total survival rate to beyond the critical period was positively correlated with the average fledging weight of the brood. This correlation was confirmed (Fig. 11a). There is, however, a potential complication if only body weight is used as a measure of condition, because about 60 per cent of the variation in the average adult body weight is genetic (Van Noordwijk *et al.* 1980). Assuming that the mid-parent value (defined as the mean of the parental weights) for body weight is a useful measure for the body size of the parents and hence of the young (Garnett 1976, Van Noordwijk *et al.* 1980) the difference between the average fledging weight of the young and the mid-parent weight is used as an indication of the condition of the brood (condition index). The mid-parent values were calculated from weights measured in spring, particularly during the nestling stage. During this period the parents weight is at its lowest (Drent unpub. data), and therefore closest to their lean weight, corresponding to their size. Garnett (1981) has shown that only about 9 per cent of the variation in fledging weight is explained by the fat content that is often taken as a measure of condition. However, particularly in 1976 the mean fledging weight of the broods was often up to 20 per cent lower than the mid-parent value. Similar results were obtained by Van Noordwijk (pers. comm.), who compared the tarsus length of parents and offspring in 1977 in the Liesbos area. These results suggest that the index for condition not only indicates a deviation in fat content but, in extreme cases, also in either protein content and or body size. Important in this respect is that body size (as measured by weight or tarsus length) is definitively determined by the 15th day of life (Garnett 1981).

In the 1976 data the variation in the condition index between broods was considerably higher than the variation in the mid-parent values (coefficient of variation 2.40 *v.* 0.48). The correlation coefficient between survival and mid-parent weight was positive but not significant ($r = 0.3182$, v. = 16, $P > 0.05$, n.s.) while that

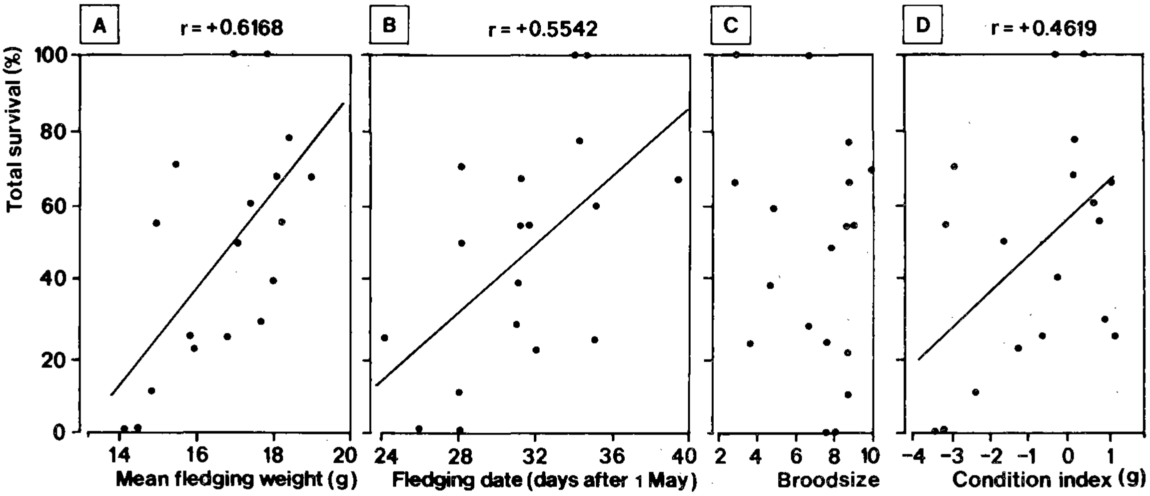

Fig. 11. The relationship between total survival within first broods in 1976 and the following parameters of these broods: A: mean fledging weight; Spearman: $T_0 = 2.6145$, $P < 0.01$; B: fledging date; Spearman: $T_0 = 2.1541$, $P < 0.05$; C: brood size; Spearman: $T_0 = 0.3894$, $P > 0.50$; D: condition index = mean fledging weight of brood — midparent weight in breeding season; Spearman: $T_0 = 2.215$, $P < 0.05$.

between survival and the condition index was positive and significant (Fig. 11d). A partial correlation analysis (Bailey 1959) showed that survival was positively correlated with both the mid-parent weight (x_1) and the condition index (x_2) ($ryx_1.\ x_2 = 0.5212$, v. = 15, $P < 0.05$ and $ryx_2.\ x_1 = 0.6021$, v. = 15, $P \approx 0.01$).

The total survival rate of the first broods to beyond the critical period was positively correlated with the fledging date (Fig. 11b). This confirms the data in the literature (Dhondt 1971, Kluyver 1951, Perrins 1965, Webber 1975).

Van Noordwijk (1980) has found that in most years there is a negative correlation between recruitment (survival to the next breeding season) and clutch size. In the present data, however, survival to beyond the critical period, was not significantly correlated with broodsize neither for 1976 (Fig. 11c), nor for the other years.

Several authors have found that clutch size decreases in the course of the breeding season, and that mean fledging weight is negatively correlated with brood size. Moreover, in a habitat such as the Hoge Veluwe the earliest first broods are hatched in many years long before the food supply is abundant thus explaining the low fledging weights (Van Balen 1973). So we may expect that the 15th day weight (x_1) will be positively correlated with the weighing date (x_2) and negatively with the brood size at fledging (x_3), and that date and brood size will be negatively correlated. In our data such correlations were present although only that between weight and date is significant ($r_{x1x2} = +0.4837$, v. = 16, $P < 0.05$; $r_{x1\,x3} = -0.3330$, v. = 16, $P > 0.05$, and $r_{x2\,x3} = -0.2982$, v. 16, $P > 0.05$). Therefore, the partial correlation coefficients between survival (y) and these three parameters were computed and tested one sided because of existing hypothesis ($ryx_1.x_2x_3 = 0.4680$, v. = 14, $P < 0.05$; $ryx_2.\ x_1x_3 = 0.3637$, $0.05 < P < 0.10$ and $ryx_3.\ x_1x_2 = 0.02216$, $P > 0.20$). This shows that after fledging it is mainly fledging weight that affected survival. In a multiple regression analysis with the above mentioned variables ($F\ 3.14 = 4.1013$, $P < 0.05$) only 46.8 per cent of the variation in the survival rate between broods could be explained by fledging weight. Data about total survival and fledging weights of first and second broods of the same pairs may throw light on this high unexplained variation in the survival rate. In 1976 a lot of second broods were produced.

The mean fledging weights of the first and second broods of the same pair were not correlated (Spearman To = 1.1930, $P_DT_O = 0.2670$) nor were the fledging dates (Spearman To = 0.09144 $P_DT_O = 0.9282$), but there was a high correlation of their survival rate (Fig. 12). Although the sets of data for the other years

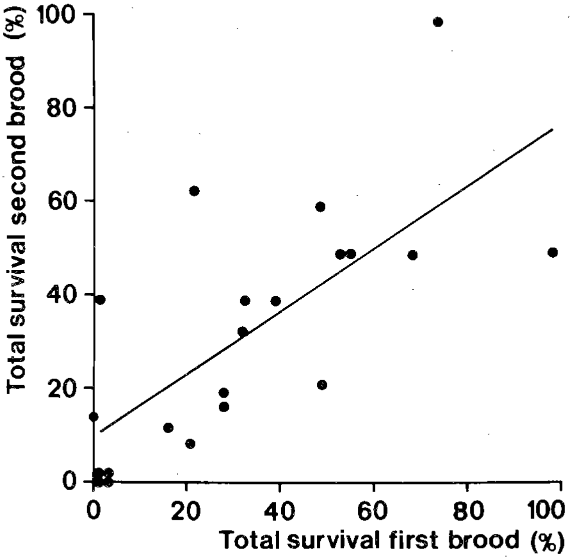

Fig. 12. The relationship between total survival (%) of fledglings of the first brood to beyond the critical period and that of the fledglings of the second brood of the same pair. Data from the Hoge Veluwe 1976, Spearman: $T_0 = 3.624$, $P < 0.001$.

were rather small, they also suggested that the survival of first and second broods to beyond the critical period of the same pair is correlated.

This effect was also found for the survival of first broods of the same parents in successive years. There was a high positive correlation between the survival rate of all the broods whose parents had young in both 1976 and 1977, (for male parents see Fig. 13, for female parents: Spearman To = 3.368, $P < 0.001$). This was in spite of the fact that the mean fledging weight (Table 14) and the average condition index (−0.9 *v.* −0.2 g., Wilcoxon, $P < 0.05$) differed between the two years. In contrast to the first broods in 1976, in 1977 there was no positive correlation between the mean fledging weight of the brood and the survival rate.

All this suggests that the young of some parents were able to survive well and the young of others not. The correlation between the mean fledging weight of a brood and its survival and also between the fledging date and survival most probably do not imply a simple causal relationship. The data presented so far indicate that most of the correlations between fledging date, fledging weight and survival rate are possibly based on either differences in local conditions between broods of different parents or differences in quality between the parents or the young themselves. Since after fledging the broods as well as the independent juveniles were assembled in the same oak-rich parts of the area of study (see 6.1), differences in condition, resulting in an effect on the survival rate after attaining independence, should already have been apparent in the nestling stage. However, regardless of whether they had a high or low survival rate the distribution of their nest sites over the parts rich in oaks or other parts of the area of study was the same ($\chi^2 = 0.9428$, $P > 0.25$). An area rich in oaks is considered to be synonymous with an abundant food supply during the nestling stage (Van Balen 1973). Thus if an abundance of food near the nest site is an important factor for later survival this is only possible on a smaller scale as it is dependent on the composition of the tree species around the nest site. Unfortunately almost all broods of the same parent had fledged within the same plot, either from the same nestbox or within 50 m. Consequently, it was impossible to separate the effects of environmental differences from those of qualitative differences between the tits. However, it could be of interest that pairs of broods

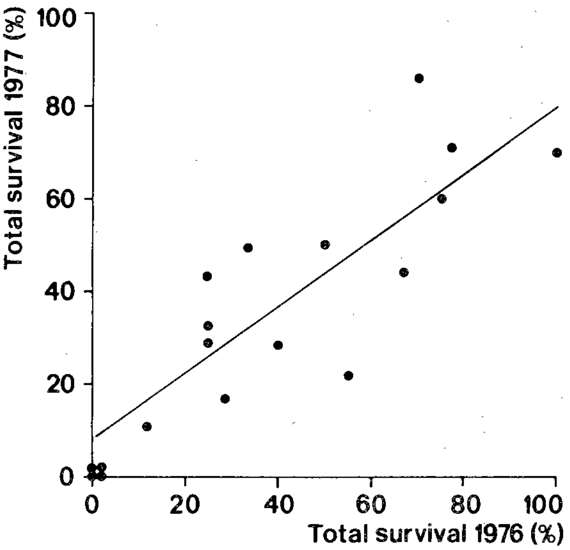

Fig. 13. The relationship between total survival (%) of fledglings of the first brood to beyond the critical period in 1976 on the Hoge Veluwe and that in 1977 of the same male. Spearman: $T_0 = 3.497$, $P < 0.001$.

with a low survival-rate score also less for other reproductive characteristics, they started their breeding attempts relatively early. Consequently particularly in areas other than where oaks are abundant the nestling-stage is very early in relation to the peak in caterpillar supply (Van Balen 1973) culminating in high nestling mortality, relatively small size and low fledging weight. The relative onset of the breeding attempt is in females partly genetically determined (Van Noordwijk *et al.* 1980). Pairs of the first category more often started a second breeding attempt (1976: $\chi^2 = 3.9996$, $P < 0.05$) which may imply that their own survival decreases (Kluyver 1971). The first brood, of pairs, for which the survival rate was low terminate more often prematurely their second breeding attempt (1976: 40 *v.* 0 per cent; $\chi^2 = 4.0725$, $P < 0.05$) and were more sensitive to disturbance by observers than pairs of which the survival rate of the first brood had been high.

10. IMMIGRATION OF JUVENILES AFTER ATTAINING INDEPENDENCE

In earlier chapters it was shown that, after they became independent, many juveniles dispersed from the areas of study, and on the other hand a number immigrated. These last ones are referred to as juveniles that immigrated individually as distinct from those that immigrated as members of a brood. Unfortunately many immigrants, of both categories, were not ringed. Moreover some of the juveniles of the immigrant broods were only ringed after the brood had separated. Consequently many immigrant juveniles that were only caught after attaining independence could not be classified in one of the two above-mentioned categories of immigrants. Therefore, the immigration of juveniles after the brood had separated has to be analysed by indirect methods: Juveniles from resident autochthonous broods present on September 1st have the same capture rate in the preceding period as those from marked immigrant broods. In addition the monthly survival rates did not usely differ between resident and immigrant juveniles (Table 13). Hence, we may assume that the distribution in time of first captures (= first local capture after fledging) is the same for juveniles of autochthonous and immigrant broods. Consequently, any deviations between the distributions of first captures of autochthonous and all immigrant juveniles must be ascribed to juveniles that immigrated after attaining independence. The distribution of the first capture of autochthonous and immigrant juveniles from first broods in Vosbergen Estate (1970) and in Hoge Veluwe (1976) is presented in Fig. 14 for both sexes. Almost all juveniles caught in June belonged to either resident autochthonous or immigrant broods. Thus the ratio of captures for June of autochthonous over immigrant juveniles reflects approximately the composition of the local population of juveniles at the moment that the first broods had dispersed. This ratio in June multiplied by the number of first captures of autochthonous juveniles in the following periods gives the expected number of first captures in that period of juveniles of broods that immigrated in June. The observed difference between the number of first captures of all immigrants and the expected value for immigrants from broods, that immigrated in June,

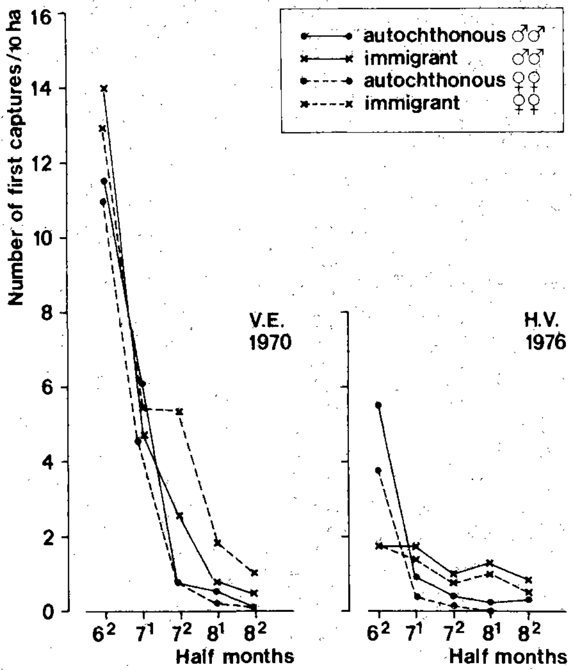

Fig. 14. The distribution of first captures of autochthonous and immigrant first brood males and females over half month period (6² = second half of June). Data from a) Vosbergen Estate 1970, and b) Hoge Veluwe 1976.

Table 18. The calculated number per 10 ha of first captures of individually immigrated first brood young males and females in half-month periods in 1970 (Vosbergen Estate) and in 1976 (Hoge Veluwe)

Capture period	V.E. 1970		H.V. 1976	
	♂♂	♀♀	♂♂	♀♀
June 2	—[1]	—[1]	—[1]	—[1]
July 1	0	0.4	1.4[2]	1.2[2]
July 2	1.7[2]	4.5[2]	0.8[2]	0.7[2]
Aug. 1	0.2	1.6[2]	1.2[2]	1.1[2]
Aug. 2	0.1	0.8	0.8[2]	0.5

[1] Immigration is assumed to be non-existing (see text).

[2] In these months the observed number of immigrants per 10 ha was significantly ($P < 0.05$) larger than the calculated number of juveniles per 10 ha from immigrant broods (explanation in text).

Table 19. The calculated number per 10 ha on 1 September of individually immigrated first brood juveniles on the Vosbergen Estate (1969—1970) and on the Hoge Veluwe (1976—1978)

Sex	Vosbergen Estate		Hoge Veluwe		
	1969	1970	1976	1977	1978
♂♂	1.0	1.3	2.7	1.7	2.2
♀♀	3.3	4.4	1.6	1.0	0.9

shows the half monthly immigration after the period of dependence (Table 18). The number of juveniles that immigrated individually and were present on 1 September in the area of study was calculated in the same way as the monthly immigration (Table 19).

To compare immigration and emigration a methodical error must be taken into account. Immigration can only be measured by the first local capture, but this is necessarily some time after arrival in the area. On the other hand emigration is assumed to have occurred directly after the date of the last capture in the area, which can be some time before real date of departure. These two methodical errors can amount to about half a month.

In the Vosbergen Estate the calculated number of first captures of juveniles that immigrated individually per half month peaked in the second half of July. The values found for the females were higher than for the males; their immigration was spread over a longer period (Table 18). The total numbers of first captures of juveniles that immigrated individually are both a minority of the total number of first captures and of the number of first captures of all immigrants (from Table 18 and Fig. 14; ♂♂: 5 and ♀♀: 15 per cent and ♂♂: 8 and ♀♀: 28 per cent, respectively). On 1 September of 1969 and 1970 more individually immigrated females than males were present (Table 19). These numbers were below the minimum numbers of autochthonous emigrants of resident first broods (Table 20). So after independence the balance between emigration and immigration was shifted in favour of emigration from the area of study. This difference would have been much larger if the number of emigrants from originally immigrant broods were included.

In the Hoge Veluwe area first captures of individually immigrated first brood juveniles occurred in more or less equal numbers throughout the summer (Table 18). In 1976 the number of first captures of males was in all periods slightly higher than that of females. In 1977 this difference between the sexes was smaller and in 1978 it was absent. Although the total of first captures of juveniles that immigrated individually was not very high, in 1976 for both sexes it was a marked proportion of all first captures (from Table 18 and Fig. 14; ♂♂: 31 and ♀♀: 35 per cent) and of the first captures of all immigrants as well (♂♂: 64 and ♀♀: 46 per cent). In the three years there were more male than female immigrants present on 1 September. For both sexes the numbers of immigrants were below the minimum numbers of emigrants of resident first broods (Table 19, 20) and hence also below those of all first broods which were present on the area of study during the period of dependence. Thus in the Hoge Veluwe region just as in the Vosbergen Estate region the balance between emigration and immigration shifted after the period of dependent life in favour of emigration.

On 1 September the densities of first-brood juvenile males, that immigrated individually

Table 20. The number of juveniles of resident first broods, emigrated from the area of study and still alive on 1 September, expressed as a drop in density on the area of study (number/10 ha)

Sex	Vosbergen Estate		Hoge Veluwe		
	1969	1970	1976	1977	1978
♂♂	3.3	3.5	3.8	3.7	2.3
♀♀	5.3	5.3	2.0	5.0	1.4

Table 21. The density (number/10 ha) of autochthonous, immigrant and all juvenile males and females, present in the area of study on 1 September, the total number present as a percentage of all locally fledged young, and the difference between the density of immigrants and the drop in the density by dispersal (see Table 20) on 1 September. Data from the Vosbergen Estate (1969-1970), Park (1970) and the Hoge Veluwe (1975-1978)

Sex Year	Density (number/10 ha)			All juveniles as % of fledged	Emigration(−) or immigration (+) surplus per 10 ha
	autochthonous juveniles	immigrant juveniles	all juveniles		
♂♂					
1969	10.9	11.5	22.4	59	+ 6.4
1970	11.8	16.0	27.8	71	+10.6
1970	0.5	3.7	4.2	25	− 5.9
1975	1.2	2.0	3.2	31	− 1.2
1976	4.3	4.3	8.6	33	− 1.3
1977	4.8	3.5	8.3	32	− 1.1
1978	2.4	4.3	6.7	37	− 0.8
♀♀					
1969	8.7	12.1	20.8	58	+ 4.8
1970	8.8	15.8	24.6	61	+ 7.4
1970	0.4	4.5	4.9	31	− 5.0
1975	0.5	1.4	1.9	18	+ 0.2
1976	0.9	2.7	3.6	16	− 2.1
1977	2.7	2.1	4.8	18	− 4.0
1978	1.5	2.1	3.6	25	− 1.4

were lower on the Vosbergen Estate than on the Hoge Veluwe. For females, however, these densities were higher on the Vosbergen Estate than on the Hoge Veluwe. The densities of first-brood juveniles that immigrated individually and were present on 1 September in the Vosbergen Estate were for both sexes a lower proportion of all first-brood juveniles and of all immigrants than in the Hoge Veluwe (all years per area together: males: 5 *v*. 31 and 10 *v*. 58 per cent and females: 17 *v*. 32 and 29 *v*. 60 per cent, respectively).

11. NUMBERS, MIGRATION AND MORTALITY: A GENERAL DESCRIPTION

The aim of this chapter is to give a summary of the changes in numbers, migration and mortality after fledging in the different habitat types, leading to the final densities of the different categories of birds (Table 5, 21) at the start of territorial activity on 1 September (Drent 1983).

11.1. ADULTS

In this study the mortality of the local territorial adults differed only slightly between the areas studied and was not different between years (Table 6). Local non-territorial pairs (guest pairs) leave the area immediately after fledging, but their subsequent survival is identical to the one of the local of the local territorial birds. Small-scale migration of the local territorial adults only occurs in the dependent period, since parents guide their young to the site where they had spent their own youth. As soon as the juveniles become independent, these adults return to their breeding territories, thus being effectively residents.

Predicting the number of adults on 1 September from the breeding numbers requires therefore knowledge about the fraction of guest pairs and the mortality rate of the territorial birds. Since the mortality of the territorial birds is relatively constant, variations in density at 1 September will be mainly due to variations in the proportion of guest breeders. Variations in the proportion of guest breeders are usually small (Table 2) as compared to variations in density of the total adult Great Tit population at 1 September (Table 5). The relatively constant mortality rate of the territorial birds and the minor effect of the emigration of the guest pairs confirms for this period the general accepted hypothesis that changes in total numbers of Great Tits must take place through juvenile mortality and/or dispersal.

11.2. JUVENILES

The patterns of juvenile mortality and migration will be described by using the data for years

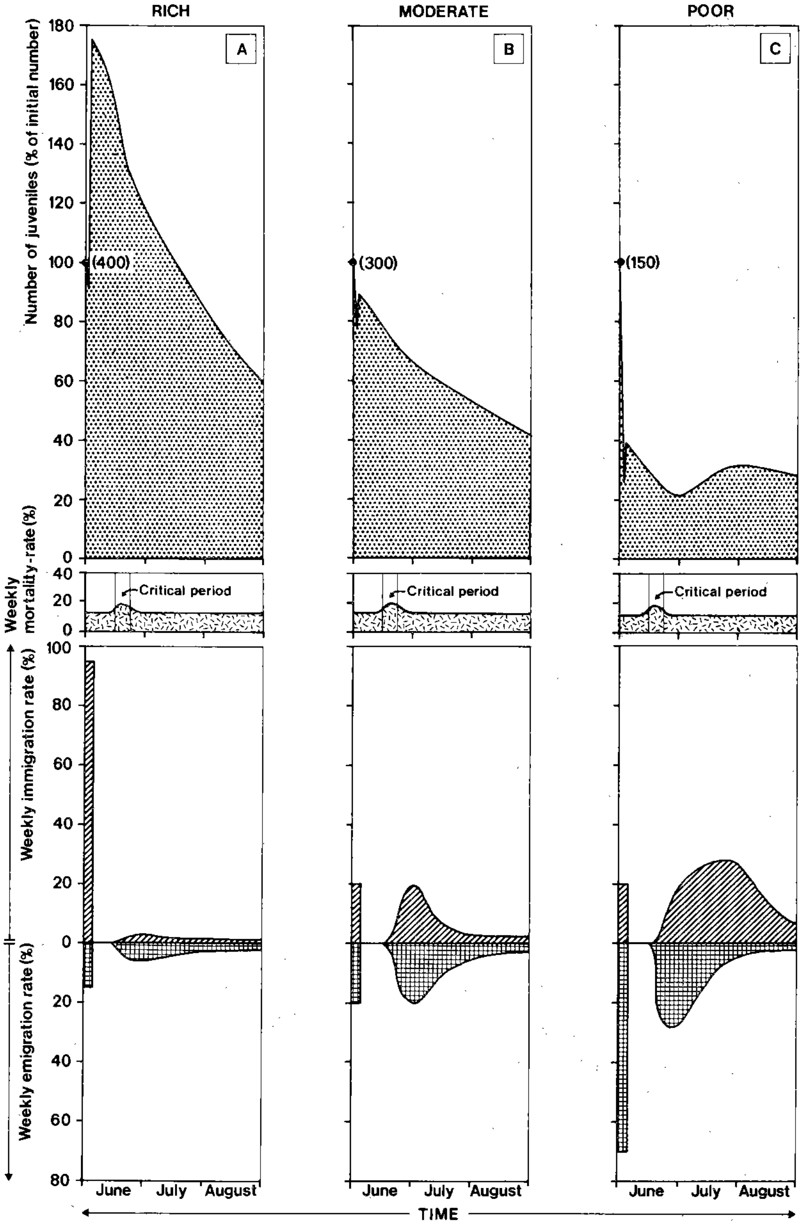

Fig. 15. Schematical representation of changes in numbers, weekly mortality, immigration and emigration rates in three different habitat types between fledging and 1 September. The habitats are surrounded by moderately rich wood and survival in the preceding winter is supposed to be high as a consequence of the winter food situation. The numbers are expressed as percentage of the numbers locally fledged. Actual numbers at fledging per 100 ha are given in parentheses. A: Rich = wood with many oaks (Vosbergen Estate); B: Moderate = mixed wood with some oaks (Hoge Veluwe); C: Poor = wood without oaks (Park). For further explanation see text.

preceded by high survival in winter. This choice is made to eliminate disturbing effects of varying immigration of potential breeding birds in spring. The most important environmental factor affecting mortality and migration is the distribution of oaks, most probably synonymous with "summerfood" (Van Balen 1973). In Fig. 15 three situations are compared: A. a rich habitat (example: Vosbergen), B. a moderately rich habitat (example: Hoge Veluwe), and C. poor habitat (example: Park). For the understanding of the emigration and immigration patterns, it is essential to realize that in all three cases the surrounding area is moderately rich. In describing the population data attention is focussed on the males only. The females give a similar picture, but because their mortality is slightly higher and their migration in the independent period more pronounced, shifts in sex ratio may occur (Table 22).

Table 22. The sex ratio (males/females) among the fledglings and among the young in the area of study on 1 September. Data from the Vosbergen Estate (1969—1970), Park (1970) and Hoge Veluwe (1975—1978)

	Ratio males/females	
	fledging	1 September
1969	1.13	1.08
1970	0.97	1.13
1970	1.10	0.86
1975	0.98	[1] 1.68
1976	1.48	[1] 2.39
1977	0.97	[1] 1.73
1978	1.23	[1] 1.86

[1] Differences between the two ratios significant ($P < 0.05$).

Situation A. Most of the pairs that nest in the oak-rich area (Vosbergen Estate) are residents, since in competition for vacant ground in the previous autumn residents gain over immigrants (Drent 1983). This means that only a small part of the breeding birds will guide their young to locations outside the rich area. However, the high number of males expelled from the rich area from the previous autumn onward will return with their young. The net result of this dispersal of family groups in the dependent period is a small drop in numbers of juveniles, directly followed by a sharp increase.

The mortality rate is constant, except for a short increase during the critical period.

After the critical period, the number of juveniles steadily decreases, due to the constant mortality rate and a decreasing emigration rate. A small influx of young males occurs, but this does not compensate for the number that emigrated. At 1 September the number of juvenile males is high (Table 21) and amounts to about 60 per cent of the number fledged. This number is higher than expected from the calculated total (= real) survival of 40 to 50 per cent between fledging and 1 September. This difference is caused by a high surplus of immigrating broods. Although the dispersal rate in females is higher than in males, the final result for the density at 1 September is such that the sex ratio did not change much in relation to that at fledging (Table 22).

Situation B. In the moderately rich area (Hoge Veluwe) the ratio of the numbers of adult males that have spent their own youth in or outside the area is more or less equal to the ratio of the numbers of males in the surrounding area that have spent their own youth in, or outside the area of study. Consequently, immigration and emigration of whole broods are similar. After the critical period immigration and emigration of individual juveniles are balanced as well; both are high in June and decrease towards 1 September.

The number of juvenile males present at 1 September amounts to 40 to 50 per cent of the number locally fledged, which is similar to the real survival rate in that period. Since there is no surplus of migration the final density is solely determined by real survival.

In contrast to the assumption of Fig. 15b, in part of the surroundings of the Hoge Veluwe area of study, the density of fledglings is small because of a shortage of nest-holes (Van Balen *et al.* 1978, 1982). In spite of identical emigration rates of the juveniles fledged in and outside the area of study, the number of immigrants is therefore smaller than the number of emigrants. This causes a lower number of juvenile males at 1 September than expected on the basis of equal densities of fledglings (Table 21). The final density at 1 September amounts to only *c* 26 per cent of the final density at the Vosbergen Estate, (Table 21) compared to 55 per cent at fledging (Table 9).

Since both migration and mortality are more pronounced in females than in males, the low number of fledglings in the surrounding area causes a significant shift in the sex ratio in favour of the males within the area of study (Table 22). Because of this shift in sex ratio only 55 per cent of the males, present at 1 September, should be able to obtain a juvenile male.

Situation C. This figure depicts the situation of a poor habitat (Park) surrounded by areas of moderate quality. Most adults that fledged their young in the poor habitat have spent their own youth in the richer surroundings. Therefore, most broods emigrate and only few immigrate directly after fledging, causing the balance to be strongly in favour of emigration. Directly after the critical period the emigration rate of the individual young is high. Immigration increases later since the surrounding area becomes gradually less attractive. At that time the number of immigrants exceeds the number of emigrants.

This surplus of immigrants, however, does not compensate for the excess of emigrated broods in the dependent period. The number present at 1 September is far below the number expected on the basis of the real survival alone, since emigration exceeds immigration (Table 21). Together with the low density of fledglings in such a poor habitat, this results in a very low juvenile density at 1 September: 17 per cent of the final density at the Vosbergen Estate compared to 40 per cent at fledging.

These examples show that the differences in density between rich and other habitats those exist at fledging increase in the period considered. At one hand this is due to a surplus of immigrants in the rich habitat, and, at the other hand to a surplus of emigrants in the poor habitat. Particular the balance in migration of family groups plays a crucial role.

The distribution and the high of seed-food in the preceding winter modify the above described differences in density between habitats. They determined the high and the composition of the breeding density and differences in these between adjacent areas (Van Balen 1980, Drent 1983). In turn these differences result in differences in fledgling density and in the net result in dispersal of family groups in favour of the oak-rich habitat with a high seed-food supply in the preceding winter.

12. DISCUSSION

Most authors agree that in a particular area of study variations in numbers of Great Tits are strongly related to the local survival of the juveniles (Dhondt 1971, Kluyver 1971, Lack 1966, Perrins 1965, Webber 1975). However, opposing views exist about when and how the crucial decrease in numbers occurs (see Chitty 1967). In this discussion we will emphasise actual small scale movements in summer as playing a crucial role in causing the variations in Great Tit numbers.

There are two different levels at which dispersal and mortality can be analysed. The first is based on comparison between years, in search of factors that explain annual levels in density within and between areas. The second poses the question which birds will be likely to disperse or die within a particular year and area. Both levels of analysis have been used to trace factors of importance in explaining the density and composition of Great Tit populations at 1 September, the start of the period of territorial strife.

Adult mortality was constant between years and differed only slightly between areas of study, and emigration of territorial birds without remigration did not occur. Therefore the number of adults on 1 September is a constant fraction of the number of local-territorial breeding birds. Changes in Great Tit numbers from fledging till 1 September are thus not brought about by variations in dispersal or survival of adult tits. In the following we will therefore focus on juvenile mortality and dispersal, and the behaviour of the parents as an indirect cause of juvenile dispersal and mortality.

Mortality of juveniles

To discuss causal factors in juvenile mortality we have to distinguish three periods: the dependent, the critical and the independent period (Fig. 16). Within years the weekly mortality rate turns out to be constant, except during the critical period (Fig. 15). In this critical period factors that are of importance in determining which juveniles will survive are condition, food availability and the quality of the parents (Fig. 16).

It was shown that the quality of the parents has a considerable influence on juvenile survival in the critical period. Transfer of foraging experience from parents to young (see also Cody 1971, Krebs *et al.* 1972, Krebs 1973, Murton 1971), and the timing of parental meanness (Davies 1978b) are likely to play a role in determining mortality at this stage. In some bird species, including the Great Tit, the parents prolong the dependent period in situations in which food is scarce (Davies 1976, Norton-Griffiths 1969, Higachi & Momose 1981, Kluyver 1951, own obs.).

During the transition period to self-feeding marked declines of body weight occur (up to 10 per cent of fledging weight, Van Balen & Drent unpub. data, Webber 1975) indicating that almost all body reserves have been used (Garnett 1976, 1981, Mertens 1977). Higher body reserves as indicated by higher weights therefore increase survival chances to some extent.

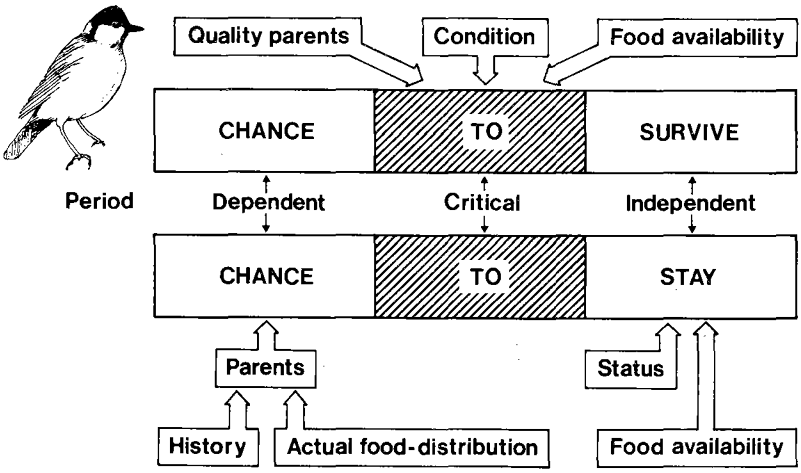

Fig. 16. Factors influencing the chance to survive and to stay of individual juveniles between fledging and 1 September for the different stages of dependency on their parents. For further explanation see text.

Considering differences in mortality between males and females, mortality in females is in general somewhat higher. The low body reserves of the females possibly explain their higher vulnerability.

Differences in summer mortality rates between years could for a small part be explained by variations in food supply, as estimated by the average yearly fledging weight (Van Balen 1973). Also these differences find their origin in the critical period. No effect of density of both adults and juveniles on juvenile mortality could be shown. Consequently, differences in juvenile survival between years can only be linked to differences in food availability.

Concluding, it was found that within years, parental quality, fledging weight and food availability, are involved in determining which young will survive. The mortality rate does not differ appreciably between years or areas of study, except for a small effect of food availability, causing in some years (and presumably in some areas) a slightly higher mortality, especially in females. The finding that juvenile mortality is relatively constant between years and areas implies that dispersal plays a crucial role in modifying densities.

Dispersal of juveniles

In understanding the dispersal of juveniles in the dependent period, the fact that males bring their broods, directly after fledging, to the area where he has spent the first two months of its own youth is of prime importance. The behaviour of the parents determines the dispersal in the dependent period (Fig. 15). Functionally speaking, this mechanism can be understood in terms of food availability for those birds that where forced to reproduce in areas which are relatively poor in oaks and in winter food. These birds normally have spent their youth in areas richer in oaks that provide more food in summer. These areas also provide more food in the following winter. The young of these parents will have better chances in such areas as well. However, the few parents that nested in oak-rich woods, but spent their youth in a nearby oak-rich area also return to this last area with their brood. This means that they leave a potentially good area in favour of the one known from their own youth. It seemed that knowledge of the local area in the same period last year is more important than recent knowledge of the breeding area itself. However the streams of emigrating and immigrating family groups cannot be understood without a quantitative consideration of the history of the parents, both in the area of study and the surroundings.

The occurrence of different types of parents is strongly dependent on the distribution of oaks on one hand and on the distribution and the abundance of winterfood on the other hand. When in an area abundant in oaks food in winter is poor, the winter mortality is high, giving immigrant males better chances to settle in spring (Van Balen 1980, Drent 1983). These males guide their young to sites outside the area of study. Thus, after a poor winter emigration of broods in the dependent period is high. When food in winter in an area rich in oaks is abundant, spring immigrants have little chance to settle (Dhondt 1970, Drent 1983, Krebs 1971), resulting in a low emigration rate of broods. In this situation many males were expelled by territorial strife and were forced to settle in the poorer surroundings (Dhondt 1970, Drent 1983, Krebs 1971, Webber 1975). These males guide their young back to the oak abundant area, resulting in a high immigration rate of family groups. In general there is a negative relation between both the abundance of oaks and winterfood in the breeding habitat and the fraction of males which guide their young to sites outside the area.

This mechanism has important implications for the so-called buffer mechanism (Kluyver & Tinbergen 1953, Dhondt 1970, Drent 1983). Directly after fledging buffering of breeding densities between good and bad habitats will be counteracted strongly by the movements of the broods, causing again large concentrations in the rich habitats. The buffer mechanism, or even territoriality, can be seen functionally as a mechanism preventing competition for food, particularly in the breeding season. Breeding Great Tits are central-place foragers and are usually single-prey loaders. The high costs of flying between nest and foraging sites restrict them in the use of foraging sites (Orians *et al.* 1979). For the same reason their prey spectrum is probably smaller than in the period just after fledging. Therefore in the nesting period the parents are presumably more sensitive to competition by conspecifics than after fledging. Some evidence that such competition may play a role is provided by the effect of the inter-nest distance on the production of young (Dhondt *et al.* 1983). Outside the breeding period the feeding range is much larger than during breeding (Drent 1983). Depletion of food on a particular site is then less likely to occur. For these reasons, a particular habitat may contain a much lower number of central-place foragers than of noncentral-place foragers. This suggests that, in the case that buffering takes place directly after fledging, it will be on a much higher density level than during nesting.

Directly after brood migration the family groups forage in fairly small areas. During the critical period, *i.e.* when the parents desert their young, movements of broods are small. The juveniles that survive the critical period move around in small sibling groups and may join other groups, although total group size generally does not exceed 30. Dominance relationships develop, whereby males become dominant over females and early-fledged young over late ones (Drent 1983). In this period groups may split and rejoin with others. In July and August foraging extends to other tree-species than oaks, presumably because food quality and abundance in oaks decrease (Van Balen 1973, Perrins 1976).

After the critical period dispersal is determined by two forces. The degree of success (status) in the regularly occurring skirmishes among the juveniles determines the tendency to stay or to depart (Drent 1983), while food availability has a similar effect (Fig. 16). These two tendencies explain why from areas rich in food emigration is low, while there is a steady influx of immigration from nearby sites. The low status of females and late-fledged juveniles explains why more of such juveniles move away than early-fledged males. Although there is a distinct dispersal in the independent period resulting in a redistribution of the juveniles, individual displacements generally do not exceed one kilometre. The birds that are forced to leave do not have a higher risk to die in late summer than the birds that stay (see also Dhondt 1979).

Earlier studies used local survival of fledglings as an estimate of real survival (*e.g.* Kluyver 1951, Lack 1966). The results of the present study show that local survival until 1 September cannot be equalled with real survival, since it is highly influenced by emigration.

Total survival, which is the recovery rate of fledglings obtained from captures and sightings not only in the area of study, but also in its surroundings, gives a better approximation of real survival. This extimate of real survival is still biased by emigration to some extent. In the present areas of study annual variation in total survival (between fledging and 1 September) is small and the large differences found in local survival are mainly caused by dispersal. These findings are in accordance with those of Dhondt

(1979), although his estimates of real survival are much lower than the estimates given in the present paper. However, Dhondt sampled only part of the surroundings, while in this study a much larger area was checked.

The redistribution caused by migration of broods has the result that the number of autochthonous juveniles fledged from the area of study gives an incomplete, possibly misleading, picture of the actual density soon after fledging. Studies where fledging densities are estimated from the number of autochthonous juveniles fledged from the area of study, without considering immigration or emigration (*e.g.* Fretwell 1972) are therefore likely to reach wrong conclusions about density dependence.

In the present study no indications were obtained that dispersal or mortality in summer were density dependent. In September, however, territory settlement by juvenile males depends on the density of the adult and the juvenile males (Drent 1983). Therefore differences in density in summer have indirect consequences for territory settlement. Ultimately, this leads to density-dependent migration and mortality (Dhondt 1973, Drent 1983).

Much more is known now than at the time of the opposing view points of Lack (1966) and Kluyver (1971) about the way in which the densities of adult and juvenile Great Tits at the start of autumnal territorial behaviour arise, as well as about the consequences of territorial behaviour. These view-points, each supported by decades of field work, led to an international debate bordering on a controversy. With the advantage of hindsight, we must conclude that elements of both have been upheld. Lack's view that the mortality among juveniles before the autumn period is of decisive importance on subsequent densities is true insofar as the number of candidates in the autumn is one of the factors determining the number that will be successful in obtaining a territory, and hence will (in many cases) survive to breed in next spring, *i.e.* spring densities are related to autumn densities. Dispersal in the post-fledging period as a factor influencing local density was overlooked by Lack. The observation that many juveniles present in the area in autumn fail to secure a territory, and in fact do emigrate, confirms Kluyver's interpretation of territorial behaviour as an expression of a density-limiting process. The interplay between the number of adult territory-owners present and the number of juveniles contending for a territory results in a density that differs in the various habitats. Study of how the number of competitors that are found to be present at the onset of autumn is determined is thus as critical for understanding subsequent breeding densities as is the study of the competitive process that gains momentum from that moment. Our conclusion must be that, far from being a choice between opposing viewpoints, the truth of the matter is that both phenomena contribute to the determination of numbers of Great Tits present in the breeding season and to differences between habitats and between years. Further advance will depend on the judicious integration of the major premises championed by these eminent biologists.

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14. SUMMARY

Numerous studies have shown that the breeding density of the Great Tit *Parus major* differs from year to year but that the level around which the density fluctuates is characteristic for the habitat. The mechanisms underlying the differences in breeding density have not yet been clarified.

The aim of the present study is to analyse these mechanisms by following the fate of individual birds. The study was performed in the areas: Vosbergen Estate (near Gro-

ningen) and adjacent Park, and Hoge Veluwe (near Arnhem). In the present paper, a part of this study, the mechanisms are analysed which determine the differences in density of both adults and juveniles at the onset of autumn, which are important for the determination of density in the following spring (Drent 1983).

The levels of breeding density in the areas of study and the differences between the years are related to the abundance of oaks and seed food in the preceding winter (beechmast crop and artificial food supply). Each year a number of the breeding birds are so-called guest birds (intruders). The proportion of guest pairs is particularly high after winters with an abundant beechmast crop, thus in years with a high breeding density.

Almost all guest parents and their young emigrate directly after the breeding season. The local survival rate of territorial birds is high and differs hardly between the two areas of study. Therefore, the differences in the density of territorial breeding birds are found back in the density of adults at the onset of autumn.

The density of fledglings is positively related to the density of breeding pairs. Moreover, in oak-rich habitats more young fledge per breeding pair, due to the high survival rate of the nestlings.

The proportion of males among the fledglings is negatively related to breeding density and positively to nestling mortality.

The local survival of the fledglings until 1 September differs between the habitats and between the years. The more oaks and the higher the survival rate of the nestlings and their fledging weights, the higher the local survival rate. When dispersal of juveniles is taken into account, the total (= real) survival rate until 1 September amounts to 40—50 per cent in both areas and in almost all years. Differences in the mortality rate arise in the period shortly after independence. This mortality affects particularly light juveniles, especially females. The total survival rate is positively correlated with the annual mean fledging weight, but neither with the density of adults and juveniles, nor with the proportion of second-brood juveniles. In a year with a relatively low total survival rate the first broods with a low mean weight and an early fledging date have the highest losses. Nevertheless these two factors explain only half the variation in the survival rate between broods. Since, irrespective of the mean fledging weight, the survival of successive broods of the same parents (first and second brood in the same year, first broods in successive years) is positively correlated, an important rôle in determining the survival chance is attributed to the characteristic timing of "parental meanness".

The major differences in local survival rate are caused by variation in dispersal. Two different types of dispersal can be distinguished. Firstly, directly after fledging, juvenile experiences of the parents and the distribution of oak patches over the adjacent areas cause a redistribution of broods favouring habitats with many oaks, particularly those in which the seed food had been abundant in the preceding winter. The consequences of this redistribution are discussed with respect to the so-called buffer-mechanism of breeding densities. Secondly, shortly after gaining independence juveniles start to disperse individually. The individual dispersal rate is correlated negatively with the annual mean fledging weight and with the abundance of oaks. Towards September the emigration rate from areas with many oaks increases while the immigration rate decreases. This runs parallel with a decrease in attractiveness of oaks for foraging. As a consequence of the difference in dominance status the change in dispersal rate particularly affects females. In the course of time males become more and more sedentary. The shift towards more emigration from the oaks results in a decrease of the marked differences in the density of juveniles between adjacent oak-rich and other forests as found shortly after independence.

Concluding, the differences in density of juveniles in oak-rich and adjacent other habitats on 1 September are much larger than can be expected from the reproductive rates and the total survival rates. This is mainly a result of dispersal by broods in the dependent period. Any differences in juvenile density at 1 September will be found back in differences in territory density in autumn and hence in spring. The consequences of the present results are discussed in the light of the controversy between Kluyver and Lack.

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16. SAMENVATTING

Verschillende onderzoekingen hebben aangetoond dat de dichtheid waarin broedparen van de Koolmees voorkomen van jaar tot jaar verschilt en dat het niveau, waaromheen deze dichtheden schommelen, karakteristiek is voor het bostype. Reeds vanaf de eerste publikaties hierover bestond over de veroorzaking ervan verschil van mening, vooral tussen de twee belangrijkste onderzoekers: Kluyver en Lack. Kluyver schreef het verschijnsel vooral toe aan beperking van dichtheden door territoriaal gedrag, waardoor een wisselend gedeelte van de jonge vogels tot emigratie wordt aangezet. In tegenstelling tot Kluyver veronderstelde Lack dat het aantal broedparen vooral wordt bepaald door sterfte onder de jonge vogels tijdens de eerste periode na het uitvliegen. Voedselschaarste werd verondersteld hiervan de belangrijkste oorzaak te zijn.

De bedoeling van het huidige onderzoek was om duidelijkheid te brengen in deze discussie. Dit werd bereikt door het lot van alle aanwezige Koolmezen, die met kleurringen individueel waren te herkennen, te vervolgen gedurende de jaarcyclus in opeenvolgende jaren. In deze publikatie worden de mechanismen besproken, die verschillen in dichtheden van zowel oude als jonge vogels op 1 september veroorzaken.

In een andere publikatie (Drent 1983) kon ik aantonen dat deze dichtheden van beslissend belang zijn om verschillen in dichtheden van territoria in de herfst en daardoor in het volgende voorjaar te begrijpen.

Het onderzoek werd in 1968 t/m 1971 uitgevoerd in twee aangrenzende gebieden bij Groningen: Vosbergen en Park, en in 1975 t/m 1979 in het zuidelijk gedeelte van De Hoge Veluwe.

De terreinen verschilden in het aantal eiken en hun grootte. Binnen een gebied verschilden de jaren in de aan- of afwezigheid van een rijke oogst aan beukenoten en van bijvoedering in de winter. In overeenstemming hiermee verschillen én de niveaus waaromheen de dichtheid van broedparen schommelt én de dichtheden van jaar tot jaar. In de meeste jaren hebben niet alle broedparen een territorium rondom de nestholte. De paren die buiten hun territoria in dat van een ander paar broeden worden gastbroeders genoemd. Hun aantal en aandeel in de totale broedpopulatie is vooral groot na winters met een rijke beukenotenoogst, dus in jaren met een relatief hoge broeddichtheid.

Bijna alle gastbroeders en hun jongen emigreren direct na het uitvliegen van de jongen uit het onderzoekgebied. De sterfte onder de territoriale Koolmezen is in alle terreinen en jaren gering, terwijl emigratie zelden optreedt. Hierdoor worden de verschillen in de dichtheden van de territoriale vogels in het broedseizoen teruggevonden in die van de oude vogels op 1 september.

De dichtheid van de uitgevlogen jongen neemt toe met de dichtheid van broedparen (het hoogste in eikenpercelen). Doordat de overleving van de jongen in het nest in het terrein met veel eiken groter is dan in de andere terreinen, vliegen daar bovendien bij dezelfde dichtheid aan broedparen nog meer jongen uit.

Het percentage mannetjes onder de uitgevlogen jongen is negatief gecorreleerd met de dichtheid aan broedparen en positief met de sterfte in het nest.

De plaatselijke overleving van de uitgevlogen jongen tot 1 september verschilt tussen de terreinen en tussen de jaren. Deze neemt toe naarmate er meer eiken in het gebied zijn, en naarmate de sterfte onder de jongen in het nest lager en het uitvlieggewicht hoger is. Wanneer we rekening houden met de emigratie van hele families en van onafhankelijke jongen, dan overleven in bijna alle jaren 40—50 procent van de uitgevlogen jongen tot 1 september. Verschillen in sterfte zijn alleen gevonden in de korte periode dat de jongen onafhankelijk van hun ouders werden. Vooral lichte jongen, met name vrouwtjes, komen om. De werkelijke overleving (overleving ongeacht de verblijfplaats) is positief gecorreleerd met het jaarlijkse gemiddelde uitvlieggewicht, maar niet met de dichtheid van de oude en jonge vogels, noch met het deel van de jongen dat afkomstig is uit tweede broedsels. In jaren met een relatief hoge sterfte werden vooral jongen van eerste broedsels met een laag gemiddeld gewicht en een vroege datum van uitvliegen door sterfte getroffen. Toch kan slechts de helft van de variatie in overleving tussen de broedsels verklaard worden. Onafhankelijk van het gemiddelde uitvlieggewicht zijn de overlevingspercentages van opeenvolgende broedsels van dezelfde ouders (eerste en tweede broedsel in hetzelfde jaar, eerste broedsels in opeenvolgende jaren) sterk positief gecorreleerd. Hieruit volgt dat de overlevingskansen van de jongen sterk beïnvloed zullen worden door wanneer en onder welke omstandigheden de ouders hun jongen aan hun lot overlaten.

De belangrijkste verschillen in plaatselijke overleving van de aldaar uitgevlogen jongen worden veroorzaakt door verschillen in dispersie. Twee verschillende types in dispersie van jongen worden onderscheiden. Ten eerste: direct na het uitvliegen vindt er een dispersie van hele families plaats die bepaald wordt door ervaringen van de ouders in hun eigen jeugd, en door de verspreiding van eiken. Deze dispersie van families veroorzaakt een herverdeling van jongen ten gunste van terreinen waarin veel eiken voorkomen, vooral wanneer in de voorgaande winters veel zaden aanwezig waren. Deze herverdeling heeft belangrijke consequenties voor het buffermechanisme dat optreedt vóór het broedseizoen, namelijk dat het bufferende effect uit het voorgaande voorjaar wordt teniet gedaan. Ten tweede: vrij snel na het onafhankelijk worden beginnen jonge vogels te migreren. De emigratie is sterk positief gecorreleerd met het jaarlijkse gemiddelde uitvlieggewicht en negatief met het aantal eiken. De mate van emigratie uit bossen met veel eiken neemt in de loop van de zomer toe, terwijl de immigratie afneemt. Dit hangt samen met de verminderde aantrekkelijkheid van eiken, gemeten aan de tijd die besteed wordt aan het voedselzoeken in eiken. Ten gevolge van verschillen in

status komt deze verandering in dispersie vooral tot uiting bij de vrouwtjes. Mannetjes worden in de loop van de tijd steeds meer plaatsgebonden. Door deze verandering in de dispersie worden de verschillen in de dichtheid van jonge Koolmezen tussen de terreinen kleiner.

Samenvattend kan gezegd worden dat de verschillen in dichtheid van de jonge Koolmezen op 1 september tussen terreinen met veel eiken en naburige armere terreinen veel groter zijn dan verwacht kan worden op grond van de aantallen uitgevlogen jongen en hun werkelijke overleving. Dit wordt vooral veroorzaakt door dispersie van broedsels in de periode dat ze van hun ouders afhankelijk zijn. Verschillen in dichtheid van de jonge mezen op 1 september werken door in verschillen in dichtheid van de territoria in de herfst en daardoor ook in het voorjaar. Verder worden de consequenties van deze resultaten besproken in het kader van de hierboven genoemde controverse tussen Kluyver en Lack.

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