Clutch size of the Reed Bunting *Emberiza schoeniclus*

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1. Introduction

The clutch size of different species of birds varies considerably. For instance, the Razorbill *Alca torda* lays clutches of one egg and the Partridge *Perdix perdix* up to twenty eggs (LACK 1947). For a certain species of bird the number of eggs laid in a clutch is less variable, although the range may still be rather large. Within a species the mode and range often vary according to time and place.

What factors determine the range and other parameters of clutch size distribution? Generally it is accepted that the clutch size of a population is adapted to time and place. The factors which have caused the clutch size to evolve to the figures found nowadays at a certain place are, on the other hand, a matter of much controversy. Before it is possible to solve such problems of general interest, much material must be gathered and analysed.

An exact knowledge of the trends of the clutch size of a species is one piece of evidence needed for determining the importance of the clutch size. Very thorough investigations have been conducted on the clutch size of certain species which nest in holes; the Great Tit *Parus major* (KLUYVER 1951, PERRINS 1965) and the Pied Flycatcher *Ficedula hypoleuca* (V. HAARTMAN 1967a, BERNDT & WINKEL 1967) have been studied most thoroughly. Some general trends on the subject of the clutch size have been presented by LACK (1947, 1948a).

In this paper I will present the trends of the clutch size in a Reed Bunting population studied by me in southwestern Finland.

The other side of the problem of clutch size is formed by the heritability of the clutch size of which there are extremely few data for wild birds. Discussion of these facts, partly on the basis of the material presented in this paper, is also given.

2. Materials and methods

The field work of this study has been conducted near the town of Pori at the mouth of the Kokemäki-River (ca. 61°32′ N, 21°44′ E) in south-western Finland. The *main study area,* to which the study of a colour-ringed population of Reed Buntings has been concentrated, is in two parts and comprises the island of Välisanta (A in Fig. 1) and the northern part of the island of Hevosluoto (B in Fig. 1). The island of Välisanta is about 25 hectares in size. The vegetation of this island is described in my earlier paper (HAUKIOJA, 1968). The northern part of Hevosluoto is about 20 hectares in area. The vegetation of this area consists largely of willow thickets (the dominating species being *Salix phylicifolia*) and marsh (the predominating species are *Carex aquatilis* and *Comarum palustre*).

The *study area* mentioned later in this paper means the main study area plus the island of Täiluoto (C in Fig. 1) and the northern part of the island of Hanhiluoto (D in Fig. 1). The vegetation of these part-areas is much like that of Hevosluoto as presented above. Besides these areas, some field work has also been done in other parts of the delta of the Kokemäki-River.

The field work was conducted during the years 1966—1969. The number of working days at the study area was 93 in 1966 and over one hundred in other years during the period when Reed Buntings, which are migratory birds in this part of their distribution area, are present. The migration times are given in an earlier paper of mine (HAUKIOJA 1969a). For the present paper the most important period of field work is the time when nests are to be found, that is from the first half of May to the end of July. During this time I have worked in the area practically daily. The most frequently examined part of the study area is the main study area. The rest of the study area has been visited less frequently, about twice per week.

The search for nests, which are regularly situated under a small willow bush or in a tussock, has been quite systematic in the main study area. Because more than 90 % of breeding birds have been individually colour-ringed in most years, and the exact number and location of pairs has thus been known, it has been possible to concentrate the search for nests to those places where a pair had been located earlier. Roughly ¾ of nests of the main study area, in which eggs were assumed to be laid, were found. In the rest of the study area, the proportion of nests found was much smaller.

323 nests of Reed Buntings were found up to the year 1969; 213 of them were from the main study area, 79 from the rest of the study area, 23 from other parts of the Kokemäki-River delta, and 8 from other parts of the town of Pori. The annual numbers of nests found have been as follows:

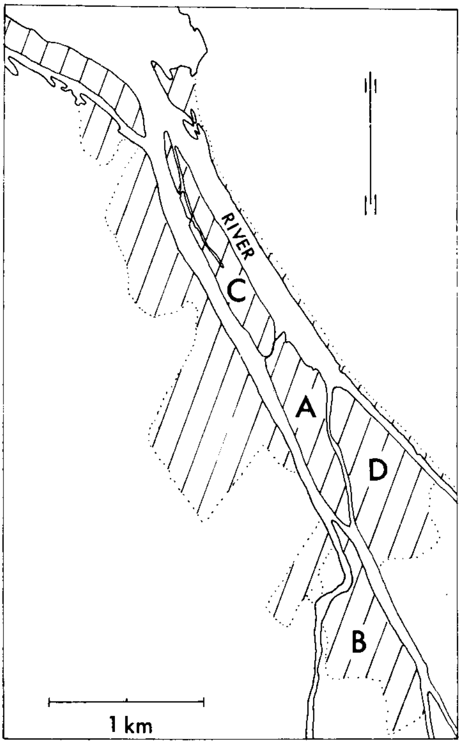

FIG. 1. Study area at the mouth of Kokemäki-River, south-western Finland. A + B = main study area, A + B + C + D = study area. Breeding sites of the Reed Bunting are striped. *(Tutkimusalue Kokemäenjoen suistossa. A + B = päätutkimusalue, A + B + C + D = tutkimusalue. Pajusirkun pesimäpaikat viivoitettu.)*

Year	Nests
1966	52
1967	73
1968	106
1969	92

Nests found have generally been examined daily or every second day in the main study area; in the rest of the study area the nests were inspected often enough to ring broods at a suitable age. The broods were ringed, if possible, at the age of five or six days, in other cases they were ringed at the age of nine days, i.e. at the age when they would have left the nest. Nestlings ringed amounted to a little over 1000 individuals.

Because special care has been taken to explain the postfledging survival of nestlings in relation to the brood size, an intensive netting programme has been conducted in the area after the end of June. Netting has been conducted on nearly every day in late summer (July and August) if weather conditions have not been unfavourable. In September netting has been less intensive. In the years 1966 and 1967 I netted in the study area only. In later years this part of the programme was the same but, in addition, netting was conducted in the lower parts of the delta by Messrs. Pertti Kalinainen and Raimo Hakila. In 1968 and 1969 the distances between the most remote netting places was about six kilometers.

For every nest a card noting every visit to the nest was made and for the present analysis an edge-notched card was made for every nest. The edge-notched cards give the following information for each nest: the year, number and location of the nest, the day the first egg was laid and the day the first young were hatched (if these were not known exactly, they were calculated from the hatching day or, after determining the age of nestlings by weighing, from this date), the number of eggs, of young hatched and of young ringed, the number of young leaving the nest, the weights of nestlings on the ringing day, the identity of parents (if ringed), the rings used for nestlings and for every young bird caught later, the sex, catching place(s) and catching date(s).

The information about the breeding biology of the Reed Bunting given in this paper is from unpublished material of mine unless otherwise specified.

3. Clutch size

I have considered a clutch as full and thus acceptable for the material if at least one of the following two conditions has been satisfied:

The number of eggs has not changed between two visits when the interval has been more than a day. This has been the most common criterion for accepting a clutch as completed. The criterion rests on the fact that eggs are laid, as in general in small passerines (Davis 1955), on successive days; in the case of the Reed Bunting in the early morning. Among several hundred possible cases, I have only twice found that the interval between two successive eggs has been two days. Both of these cases occurred in unusually cold periods in May and, consequently, they do not invalidate the argument. If there has been any doubt that the nest was deserted when found, the clutch has not been included in the material.

Another criterion for a full clutch has been that the young have been found in the nest after a shorter period than the minimum incubation period (12 days). In such cases it is probable that incubation had already begun when the nest was inspected for the first time and the clutch was then full.

In both above arguments it has been supposed that single eggs are normally not lost during the incubation period. In those nests I have visited at least twice during the incubation period, the loss of a single egg was verified only once. This source of error is therefore negligible.

3.1. *Variation within population*

The following tabulation gives the numbers of different clutch sizes of Reed Buntings found in the study area:

Clutch size	6	5	4	3
Number of clutches	68	105	21	9

The mean (n = 203) is 5.14 ± 0.05. This value, however, says very little because there are variations of several kinds in the clutch size.

The most distinct variation within a population is the change in average clutch size within a season. The mean clutch size in ten-day periods is given in Fig. 2. According to it the mean clutch size during May and the first third of June is about the same, 5.3, but after the middle of June it falls sharply and is less than four eggs per clutch on an average in July.

Changes of this kind in the mean clutch size are typical for some species of birds which lay more than one clutch per season (Snow 1955, Newton 1964, v. Haartman 1967a). The decrease in the mean clutch size during a season is probably adaptive (see later). One factor affecting this is probably that the young of the first broods are mostly fed

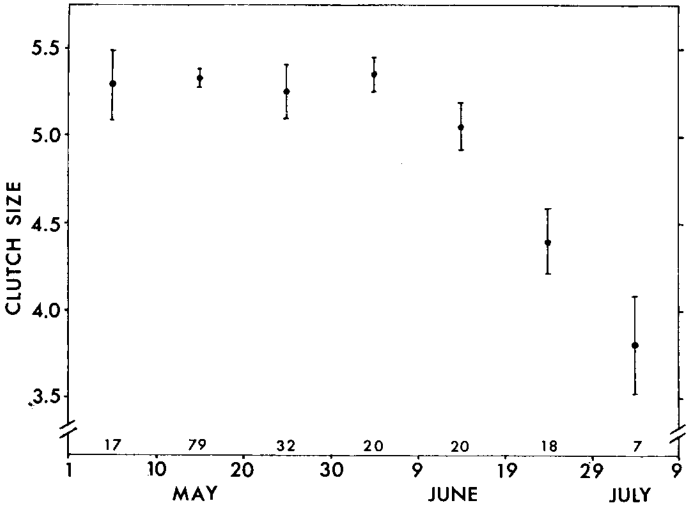

FIG. 2. Mean clutch size of the Reed Bunting in ten-day periods at Pori in 1966—1969. Range is the mean ± standard error. Sample sizes given below. *(Pajusirkun keskimääräinen pesyekoko vuosina 1966—69 Porissa kymmenpäiväjaksoina. Jana = keskiarvo ± keskivirhe. Aineiston koko alla.)*

on caterpillars but those of the last broods on adult insects (*Diptera, Lepidoptera* etc.) whose nutritional value is probably less. It may also be important in order for the female to survive not to produce so many eggs just before moulting; the weights of females feeding late broods are rather low (HAUKIOJA 1969a). This may be an indication of stress.

Because the mean clutch size varies according to the season, it is not reasonable to make any comparisons between all clutches but only between clutches laid during the phase when the mean clutch size is about the same (see Fig. 2). For this early period I have used those clutches laid in May. The justification for using a fixed date as the cessation day of "early clutches" is discussed later.

Before studying the change in the mean clutch size given in Fig. 2, it is reasonable to study how stable or unstable the clutches of an individual are and thus to try to find out whether the clutch size is environmentally or genetically determined.

If the clutch size of the Reed Bunting is genetically determined at all, it is probable that the clutch size of an individual varies less in different years than that of the population in general. It has been generally regarded that the male of a pair of birds does not determine the size of the clutch laid in the nest of the pair. This can be solved by a single test, viz. by seeing whether the clutches of the same female in successive years in the same phase of breeding vary less than those of the same male. The mean difference in the clutches of the same male laid in May in different years (largely by different females) has been 0.9 ($n = 11$). The same difference in the clutches laid by the same female has been 0.4 ($n = 21$). The difference between the sexes is statistically significant ($p < 0.05$, one-tailed Mann-Whitney U-test). So it is obvious that the clutch size is determined by the female of the pair and that it is determined, at least partially, on a genetic basis. The above test also excludes the possibility that females lay clutches of a certain size because they live in a certain territory.

Exceptionally, however, an individual female may lay clutches which vary considerably, e.g. a female which laid six eggs in May, 1967, laid three eggs during

TABLE 1. Clutch sizes of individual Reed Bunting females in the first vs. second or replacement clutches in the same season. *(Pajusirkkunaaraiden ensimmäisen/toisen tai uusintapesyeen koko samana kesänä.)*

Size of the first clutch *Ensimm. pesyeen koko*	Size of the second or replacement clutch *Toisen tai uusintapesyeen koko*			
	6	5	4	3
6	8	11	1	1
5	—	5	5	3
4	—	—	—	—
3	—	—	1	—

TABLE 2. Size of May clutches of Reed Buntings in relation to the age of the female. *(Toukokuisten pajusirkkupesyeiden koko suhteessa naaraan ikään.)*

Clutch size *Pesyekoko*	Age of female *Naaraan ikä*		
	Old *Vanha*	Unknown *Tuntematon*	Young *Nuori*
6	25	32	2
5	14	57	4
4	1	8	—
3	1	1	1
Mean *Keskiarvo*	5.5	5.2	5.0
N	41	98	7

a cold spell in May, 1968. It is obvious, therefore, that environmental factors also affect the clutch size of the Reed Bunting.

If a nest is destroyed, the female generally lays a new clutch, at least in the first and middle parts of the laying period. True second broods are probably laid only by females more than one year old. The sizes of the first clutch and of one laid later the same season by the same female are given in Table 1. The size of the second clutch is generally the same or lower than the size of the first clutch. The only exception is the female which was mentioned to be exceptional also in regard to the clutch size of different years (see above). Whether the second clutch in a season is the same or lower in size compared with the first one is largely determined by the phase of the breeding season at which the second clutch is laid. The fact that the clutch size does not in general rise in successive nestings is probably an indication that environmental factors do not greatly affect, at least directly, the clutch size of an individual female, or that the clutch size is genetically determined, not as a certain size, but as an upper limit which may or may not be arrived at.

A non-environmental factor greatly affecting the clutch size of an individual female at a certain phase of the egg-laying period is the age of the female, that is if it is one year old or older. In Table 2 the May clutches of females more than one year old and of unknown age as well as of one-year-old females are given. All age-determinations are from individuals which were ringed in an earlier year. Because the clutch size distributions are not normal, I have tested only the proportions of clutch sizes of six and five, the most common clutch sizes. The difference is significant between females known to be old and other females (which very probably also contain some old individuals) ($\chi^2 = 7.88, f = 1, p < 0.01$).

It is also possible to trace the rise in mean clutch size between successive years from the tabulation below. It gives the clutches of females found breeding for the first time in the main study area in the year 1967 or later, when females arriving in spring were largely colour-ringed. All unringed birds, however, were probably not one year old when breeding for the first time in the main study area.

First year clutch size	Second year clutch size	
	6	5
6	4	0
5	3	1

Table 3. Numbers of completed Reed Bunting clutches found in the years 1966—1969 in Pori. Only clutches laid in May are taken into account. *(Toukokuisten pajusirkkupesyeiden koot vuosina 1966—69 Porissa.)*

Year *Vuosi*	Clutch size *Pesyekoko*				Mean *Keskiarvo*	N
	6	5	4	3		
1966	9	7	—	—	5.6	16
1967	21	13	1	1	5.5	36
1968	23	26	5	2	5.3	56
1969	6	29	3	—	5.1	38
Σ	59	75	9	3	5.3	146

The differences in the clutch sizes of age groups might theoretically be the reason for the seasonal trend in the clutch size of the Reed Bunting. This would be true if the decline in the mean clutch size (Fig. 2) were due to young females laying their smaller clutches at later phases of the breeding season. However, late clutches are practically all laid by old females, which only lay true second clutches, and so the above possibility is ruled out.

Lack (1954a) assumes that the lower clutch size of first year birds found e.g. in many passerines (Great Tit, Kluyver 1951, Pied Flycatcher v. Haartman 1967a) is an adaptation, for females breeding for the first time are on average not able to raise as large broods as old females. This has been verified, among others, for the Blackbird *Turdus merula* (Snow 1958) and the Great Tit (Perrins 1965). The situation is obviously the same for the Reed Bunting (p. 116).

The differences in the clutch sizes of different age classes and within an individual are thus quite small. With this in mind it is assumed that the annual differences in the mean clutch size in May are not great. These data are given in Table 3. When testing different years I have again used the proportions of clutch sizes of six and five, the most common clutch sizes. The proportions of these clutch sizes differ significantly in different years ($\chi^2 = 8.82$, $f = 3$, $p < 0.05$).

A possible bias causing differences might arise if the proportion of young females in the population varies considerably from year to year. If this were so, the breeding population of the year 1969 should probably contain the greatest proportion of young females. However, in this year the proportion of old, colour-ringed females was the largest among females arriving during the springs of 1967—1969 when it was expected that in the preceding year nearly all breeding females were colour-ringed. This material will not be dealt in this paper.

Obviously environmental factors are the reason for differences in the mean clutch size between different years. The start of laying varies in different years. In the following tabulation the mean date of clutches laid in May has been used as a measurement of the earliness of the laying. Only nests from the main study area are taken into account because in this area the search for nests has been most even during all phases of the breeding season. Day No. 1 is the first of May.

1966	22 ± 1.1	(22)
1967	19 ± 0.8	(31)
1968	13 ± 1.1	(39)
1969	21 ± 1.1	(28)

So the only year when the mean laying date differs considerably from others is

TABLE 4. Mean daily temperatures in May, 1966—1969, in Pori during the time 5 days before — 5 days after the mean laying date in May. *(Vuosien 1966—69 keskimääräiset vuorokausilämpötilat Porissa 5 vrk ennen — 5 vrk jälkeen toukokuun keskimääräisen munintapäivän.)*

Year *Vuosi*	Period *Jakso*	(°C)
1966	17.—26.5.	11.7°
1967	14.—23.5.	9.6°
1968	8.—17.5.	6.3°
1969	16.—25.5.	6.9°

1968, but the mean clutch size of this year is very near the mean value for the whole material. It is thus evident that differences in the start of laying are not the reason for annual variations in the clutch size. Also the use of May clutches as "early clutches" is thus reasonable.

The lowest mean clutches occurred in the years 1969 and 1968 when the temperature of the middle of May was also the lowest (Table 4). It may be mentioned that during a cold spell in May, 1969, several females in the main study area deserted their clutches during the egg-laying period although they were not disturbed by me and in 1968 the only dwarf-eggs of the Reed Bunting I ever have found were laid in two nests during the cold spell in May. Also the intervals of more than one day between the laying of successive eggs mentioned earlier are both from these cold periods in May. Because the weather leads to abnormalities in egg-laying (there are possibly difficulties in forming eggs) it seems quite natural that it may also result in reduced clutch size.

The clutch size of the population studied varies, according to the above treatment, with the season, the age of the female, and there are, in addition, differences between years. All these differences have been verified, e.g. for the Great Tit (KLUYVER 1951), the Pied Flycatcher (v. HAARTMAN 1967a), and the Blackbird (SNOW 1958).

3.2. *Differences between populations*

In addition to the intrapopulation variations in the clutch size there is a marked difference between different populations. In the following tabulation the clutch sizes of my study area (May) and those given by GÉROUDET (1962) from Switzerland from April—May are presented.

	Clutch size				Mean
	6	5	4	3	
Southern Finland	59	75	9	3	5.30
Switzerland	3	48	6	1	4.91

The difference between proportions of six and five eggs is statistically significant ($p < 0.001$, Fisher exact probability test).

From northern Scandinavia I know two places from where there are published data on the clutch size of the Reed Bunting (LENNERSTEDT 1964 from Ammarnäs, Swedish Lapland, and HILDÉN 1967 from Karigasniemi, Finnish Lapland). These data are as follows:

	Clutch size				Mean
	7	6	5	4	
Karigasniemi (69° N)	—	11	8	2	5.4
Ammarnäs (66° N)	1	10	—	—	6.1

The materials from Karigasniemi and Ammarnäs differ significantly in the proportions of six and five eggs ($p = 0.02$, Fisher exact probability test). My material from Pori differs significantly from that of Ammarnäs ($p < 0.001$, Fisher exact probability test) but does not differ from that of Karigasniemi ($\chi^2 = 0.79$, $f = 1$).

From Estonia ONNO (1968) gives the following clutch sizes of Reed Buntings from Matsalu Bay (59° N):

6	5	4	3—1	Mean
18	24	6	1	5.20

Because clutches of whole seasons have

been combined in ONNO's material, the comparisons with my material are best done by comparing the whole of my material with his. There is no significant difference between these two materials ($\chi^2 = 0.15$, $f = 1$).

As considered by LACK (1947), the longer daylight hours may be the reason why the clutch size tends to rise from southern Europe to north. This enables the parents to feed more young during the long days in the north. This, however, presupposes that food for the young is the ultimate limiting factor in clutch size. The author (LACK 1954a, 1966 etc.) has produced much evidence, indeed, to show that the amount of available food is at least on some occasions the correct explanation; what the significance of the number of daylight hours is, however, is not known. CODY (1966) has presented a general hypothesis of clutch size according to which the clutch size is low in areas where there are stable environmental conditions. According to this hypothesis the clutch size is determined by how an individual bird uses its existence energy for reproduction, avoiding predators and for competition, and this varies in different areas. LACK's (1947) explanation is a part of CODY's (1966) hypothesis.

The biotopes most preferred by the Reed Bunting differ in various parts of the species' distribution. From Neusiedlersee we know that the most preferred habitats of the Reed Buntings are reed beds (ZIMMERMANN 1944, KOENIG 1952) but in Finland FRITZÉN & TENOVUO (1957) have shown that the most preferred habitats are low thickets of willow (*Salix*), which in my study area also form the area of the densest population (HAUKIOJA 1969a). It has been shown in many species that the habitat has an effect on the mean clutch size (in the Great Tit (KLUYVER 1951), the Pied Flycatcher (LÖHRL 1965), and the Blackbird (SNOW 1958). If the situation is the same for the Reed Bunting, then it may be a possible reason for the differences between different areas. It is not possible to test whether the clutch size of the Reed Bunting varies according to the habitat using my nesting material because I have not much material from biotopes other than those usual in my study area.

An interesting aspect is still worth discussing. For 21 broods hatched from eggs laid in May (1966—1967 material analysed), the mean nestling period was 9.2 days (range 9—10 days) in my study area. These broods were not handled by man after the sixth day of life. From Switzerland GÉROUDET (1962) gives the following nestling periods: 10, 11—12, and 12—13 days. The difference between these and the values from my study area is statistically significant ($F = 45.79$, $f = 1, 22$, $p < 0.001$). From England BELL (1967) mentions having ringed a brood of Reed Buntings at the age of eight days and at the age of ten days the young were still in the nest. This would be quite impossible in my study area; it is extremely difficult to succeed in getting a seven-day-old brood to stay in the nest.

The nestling period is thus longer in Switzerland and possibly also in England where WITHERBY *et al.* (1958) give the clutch size for the Reed Bunting as 4—5 normally, occasionally 6, rarely 7 in Scandinavia. If the clutch size of the Reed Bunting were adapted to produce as many young as possible in all areas, and this were the only aim, then why are there no clutches of seven or eight eggs in my study area when it is possible to shorten the nestling period? A logical answer to this question would be that the shorter nestling period per se may be very important in Northern Europe in order to avoid predators or for some other reason. However, in my main study area the mean percentage of eggs producing fledglings (nine days old) has been

48 % for the years 1966—1967, which material has been analysed so far. This does not deviate much from the figure given by NICE (1957) for birds building open nests (46.9 %). HILDÉN (1967) reports a still lower predation rate for the Reed Bunting from Finnish Lapland; this, however, is based on a very small amount of material. It is, therefore, not clear whether the mere struggle for as high a production of young as possible is the only factor in operation.

This question relates to another important question in this paper. Why do the Reed Buntings of my study area in an early phase of the laying period lay almost exclusively clutches of five and six? The skewness of this distribution (—0.879 with standard deviation of 0.211) differs significantly from the normal distribution (t-test, $p<0.001$). Especially the upper portion of the clutch size distribution is much truncated. Studying these matters is important because answers to above questions are needed in order to solve more general aspects of the clutch size.

4. Productivity of different clutch and brood sizes

According to LACK (1947 and later) the most common clutch size is that which produces most surviving young for the population. According to SKUTCH (1949, 1967) this, at least in tropical areas, does not hold true and the clutch size is determined, not by the upper limit of parents' ability to feed their young, but by the need to maintain the population at a reasonable level. WYNNE-EDWARDS (1962) discusses possible mechanisms leading to this. CODY (1966) has shown that these opinions are not necessarily alternatives but may each form a part of a more general explanation.

If birds of the northern temperate zone produce as many offspring as they can, then the Reed Bunting, which is a typical species of this region, would do likewise. I shall next examine whether clutches of a certain size are more or less productive than others. Because the clutch size of the Reed Buntings studied declines in the middle of June it is not reasonable to combine early and late clutches.

4.1. *Early broods*

Early broods mentioned later are those in which young have hatched not later than June 15th. I have shown earlier (HAUKIOJA 1969a) that according to the post-fledgling weight development this date of hatching is a suitable criterion for classing young Reed Buntings of my study area as early and late ones.

Nestling period — If there are any differences in the proportional or absolute productivity of different sizes of clutches, then the first possibility is that total losses (mainly as a result of predation) are dependent on the clutch or brood size. The material from my study area is given in Table 5. There are no significant differences in relation to clutch ($\chi^2 = 0.84$, $f = 2$) or brood ($\chi^2 = 0.78$, $f = 2$) sizes.

The following possible source of difference occurs if the hatching percentage is dependent on the clutch size. Table 6 gives this material and there are no significant differences in relation to clutch size ($\chi^2 = 0.01$, $f = 2$).

During the nestling phase the loss of individual young from early broods of Reed Buntings of my study area after the hatching day when some young perish is negligible. The nestlings have been ringed at the age of five or six days and the size of broods at this time in relation to the size at hatching is given in Table 7. Losses (largely during the first day of life) are not statistically dependent on the brood size ($\chi^2 = 2.81$, $f = 3$).

TABLE 5. Total losses of Reed Bunting clutches and broods in relation to original clutch and brood size in early broods. *(Tuhoutuneet pajusirkkupesyeet ja poikueet suhteessa pesyekokoon aikaisissa pesyeissä.)*

Size of clutch/brood *Pesye-/poikue-koko*	Clutches *Pesyeitä* N	Clutches *Pesyeitä* Total losses *Tuhoutunut*	Clutches *Pesyeitä* %	Broods *Poikueita* N	Broods *Poikueita* Total losses *Tuhoutunut*	Broods *Poikueita* %
6	46	25	54	14	2	14
5	39	19	49	22	6	27
4 1—3	5	4	80	17	3	17
Σ	90	48	53	53	11	21

It is, however, possible that large broods of Reed Buntings are undernourished. If so, this would be seen from the weights of nestlings. After the sixth day of life it is often not possible to leave nestlings in the nest after weighing. Therefore I have used as the weights those which have been obtained in connection with the ringing of nestlings. These weights in relation to the brood size at the ringing age are given in Table 8. There are no significant differences between broods of different size at least up to this age. It is still possible that although mean weights do not differ significantly, there are differences in the weight of the lightest young in relation to the brood size. Table 9 gives the numbers and percentile proportions of those broods in which the lightest young weighed less than $^4/_5$ of the mean weight of young in the whole brood. The greater the brood size the more broods there seem to be in which such light young are found. The difference is statistically not significant ($\chi^2 = 1.97$, $f = 3$), however. When we take into account that large broods contain more young than small broods it seems that only in broods of six young, if any, is the proportion of light young greater (right column in Table 9). The difference is, however, statistically not significant ($\chi^2 = 0.40$, $f = 3$).

After the ringing age (five or six days) there are practically no losses (excluding total losses) during the rest of the nestling period (Table 10). The

TABLE 6. Unhatched eggs in relation to clutch size in the Reed Bunting. (*Pajusirkun kuoriutumattomat munat suhteessa pesyekokoon.)*

Clutch size *Pesyekoko*	Unhatched *Ei kuor.* 0	1	2	3	4—6	Clutches *Pesyeitä*	Eggs *Munia*	Unhatched *Ei kuor.*	%
6	26	14	6	—	—	46	276	26	9.4
5	38	11	3	3	—	55	275	26	9.5
4	6	1	—	—	—	9	34	3	8.8
3	1	—	1	—	—				
Σ	71	26	10	3	—	110	585	55	9.4

TABLE 7. Size of Reed Bunting broods at the age of 5 or 6 days in relation to the number of nestlings hatched. *(Pajusirkkupoikueiden koko 5—6 vrk:n iässä suhteessa poikuekokoon kuoriutuessa.)*

Hatched *Kuor:t*	Brood size at ringing *Poikuekoko reng.iässä*						Hatched *Kuor:t*	Young lost *Poikasia tuh.*	
	6	5	4	3	2	1		N	%
6	19	1	1	—	—	—	126	3	2.4
5		33	9	1	—	—	215	11	5.1
4			14	3	3	—	80	3	3.8
3				4	—	1	21	2	9.5
2					3	—			
Σ							442	19	4.3

TABLE 8. Weights (g) of Reed Bunting nestlings at the age of ringing in relation to brood size. *(Pajusirkun pesäpoikasten painot (g) rengastusiässä suhteessa pesyekokoon.)*

Brood size *Poikuekoko*	Age *Ikä*			
	5 days *vrk*	N	6 days *vrk*	N
6	10.7±0.3	8	13.3±0.5	13
5	10.5±0.4	17	12.6±0.4	13
4	11.2±0.6	12	13.9±0.3	10
1—3	11.0±0.9	3	13.3±0.4	8

situation is thus the same as before the ringing age excluding the first day of life.

It is obvious, consequently, that in early broods large and small broods are percentagewise about equally productive as regards the time of nest-leaving.

After the fledgling period — A quite different picture is obtained from Table 11 which gives the numbers of young captured after the beginning of July in relation to the brood size at the age of ringing.

There is the same tendency in all catching periods; percentually very few young have been caught from large broods and many from small ones. By

TABLE 9. The number of Reed Bunting broods and young in broods where the lightest young weighed less than $^4/_5$ of the mean of the brood at the age of ringing and their relation to brood size. *(Pajusirkkupoikueiden määrät, joissa kevein poikanen painoi alle $^4/_5$ poikueen keskipainosta, suhteessa poikuekokoon.)*

Brood size *Poikuekoko*	Young *Poikasia*	Light young *Keveitä poikasia*	% Out of broods *Poikueista*	% Out of young *Poikasista*
6	126	6	29	4.8
5	150	5	17	3.3
4	84	3	14	3.6
2—3	28	1	9	3.6
Σ	388	15	17	3.9

TABLE 10. Number of Reed Bunting young leaving the nest in relation to the brood size at the time of ringing. *(Pesästälähtevien pajusirkkupoikueiden koko suhteessa poikuekokoon rengastusiässä.)*

Brood size at ringing *Poikuekoko reng.iässä*	Broods leaving the nest *Pesästäläht. poik.* 6	5	4	3	2	Young *Poikasia*	Lost *Tuh.*
6	12	—	—	—	—	72	0
5		16	1	—	—	85	1
4			12	—	1	52	2
3				2	—	6	0
2					3	6	0
Σ						231	3

adding together the numbers caught in each brood size we get the values given in Table 11 (right). These numbers differ significantly from an assumed stable catching probability of each brood size ($\chi^2 = 15.00$, f = 3, $p < 0.01$). During single periods, the deviation from equal catching probability in relation to brood size is directive for the period 1—15.7. ($\chi^2 = 6.82$, f = 3) and significant for the period 16.7.—15.8. ($\chi^2 = 10.66$, f = 3, $p < 0.025$). Combining all catching periods is justified because the proportions from different brood sizes do not significantly change after the first half of July:

1—15.7./16.7.—15.8. $\chi^2 = 1.06$, f = 3
1—15.7./16.8.—30.9. $\chi^2 = 1.31$, f = 3
1—15.7./later years $\chi^2 = 2.16$, f = 3

It is thus obvious that the brood size at the age of ringing, which is practically the same as that at the age of leaving the nest (Table 10), affects the survival of young after leaving the nest. Because the proportions between different brood sizes do not change significantly after the beginning of July, it is evident that the effects of brood size on the survival of young occur largely up to this time. This means that the time between nest-leaving (at the age of about 9 days) and independence (at the age of about 30 days) is the time of real crisis for the Reed Buntings studied.

Because the category of "early broods" contains broods hatched up to the 15th June and on the other hand the catching files presented in Table 11 contain recoveries made after the first of July, it is evident that mortality dependent on brood size has occurred nearer the time of nest-leaving than the time of becoming independent. If it were other-

TABLE 11. Recaught Reed Buntings after the 1st July in relation to brood size at ringing. *(Kontrolloidut pajusirkut heinäkuun alun jälkeen suhteessa pesyekokoon rengastusiässä.)*

Brood size *Poikuekoko*	Young *Poikasia*	Recaught *Kontrolloitu* 1—15.7. N	%	16.7.—15.8. N	%	16.8—30.9. N	%	Later years in Pori *Myöhemmin Porissa* N	% *	Σ N	%
6	132	7	(5.3)	5	(3.8)	5	(3.8)	8	(7.5)	25	(18.9)
5	215	20	(9.3)	22	(10.2)	21	(9.8)	10	(7.4)	73	(34.0)
4	111	14	(12.6)	10	(9.0)	12	(10.8)	6	(6.9)	42	(37.8)
1—3	44	8	(18.2)	9	(20.5)	4	(9.1)	3	(15.0)	24	(54.5)
Σ	502	49	(9.8)	46	(9.2)	42	(8.4)	27	(7.7)	164	(32.7)

* Calculated from young ringed in 1966—1968. *(Laskettu vuosina 1966—68 rengastetuista poikasista.)*

wise, the proportions of recaught young would probably have been higher in small broods from the first half of July onwards, because the latest broods among "early broods" have not become independent at the beginning of July but some of these have been caught after attaining flying capacity at the age of about fifteen days.

Differences between sexes — Young Reed Buntings have been sexed (for criteria see HAUKIOJA 1969a) when caught after leaving the nest. The numbers of recaught males and females in relation to the brood size at the age of ringing are given in Table 12. The tendency of large recovery percentages for small broods and vice versa is obvious for both sexes but statistically not significant ($\chi^2 = 2.32$ for males and 4.95 for females, f = 3 for both sexes). The table indicates that the small percentile proportion of recaught birds from the broods of six young is principally caused by the fact that not many females from these broods have been recaught. This is based on a rather small amount of material but on the other hand it does not seem impossible that females, which are smaller than males even during the nestling period, are less efficient at begging food than larger males during critical periods. Another possibility is that the runts in nests are largely females and that these from broods of six soon perish after leaving the nest. That the runts may be largely females, is shown by GAVRILOV (1968) for the Spanish Sparrow *Passer hispaniolensis*.

TABLE 12. Female and male Reed Buntings recaught after 1st July in relation to brood size at the time of ringing. *(Heinäkuun alun jälkeen pyydystetyt koiras- ja naaraspajusirkut suhteessa pesyekokoon rengastusiässä.)*

Brood size *Poikue-koko*	Young *Poika-sia*	Recaught *Kontrolloitu* ♂ N	%	♀ N	%
6	132	11	8.3	11	8.3
5	215	21	9.8	33	15.3
4	111	14	12.6	18	16.2
1—3	44	7	15.9	9	20.5
Σ	502	53	10.6	71	14.1

TABLE 13. Mean distances from birth site of female and male Reed Buntings ringed as nestlings and later recaught during their first summer after the 15th July in relation to brood size at ringing age *(Pesäpoikasina rengastettujen, ensimmäisenä kesänä heinäkuun puolivälin jälkeen kontrolloitujen koiras- ja naaraspajusirkkujen keskimääräiset etäisyydet syntymäpaikalta suhteessa pesyekokoon.)*

Brood size *Poikuekoko*	Distance from birthplace *Etäisyys syntymäpaikalta* km ♀ x̄	N	♂ x̄	N
6	0.3	3	1.0	5
5	1.2	28	0.9	12
4	0.8	15	1.6	9
1—3	0.6	7	1.1	3

Above I have used recoveries as a measurement of survival. This, of course, is permissible only if the brood size at the age of ringing does not affect the dispersal of young during their first summer and later. It is not easy to verify this in a study area only a few kilometers in diameter. I have calculated the mean distances between the birth place and the place where young were recaught during the time 16th July—20th September the first summer (Table 13). In the years 1966—1968, when catching was conducted principally in the main study area, only broods ringed in this area were taken into account. In the year 1969 when there were catching points all over the delta of the Kokemäki-River, all broods ringed in the delta-area were included. There are no significant differences among the recovery distances of males ($F = 1.91$, $f = 3, 25$) or among recaught females ($F = 2.66$, $f = 3, 49$) in relation to the original brood size. Therefore, to use the recovery numbers as a measurement of survival has seemed justified. It may still be possible that the original brood size results in long-distance wandering after independence, but this kind of phenomenon does not seem probable. It may be stressed that the values in Table 13 as such have no biological equivalents; they only show what *I* have observed, but I think there is no reason to believe that they were not comparable with each other.

The difference in numbers of recaught females (71) and males (53) is statistically not significant. The most evident cause of this uneven distribution is that females probably stray less than males during their first summer. This topic will be treated more thoroughly in a later paper. That the numbers of females and males are at least nearly equal among young Reed Buntings is shown by the fact that during August, 1966—1969, 292 ♂♂ and 305 ♀♀ were among the sexed young Reed Buntings captured for this study.

Table 12 gave the percentages of recoveries from broods of different size. The importance of these figures for the population is obvious only when the absolute brood size is taken into account. In the following tabulation I present the productivity (= recovery) indices (recovery per cent/100 × brood size) for both sexes as calculated from the data of Table 12.

Brood size	Productivity index ♂	♀
6	0.50	0.50
5	0.49	0.77
4	0.50	0.65
1—3	0.41	0.53

According to the tabulation the brood sizes of 4, 5 and 6 young are equally efficient for producing males and smaller brood sizes are nearly as efficient. For females the brood size 5 which also is the most common in my material (43 early broods ringed) is the most productive. The second is the brood size of 4 young which is the second in order among ringing material (28 early broods) and the least productive have been small broods and broods of 6 young, the numbers of which in the ringing material of early broods are 17 and 22 respectively.

If we weight the recovery numbers for males and females we arrive at the following values and combined productivity indices:

Brood size	Relative productivity index ♂	♀	Combined
6	0.26	0.20	0.46
5	0.26	0.31	0.57
4	0.26	0.27	0.53
1—3	0.22	0.22	0.44

The order of these combined values is the same as that of the numbers of broods of different size ringed.

In the above indices the deviation from the mean is greater for females than for males ($p = 0.03$, one tailed Mann-Whitney U-test). This topic is discussed later.

The clutches from which the early broods have hatched were laid in May. According to Table 3 the dominant clutch size is 5 in May broods; clutches of 6 eggs are also common but clutches of 4 and 3 eggs occur much less.

In Table 14 I have calculated (according to binomial distribution) the probable distribution of broods of different sizes which come from a certain clutch size (excluding total losses) at the age of ringing. In these calculations the hatchability of eggs was regarded as 90.6 % (Table 6) and the survival of young up to the age of ringing as 95.7 % (Table 7). These values were assumed to be independent of the clutch size.

In Table 14, the calculated mean productivity indices for each clutch size are also given. These have been calculated by using both the productivity indices of females alone and the combined indices for each brood size. Both methods provide us with the result that the most

TABLE 14. Calculated brood size distribution at the ringing age in the Reed Bunting per 100 nests and their productivities in relation to the original clutch size. *(Laskettu pajusirkun poikkuekokojakautuma rengastusiässä 100 pesää kohti tuottoisuusindekseineen suhteessa alkuperäiseen pesyekokoon.)*

Clutch size *Pesyekoko*	Brood size *Poikuekoko*						Relative productivity index *Suhteellinen tuottoisuusindeksi*	
	6	5	4	3	2	1	♀	♂ ♀
6	43	39	15	3	—	—	0.25	0.26
5		50	37	11	2	—	0.28	0.27
4			57	34	8	1	0.25	0.25
3				66	30	4	0.22	0.22

productive clutch size is five. Six eggs, closely followed by four eggs are the following in order and then come clutches of three. The order of the combined values is exactly the same as that occurring naturally, and that based on females alone is nearly the same. Thus it seems evident that the clutch size of the population studied is adapted to produce clutches from which the number of offspring produced is the largest. This optimum clutch size for efficient reproduction is a little higher than the optimum brood size and so allows normal losses of single eggs and/or young.

4.2. *Late broods*

By late broods is meant those from which young have hatched on or after the 16th June. I have further divided these into two groups: those hatched before the end of June and those hatched afterwards. This practice has been adopted because the earliest of the late broods have mainly been laid during the phase of the laying period when the mean clutch size is high (Fig. 2). The later broods from these late clutches are from the phase of laying period when the mean clutch size is declining. The earliest of the late clutches probably give rise to broods of about the same size as in ”early broods” but for reasons of caution I have not combined these. Those clutches hatched after the beginning of July clearly form a group of their own.

In Table 15 young recovered from broods hatched during the latter half of June are given in relation to brood size at the age of ringing.

TABLE 15. Reed Buntings hatched during 16—30.6., ringed as nestlings and recaught after the 15th July in relation to brood size at the age of ringing. *(16—30.6. kuoriutuneet, pesäpoikasina rengastetut ja heinäkuun puolivälin jälkeen kontrolloidut pajusirkut suhteessa poikuekokoon rengastusiässä.)*

Brood size *Poikuekoko*	Young *Poikasia*		Recaught *Kontrolloitu*						Productivity index *Tuottoisuusindeksi*
			♂		♀		Σ	%	
6	42		4		3		7	16.7	1.00
5	130		13		14		27	20.8	1.04
4	20	27	1	4	—	1	5	18.5	0.56
1—3	7		3		1				
Σ	199		21		18		39	19.6	

TABLE 16. Reed Buntings hatched in July, ringed as nestlings and recaught after the beginning of August in relation to brood size at the age of ringing. *(Heinäkuussa kuoriutuneet, pesäpoikasina rengastetut ja elokuun alun jälkeen kontrolloidut pajusirkut suhteessa poikuekokoon rengastusiässä.)*

Brood size *Poikuekoko*	Young *Poikasia*	Recaught *Kontrolloitu*				Productivity index *Tuottoisuusindeksi*
		♂	♀	Σ	%	
6	—	—	—	—	—	—
5	40	1	6	7	17.5	0.88
4	51	5	4	9	22.5	0.90
1—3	23	1	3	4	17.4	0.50
Σ	114	7	13	20	17.5	

Table 16 gives the same information for broods hatched in July.

Because these tables are based on much smaller data than those of early broods I think that there is no good reason to analyze these as carefully as those of early broods. Some features may, however, be mentioned.

Table 15 gives much the same kind of picture as Table 11 for early broods and it seems apparent that, in relation to brood size, no great changes as regards survival have taken place. The most productive brood size seems to be five, which is also the most common. The brood size of six gives nearly the same productivity, which, however, is based on much smaller material. Those broods hatched in the latter half of June were nearly all fed by both parents. The broods can thus be compared with each other. The earliest broods hatched in July are generally fed by both parents but later broods are as a rule fed by the female alone. The material in Table 16 is rather heterogeneous in this respect. Out of broods of five young, two broods were fed by the female alone; no young from these broods were recaught later. Of the remaining six broods fed by both parents, five produced at least one young bird recovered later. From smaller broods there are young recovered from broods fed either by the female or by both of the parents.

The most common brood size in later broods has been four and, according to Table 16, this has also been the most productive. Because the mean clutch size decreases by more than one egg per clutch during the time when broods hatching in July are laid, this, perhaps, indicates that the most productive clutch and brood size varies even during this period. This, however, is circular reasoning. This period should be divided into separate smaller periods but the paucity of the material does not allow it.

4.3. *Production of young in relation to the age of parents*

The numbers of young caught after the beginning of July in relation to the brood size of those broods fed by an old female (aged on the basis of being ringed in an earlier year) are given in Table 17 where also the numbers of young caught produced by other females (among which there are probably old individuals, too) are given. The mean percentage for the former group is 30, that of the latter 23. The difference is, however, statistically not significant; the trend is nevertheless the same for all common brood sizes: old females have produced percentually and absolutely more young from their first broods than young females.

TABLE 17. Reed Buntings from early broods recaught after the beginning of July in relation to brood size at ringing and the age of female. *(Aikaisin kuoriutuneiden ja heinäkuun alun jälkeen kontrolloitujen pajusirkkujen määrät suhteessa naaraan ikään ja poikuekokoon rengastusiässä.)*

Brood size *Poikuekoko*	Young ringed from *Poikasia rengastettu*		Young recaught from *Poikasia kontrolloitu*			
	Old ♀ *Vanha*	Unknown age ♀ *Ikä tuntematon*	Old ♀ *Vanha*		Unknown age ♀ *Ikä tuntematon*	
			N	%	N	%
6	58	84	11	23	11	13
5	30	185	9	30	44	24
4	28	83	12	43	20	24
1—3	3	41	1	(33)	15	37
Σ	109	393	33	30	90	23

The corresponding figures for broods fed by an old male or by a male of unknown age are given in Table 18. The mean numbers of recovered young are 34 and 21 % respectively. The difference is not significant between groups here, either, but the trend is again the same. My material is rather small to make it possible to test the productivity indices for broods fed by two birds known to be old, by two birds one of which was known to be old, and by two young birds. 86 young, produced by two old parents gave 22 recaught young (26 %). 87 young, produced by one parent known to be old, gave 29 recaught young (33 %).

It is possible that the differences observed between the percentile productivity of young and old parents is due to old females laying earlier and young ones later. However, this is not a plausible explanation because only early broods were considered, all of which were laid in May and the difference between the mean laying dates of old and young females is less than a week.

TABLE 18. Reed Buntings from early broods recaught after the beginning of July in relation to brood size at ringing and the age of male. *(Aikaisin kuoriutuneiden ja heinäkuun alun jälkeen kontrolloitujen pajusirkkujen määrät suhteessa koiraan ikään ja poikuekokoon rengastusiässä.)*

Brood size *Poikuekoko*	Young ringed from *Poikasia rengastettu*		Young recaught from *Poikasia kontrolloitu*			
	Old ♂ *Vanha*	Unknown age ♂ *Ikä untematon*	Old ♂ *Vanha*		Unknown age ♂ *Ikä tuntematon*	
			N	%	N	%
6	48	84	9	19	13	16
5	50	165	22	44	31	19
4	48	63	18	37	14	22
1—3	9	35	3	33	13	37
Σ	155	347	52	34	71	20

5. On the genetic basis of the clutch size

In some species of birds whose clutch size variation is well known (especially the Great Tit) there are very great environmental modifications to the clutch size in addition to the possible genetic basis. This, above all, is the factor making a field study of the heritability of the clutch size of wild birds very difficult. So it is not astonishing that very little is known about this phenomenon. In the following I shall discuss some problems relating to the topic because the genetics of clutch size is of prime importance in developing theories of the evolution of the clutch size (see BIRCH & EHRLICH 1967).

5.1. *The probable nature of heredity*

Several kinds of evidence have been presented in order to show that clutch size is genetically determined. The laying qualities of poultry are known to be at least partially determined by genetic factors because selection may improve egg-production in some strains (e.g. NORDSKOG *et al.* 1967). This, however, is not equivalent to the situation in wild birds because poultry do not generally lay clutches. The second kind of evidence of genetic determination of the clutch size of birds is the fact that the clutches of the same female in successive years vary less than those of the whole population. This has also been verified in this study of the Reed Bunting. The same kind of situation has been found e.g. in the Alpine Swift *Apus melba* (LACK & ARN 1947), the Swift *Apus apus* (LACK & LACK 1951), the Starling *Sturnus vulgaris* (LACK 1948b), the Velvet Scoter *Melanitta fusca* (KOSKIMIES 1957), the Collared Flycatcher *Ficedula albicollis* (LÖHRL 1957), the Pied Flycatcher (CURIO 1959), the Skylark *Alauda arvensis* (DELIUS 1965), the Kittiwake *Rissa tridactyla* (COULSON & WHITE 1961), and the Great Tit (KLUYVER 1951, v. HAARTMAN 1969).

Although it has been found that the clutch size of an individual is less variable than that of the population, this does not necessarily prove a genetic basis. KLUYVER (1951), finding individual stability in the Great Tit, regards the constancy of the clutch size of an individual female not necessarily as a mark of inheritance but states that birds living permanently in a certain environment may lay clutches of a certain size and this might perhaps not be genetically but environmentally determined constancy. In the Reed Bunting territorial determination was ruled out as a probable mechanism leading to stable clutch sizes in the same female (p. 104). As another argument against the heritability of clutch size in the Great Tit KLUYVER (1963) states that females producing most ringed young also produce most young for the subsequent population. But the number of ringed young per female was the combined value from the first and possible second brood, and thus it had very little to do with the genetics of the clutch size (but rather with the possible genetics of the number of clutches in a season).

In his earlier analyses, LACK has treated the topic of clutch size evolution as if the heritability of clutch size were selfevidently high. WAGNER (1957) has criticized this and regarded the upper limit of the clutch size as the only heritable factor. He stresses the great importance of environmental factors for the determination of the clutch size. LACK (1958) has also discussed phenotypic modifications of the clutch size especially in the Great Tit. Thus it is worth discussing what is most probably inherited.

On the basis of the present investigation (p. 105) I see no reason to think that the clutch size is genetically determined in terms of the number of eggs. It seems more reasonable that the clutch size is determined genetically by how an individual female responds to certain environmental stimuli; there are thus thresholds for certain stimuli which are probably genetically different. The results presented by MILLER (1960) for the *Zonotrichia* species is an indication that genetic differences exist between threshold values in populations of the same species in their responses to photoperiodism, which is an example of much the same kind of nature. Of course, these genetically determined responses must be such that, in certain environmental conditions, they produce a clutch whose size is adapted to probable conditions during the raising of the young. I think this best explains the general constancy and at the same time makes the great potential range and flexibility of an individual's clutch comprehensible. ''Nongenetic variation is usually adaptive and controlled by natural selection, since genetic factors determine the amount and the direction of the permissible flexibility of the phenotype'' (MAYR 1966, p. 139).

The clutch size distribution found in the Reed Bunting deviates significantly from a symmetric distribution. Although we may suppose that clutches of seven eggs would be very nonproductive (this is treated later, there is a very large drop in the clutch size distribution of my material at the upper end — 68 nests with six eggs (in two Mays of four possible even the mode) and not a single nest with seven eggs has been found. This is best explained, I think, by supposing that there is an upper limit to the clutch size between six and seven eggs, which was not exceeded in the population I studied. The same limit is probably also found in most populations studied elsewhere (Switzerland, Estonia, Northern Lapland, see p. 107). Only the material originating from Swedish Lapland (Ammarnäs) contains a clutch with seven eggs. v. HAARTMAN (1969) also mentions two nests with seven eggs from Finnish Lapland.

The above opinion that the limit(s) of the clutch size and responses to certain environmental stimuli (and not the number of eggs laid) are determined genetically excludes the opinion that clutch size is a form of balanced polymorphism (LACK 1948b, HUXLEY 1955). It also explains well small differences in mean clutch sizes and small or negligible differences in range when comparing different populations (see v. HAARTMAN 1954, JOHNSTON 1954). Whether these differences in mean clutch sizes are due to differences in environment or in genetically determined responses to these environmental stimuli, is very difficult to judge without experiments. However, because the heritability of the clutch size is probably not high (p. 121), it is evident that changes in genetic factors are not of the first importance when clutch sizes change with changing environmental conditions (introduced species, MOREAU 1944, form an extreme case) (see also v. HAARTMAN 1954, and for an opposite opinion LACK 1947).

The above model of the genetics of the clutch size partly contains the opinions presented by LACK (1954b) and JOHNSTON (1956).

5.2. *The ways of inheritance*

In what ways is the genetic basis of the clutch size transferred to the following generation? I have the impression, although I have not found it expressed, that the hypothesis that the determination of the clutch size is based on individual selection (for birds formulated in detail by LACK 1947 and later) rests on the following assumptions: the genetic factors determining clutch size are transferred to the following generation by female and male alike and the most productive clutch size is at least in general that which produces most progeny (females and males). Löhrl (1957), however, mentions that the possible share of both parents in this respect is not known. Because the most productive and common clutch size of the Reed Buntings is that which produces most females but no more males than other common clutch sizes, two possibilities as to genetic influence on the clutch size remain open. These alternatives are that the genetic factors affecting clutch size are either inherited from the female only or from both parents. As far as I know, practically no attention has been paid to the different survival rates of both sexes in relation to clutch size and the possibility that the clutch size of birds is maternally inherited. Although no final solution is likely to be found without experiments into the ways of inheritance, it is necessary to discuss some aspects which are important in explaining the results of studies of the same kind as this.

If the clutch size of the laying female is determined by genetic factors inherited from the mother bird of this female only, the laying female in question has more probably been born in a clutch belonging to the most common and productive size than to some other clutch size. The male of this pair may, on the other hand, have been born in a less superior size of brood. However, if it does not affect the clutch size of the females of the subsequent generation, the clutch sizes of the following generation will again be as well or better adapted to prevailing conditions. The evolution of the most productive clutch size to the most common one by individual selection will not only be possible but also obvious and probably comparatively quick.

If the clutch size of the following generation is determined by genetic material from both parents and if in some broods more females are produced than in others, these broods will probably dominate although males are produced in equal numbers from all brood sizes. The laying female is quite probably born in a clutch of the most common size according to results given earlier for the Reed Bunting. That the male of this pair is also a descendant from such a common clutch size is almost but not quite as probable. Such a situation is not impossible, and the evolution towards a certain dominant clutch size or certain sizes in a certain place and at a certain time is probable through apparently not so quick as with the former alternative.

The ways of inheritance from both parents are easily understood. Also there are no difficulties in principle to the other alternative. These possible ways are plasmatic or maternal inheritance (found to affect e.g. the size of the poultry, Cock & Morton 1963) and perhaps also inheritance through the Y-chromosome of the female is not impossible.

The supposed heritability through females or both of parents gives roughly the same order of clutch sizes as that found in the field in the Reed Bunting. I cannot therefore find any support for either possibility from this (and in positive cases it would be circular reasoning). Thus both ways are possible and, as our knowledge of these facts is only in its infancy, it is not reasonable to favour either of them, but keep both possibilities in mind when treating the topic.

It may be mentioned that the analyses made earlier, principally by Lack (1948 and later), of the most productive clutch size are as well explained on the basis of clutch size inheritance through females alone as on the basis of inheritance through both parents. As a matter of fact the views of this paper reveal further possible sources of error which may have arisen in earlier treatments. E.g. if the trapping of birds is concentrated to the ringing place as in the work of Perrins (1963) on the Great Tit, then, according to the findings of Dhondt & Hublé (1968), more males than females will probably be caught. If proportionally more males than females are produced from clutches of a certain size as in the Reed Bunting, it is probably that a biassed distribution of young in relation to brood size will result. In general, it is possible that the production of males and females in relation to brood size differs. If, for instance, many males are produced in relation to females from large broods, as is the case with the Reed Bunting, and the clutch size is inherited by one generation from another through females alone, selection will not favour these large broods in spite of the fact that they may produce many young according to catching files. It is therefore highly desirable that analyses of the same kind as in this paper dealing with the proportional production of females and males in relation to clutch size should be made. It is probably not possible to get information of this kind from the ringing recoveries of ringing centres because the birds recovered are seldom reliably sexed. The best (and probably only) way is field work of the same kind as that described here. The easiest way to get this kind of material is to obtain it from birds nesting in nest-boxes but, as will be discussed later, this material is not quite comparable in all respects with that presented in this paper.

5.3. *Heritability of clutch size*

It has been found in this paper that some, perhaps many, environmental factors can modify the clutch size of the Reed Bunting. The great importance of environmental factors was shown when, in different environmental conditions, the same female laid early clutches whose size varied between six and three. According to this large potential range in the clutch size of an individual and the probable nature of inheritance it is assumed that the heritability of the clutch size is not high or at least that the correlation between the clutch size of females and their daughters is not high. It is laborious to collect field data on this matter, and my material is also limited in this respect. As two early clutches with three eggs (out of three possible) are included in the material (following tabulation) which shows the relation between the clutches of mothers and daughters, it is evidently biassed in this respect. Heritability cannot be high, however.

Clutch size of	
Mothers	Daughters
6 (10.5.), 6 (18.5.), 6 (5.6.)	3 (27.5.)
3 (30.5.)	6 (15.5.)
6 (10.5.), ≧ 5 (3.6.)	5 (15.5.)
≧ 6 (25.5.)	5 (22.6.)

The dates on which the first egg of the clutch was laid is given in brackets. All clutches of daughters are from their first breeding season.

A similar table given by LÖHRL (1957) for the Collared Flycatcher possibly indicates somewhat higher heritability.

6. On the determination of range, mode, and distribution of the clutch size

Clutch size evidently possesses survival value if, the following season (for species breeding when one year old), the gene pool of the breeding population contains genes from this particular clutch or from parents of this clutch. This means that not only the young but also the parents are important. As a matter of fact, if selection is to favour a certain genotype, it is very important that the parents live after the breeding attempt, because in stable populations they, more probably than their descendants, are those that live the following breeding season if the annual adult mortality rate is less than 50 %. The situation is in practice not so simple because not all adults breed every year. This makes the adults still more important if the size of the population is to remain the same. Another complicating factor is that the mortality rates of adults and first-year birds are probably interdependent (see KLUYVER 1966).

It is therefore important to know whether it is deleterious for the parents to raise large broods. According to weight data for the Reed Bunting HAUKIOJA 1969a) it is evident that if the brood size affects the survival of the parents then this would be seen in females. However, in my small material (Table 19) there is no indication of this. It is, however, still possible that the size of the second clutch is that which affects the survival of females. However, second broods are only laid by old females, which have earlier been shown to lay large clutches in the early phase of the breeding cycle. According to Table 19 this does not lead to their lowered survival. Thus there is no indication that mortality is dependent on brood size in breeding Reed Bunting females. This was to be expected in view of the fact that the annual mortality rate of adults is probably less than 50 % (e.g. Table 19 shows that 19 out of a possible 36 breeding females returned the following year and it is improbable that all females returned to exactly the same breeding site and were thus recorded; this topic will be treated in more detail in a later paper). Because even the largest broods are evidently small enough not to diminish markedly the survival of the parents, it is evident that among clutches of different sizes occurring naturally, selection favours those clutch sizes which produce most surviving descendants. These are, in the population studied, clutches of five, six, four and three, which was the order of their natural occurrence, too.

TABLE 19. Return tendency of female Reed Buntings in relation to the brood size raised in the first brood the preceding summer. *(Naaraspajusirkkujen palaaminen suhteessa edellisen kesän ensimmäisen poikueen kokoon.)*

No.of fledglings in the first brood *Poikasia ensimmäisessä pesyeessä*	♀-parents ringed *Emoja rengastettu*	Returning following year *Palasi seur. vuonna*
6	10	6
5	10	5
4	12	8
2—3	4	0
Σ	36	19

Now it is reasonable to study whether the clutch size distribution of the Reed Bunting can be understood as a sign that it has adapted to prevailing conditions when trying to raise young as efficiently as possibly. In the following I shall consider different features of the clutch size distribution of the Reed Buntings studied. Only "early broods" are dealt with.

The absolute productivity index for broods of six young is rather low in the Reed Bunting. So it is worth studying what would be the productivity index for clutches of seven eggs. I have not made field experiments by adding extra eggs to nests, and there is no proof that this would give results comparable with "natural" brood sizes (see WYNNE-EDWARDS 1964). We can, however, calculate what would be the probable brood size distribution for early clutches of seven eggs assuming that the hatchability and first-day mortality is the same as for other brood sizes. The distribution of broods/100 clutches of seven eggs are as follows:

Young	Nests
7	38
6	39
5	18
4	4
3	1

The productivity index of broods with 3—6 young would be according to Table 14 and using both sexes 0.26. Because the recovery percentage tends to decrease as brood size rises, it is probable that broods of seven young would be less productive than broods of six young, which were already rather non-productive. So it is probable that clutches of seven eggs, which have not been found in my study area, would be less productive than clutches occurring naturally, or about as productive as the most non-productive clutch sizes. So the ± rigid upper limit of clutch size distribution occurring naturally seems to have been formed to suit prevailing conditions and in order to prevent breeding attempts which were doomed to be unsuccessful. Three complicating points of view are worth mentioning. The first is that old females, whose clutch size is higher than in young females, would be the most likely to lay clutches of seven eggs. Earlier I have presented material which suggests that old females are more efficient in raising broods. However, the tendency of the productivity index to be low in broods of six young also holds true for old females as calculated from the small material presented in Table 17:

Clutch size	Old	Young
6	1.38	0.78
5	1.50	1.00
4	1.72	0.96

The absence of very large broods is thus understandable.

The second complicating fact is that all broods have been about as efficient in producing males but the proportion of females produced in broods of six young is small. Thus the production of young from clutches of seven eggs might still be rather high. This, however, is no valid argument if the clutch size is inherited through females only, but neither is this, of course, proof of female-bound inheritance. However, it seems probable that the production of males would not be higher in clutches of seven than in smaller clutches.

The third point is that the hatchability and/or nestling survival might be lower in clutches of seven eggs than in smaller clutches. This would cause higher productivity indices but, on the other hand, the females would have to lay an extra egg which does not seem to be a reasonable situation.

Thus there is no reason to believe that clutches occurring naturally were not determined so as to produce as many genes as possible for the gene pool of the following breeding population.

In the Reed Bunting, the truncation of the upper portion of the clutch size distribution leads to the non-existence of clutches of seven. This or a large clutch size seems to be uncommon in other passerines nesting in the open, too (see v. HAARTMAN 1969). In an arctic environment such clutches are, however, less uncommon (HILDÉN 1967) and in passerines nesting in holes they are not uncommon at all (v. HAARTMAN 1969).

In the arctic environment, a possible and much discussed cause is a longer working day for parents. It is, however, improbable that this is the sole reason, if it is a reason at all. For species breeding in holes, the above explanation cannot be the correct one. LACK (1947) gives the explanation that species breeding in holes, where the rate of predation is lower compared with open nesting species (NICE 1957), have evolved a slower rate of development. v. HAARTMAN (1954) has shown that the nestling periods are not a good measurement in this respect because in hole-nesting species the young stay in the nest some days after achieving their maximum weight while open-nesting species do not. RICKLEFS (1968), studying the weight curves of nestlings, came to the conclusion that LACK's (1947) explanation cannot be the correct one.

ROYAMA (1966) has presented a reasonable hypothesis according to which ”the optimum working capacity” of parent birds varies, and the bottle-neck in feeding young may fall at different phases of the nestling or fledgling period. The most obvious periods of crisis are the nestling time or the period just after that. In Reed Buntings, as well as possibly in other temperate zone passerines which leave the nest before they are able to fly, this period is just after leaving the nest (see MARLER 1956). In early broods of the Great Tit it is evidently during the nestling period (ROYAMA 1966). According to this author, the differences are based on the fact that in hole-nesting species the brood remains in the nest long after the time when the main demand on their energy is for growth. They stay in the nest also during that phase when the main demand on their energy is for maintenance. Before homoiothermy has developed (for passerine species, see DAWSON & EVANS 1960, MAHER 1964) and to some extent after it, the food requirements of the whole brood are not proportional to the size of the brood; great broods are proportionally easier to raise than small ones. In species breeding in open nests, the situation is principally the same, except that their nests are generally less well insulated and thus the heat loss of nestlings is higher. They also leave the nest proportionally earlier (adaptation for heavier predation, NICE 1957). The greatest energy demand occurs at the phase when young birds leave the nest and the energy demand per individual nestling is much more than if they remained in the nest.

We may thus ask the following important question: are the large clutches of hole-nesting species caused by the fact that they are able to eliminate the difficult phase of feeding single young which are unable to fly and follow the parent but nevertheless consume more energy than the same number of young in the nest?

If this reasoning holds true, we have three possible ways in which to study the matter. The first is that the weight distribution of young birds in relation to brood size would be more affected by the clutch size in hole-nesting species than in those nesting in the open. This would be true if the amount of food were the limiting factor and the clutch size of hole-nesting species were adapted to the maximum mean which parents are able to raise during the nestling period. The second aspect is that, if the crisis period occurs in hole-nesting species during the nestling period, the energy demand of the brood is not proportional to the number of nestlings as has been mentioned earlier. If this is true, it is assumed that the upper portion of brood and clutch size distribution, that is clutches larger than the mode, in hole-nesting species do not have such a deleterious effect on the survival of the whole brood as in open-nesting species. It is evident, then, that the upper portion of the clutch size distribution would be less abrupt in hole-nesting species than in others. The third possible way of proving plausibility of the reasoning is to study domesticated birds.

I shall now study some published figures on the weights of passerines in relation to the brood size. LACK (1948b) found differences in weight in relation to brood size in the Starling. The material was, however, very small. PERRINS (1965) has assembled a lot of data on the Great Tit in this respect and there was a tendency for nestlings in large broods to be lighter than those in small broods. ROYAMA's (1966) data show the same trend. The same thing has also been shown for the Blue Tit *Parus caeruleus* (LACK *et al.* 1957). v. HAARTMAN (1954) has shown the same kind of trend in the Pied Flycatcher. SEEL (1970) reports lowered survival and low weights in House Sparrow *Passer domesticus* nestlings in large broods but not in the Tree Sparrow *Passer montanus*.

In open-nesting passerines the following are known to me where similar weights have been taken: SCHRANTZ (1943) for the Eastern Yellow Warbler *Dendroica aestiva,* LACK & SILVA (1949) for the Robin *Erithacus rubecula,* SNOW (1958) for the Blackbird, and TYRVÄINEN (1969) for the Redwing *Turdus iliacus.* In none of these species did the young in large broods weigh less than those in small broods, but the young in broods of the most common size were on some occasions heavier than those in small broods. This possibly indicates that the feeding efficiency of parents is at least partially regulated by the need to feed or small broods consume very much energy. The former might be confusing when interpreting the above results. Another thing is that we have very little information about the importance of nestling weights. However, the predictions presented earlier do not contradict the data presented here.

In Fig. 3 I have given the clutch size distributions of some Finnish passerines. The material is mainly from v. HAARTMAN's paper (1969). This figure accords with the predictions presented earlier; that is, those species breeding in holes seem to have more symmetric clutch size distributions than those breeding in the open. In order to examine the skewness of clutch size distributions more precisely, I have computed skewness values (by using the momentum method, SNEDECOR & COCHRAN 1968) for those distributions of small and medium-sized passerines presented in Fig. 3 when the material comprises more than 100 clutches and also for those monthly clutch size distributions which are larger than 100 in the material concerning Swiss passerines presented by GLUTZ (1962). These figures are given in Table 20. Species which raise their young almost or up to the age of flying capacity in the nest have significantly lower skewness values than those species nesting in the open ($p < 0.05$, one-tailed Mann-Whitney U-test).

Because hens do not lay ordinary clutches, this species has to be disregarded when studying domesticated birds in order to prove the plausibility of the above reasoning. HINDE (1959) has given data for domesticated Canaries *Serinus canaria.* This is an open-nesting species, and if the clutch size distribution is the same as for wild birds of the same kind, it may be assumed that the skewness of the clutch size distribution is negative. However, the skewness of the clutch size distribution is clearly positive (+0.334, with SD of 0.148) if only clutches showing some embryonic development are taken into account. For other, "all-clear", clutches the skewness is 0.393 (with SD of 0.185). These values are more positive than in any other species analysed in this paper, including hole-nesting species.

Two possible explanations are obvious: the first is that in domesticated Canaries, food is no limiting factor in raising broods and thus large broods are not deleterious but very productive and that is why the disribution is positively skewed. This is what might be expected on the basis of the above reasoning. However, it is also possible, that Canaries are heterogeneous in relation to their native areas and thus the positive skewness might be due to a large proportion of birds producing clutches typical of those regions where the clutch is small and a small proportion of clutches from those regions where the clutch size is large. However, the small clutch size data of wild birds given by CHARVOZ & GÉROUDET (1962) do not show positive skewness and the material presented by HINDE (1959) is clearly one-topped. Thus the first explanation seems the most probable.

Now we can turn to our original question; can the skewed clutch size distribution of the Reed Bunting be regarded as a result of individual selection? Because the above predictions

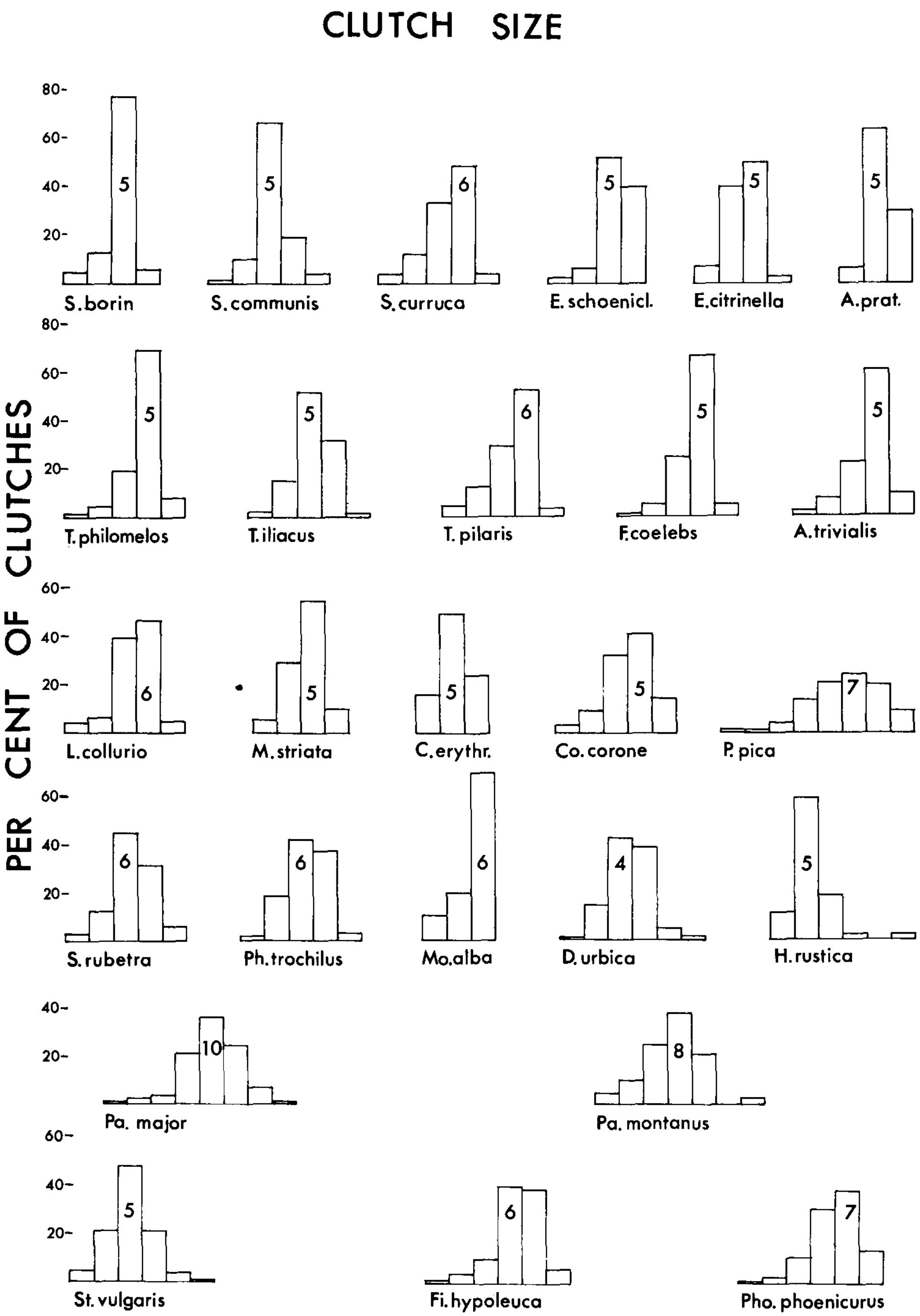
CLUTCH SIZE
PER CENT OF CLUTCHES
80-
60-
40-
20-
S.borin
5
S.communis
5
S.curruca
6
E. schoenicl.
5
E.citrinella
5
A.prat.
5
T.philomelos
5
T.iliacus
5
T. pilaris
6
F.coelebs
5
A.trivialis
5
L.collurio
6
M.striata
5
C.erythr.
5
Co.corone
5
P. pica
7
S.rubetra
6
Ph.trochilus
6
Mo.alba
6
D.urbica
4
H.rustica
5
Pa. major
10
Pa. montanus
8
St.vulgaris
5
Fi.hypoleuca
6
Pho. phoenicurus
7

TABLE 20. Skewness of clutch size distributions of some passerines, H = v. HAARTMAN 1969, G = GLUTZ VON BLOTZHEIM 1962. (*Eräiden varpuslintujen pesyekokojakautumien vinoudet,* H = v. HAARTMAN 1969, G = GLUTZ VON BLOTZHEIM 1962).

Species *Laji*	Source *Lähde*	Clutches *Pesyeitä*	Skewness *Vinous*	SD	Security of nest *Pesän suojaisuus*
Parus major	April, G	534	0.214	0.106	+
Sturnus vulgaris	H	192	0.117	0.175	+
Parus caeruleus	April, G	125	0.055	0.217	+
Sturnus vulgaris	April, G	199	0.042	0.172	+
Parus major	May, G	353	0.024	0.130	+
Turdus merula	April, G	380	—0.005	0.125	—
Delichon urbica	June, G	128	—0.194	0.214	+
Passer montanus	May, G	138	—0.198	0.206	+
Turdus iliacus	S-Finland, H	285	—0.247	0.144	—
Saxicola rubetra	H	111	—0.281	0.229	—
Phyll. trochilus	S-Finland, H	127	—0.353	0.215	—
Muscicapa striata	S-Finland, H	266	—0.393	0.149	—
Ficedula hypoleuca	May, G	434	—0.428	0.117	+
Ph. phoenicurus	H	114	—0.492	0.180	+
Turdus merula	May, G	302	—0.541	0.140	—
Parus major	Early, H	225	—0.577	0.162	+
Sylvia atricapilla	May, G	193	—0.637	0.175	—
Ph. phoenicurus	May, G	182	—0.649	0.180	+
Fringilla coelebs	H	318	—0.691	0.137	—
Lanius collurio	H	108	—0.806	0.233	—
Acroceph. scirpaceus	June, G	135	—0.828	0.209	—
Turdus pilaris	S-Finland, H	292	—0.886	0.143	—
Ficedula hypoleuca	H	1210	—1.081	0.070	+
Turdus philomelos	S-Finland, H	221	—1.196	0.164	—

were shown to be valid or not at least invalid for several temperate zone passerines, individual selection for determining the most productive clutch sizes would probably give the frequency distribution occurring naturally in the Reed Bunting. It is therefore possible to explain the very abrupt upper limit of the clutch size distribution found in the Reed Bunting on the basis of individual selection.

A factor probably contributing to the decided abruptness of the upper limit is the shortening of the nestling period, at least from Switzerland to southern Finland, in the Reed Bunting. I think it is best explained as a way of maximizing the production of young in conditions

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FIG. 3. Clutch size distributions of some Finnish passerines. The material is taken from v. HAARTMAN's work (1969) except for the Reed Bunting, which is from this study. Size of the mode is given. Abbreviations of generic names are as follows: S. = *Sylvia,* E. = *Emberiza,* A. = *Anthus,* T. = *Turdus,* F. = *Fringilla,* L. = *Lanius,* M. = *Muscicapa,* C. = *Carpodacus,* Co. = *Corvus,* P. = *Pica,* S. = *Saxicola,* Ph. = *Phylloscopus,* Mo. = *Motacilla,* D. = *Delichon,* H. = *Hirundo,* Pa. = *Parus,* St. = *Sturnus,* Fi. = *Ficedula,* Pho. = *Phoenicurus.* (*Eräiden suomalaisten varpuslintulajien pesyekokojakautumat. Aineisto* v. HAARTMAN'*in teoksesta (1969) paitsi pajusirkku, mikä tästä kirjoituksesta. Runsaslukuisin pesyekoko mainittu. Sukunimien lyhennykset yllä.)*

where it is not possible to raise a brood of seven fledged young easily. This is arrived at by shortening the vulnerable nestling period. Shorter nestling periods in northern populations have been noted to exist in the Redwing (ARMSTRONG 1954, TYRVÄINEN 1969) and the Gambel's Sparrow *Zonotrichia leucophrys gambeli* (OAKESON 1954).

Also the lower limit of the clutch size distribution found in the Reed Bunting is rather distinct, three eggs in the population I studied. The probability of finding clutches of two eggs is, however, rather small because clutches of three eggs are not common in my material, either. Whether there is any fixed lower limit to the clutch size as presented by JOHNSTON (1956) is not easy to verify. The lower limit of clutch size distribution can be thought to have formed in the following way. (This has been presented in part in another paper, HAUKIOJA & KALINAINEN 1970). The lowest clutch sizes which the females lay are such that breeding attempts are on an average profitable for preserving genes of the parents for the gene pool of the following breeding population. As the breeding cycle continues, the most productive clutch size decreases according to the above treatment. On the other hand the time which the parents (in late broods of the Reed Bunting females alone) have left for moulting and other premigratory phases becomes shorter. The postnuptial moult of the Reed Bunting lasts a little less than two months (unpublished) and the premigratory fat deposition probably a week or so. Moulting may in some conditions be a dangerous period (see DAWSON 1967, HAUKIOJA 1969a) and when it has to be gone through quickly it is probably still more dangerous. Now it is evident that selection favours such breeding attempts which are made at that period when parents and young have enough time for normal late summer phases. When it is evident that the most productive clutches which females at a certain time and place lay are determined by individual selection, it is a good reason to stop the breeding phase when the losses of parents are greater than the production of young. At this phase the most productive clutch size has evidently fallen to or near three eggs in the Reed Bunting population I have studied.

It is therefore possible to understand the present situation as the result of selection favouring individual parents and their young. The commonest clutches are those which are at present most productive and the limits of clutch size distribution are found where productivity becomes too low.

The situation examined in this paper is principally that of the Reed Bunting but because other species, treated in Fig. 3 and Table 20, showed similar tendencies, the concepts of this paper are in most points acceptable also for other nidicolous species in the temperate zone.

Although accepting individual selection as a force leading the evolution of clutch size on the basis of facts presented in this paper, it is also reasonable to discuss the possibilities of group selection in the population studied. Finding the most common clutch size to be the most productive we only show that individual selection is in operation; this, as such, does not necessarily disprove group selection (see v. HAARTMAN 1954, p. 71). The possibility of group selection is not ruled out but because nesting success and the size of subsequent breeding bird populations are generally not well correlated (e.g. TOMPA 1964, LACK 1966), possibilities of group selection in a species whose dispersal is considerable (as is probable in the Reed Bunting, Haukioja, in prep.), are small. It is, of course, possible that the situation has been different in the past but in speculating on these possibilities we are on very uncertain ground (see BIRCH & EHRLICH 1967).

7. Discussion

An evident ultimate reason for limiting the clutch size in nidicolous birds from the temperate zone has in some cases been shown to be the lowered survival of nestlings from big broods (e.g. LACK & LACK 1951). Important factors involved are probably the amount of available food and factors affecting the food requirements of the young and the capacity of the parents to collect food (ROYAMA 1969). Other factors are probably in operation, too, or operate together with the former. ROYAMA (1966) has paid considerable attention to the heat-insulation of nests, which helps in lowering the maintenance cost per nestling and is therefore a factor affecting the rather high clutch sizes found in hole-nesting species. These are able to build a well insulated nest and, furthermore, hide it well.

Another possible group of factors which may have an influence either by themselves or together with the former is the lowered survival rate of parents when raising large broods. This has, so far as I know, not been shown to be the correct explanation in any species of birds but the materials presented when studying this phenomenon (KLUYVER 1963, PERRINS 1965, LACK 1966) are difficult to interpret because dispersal of breeding birds is a very laborious and difficult field to study. The above papers all consern the Great Tit which, like the Reed Bunting, has an annual adult mortality rate rather less than 50 % (HAUKIOJA 1969b). The survival of parents must therefore be important.

It is obvious that the above factors (at least) are selected in such combinations that as many genes as possible are carried to the gene pool of the following breeding population. Bearing this in mind, it is assumed that no single factor can explain the whole complex phenomenon of clutch size evolution in different species and CODY's (1966) work is a good attempt to find possible interacting factors.

As far as I know, all attempts, excluding the paper by LACK (1949), to show links between the final productivity index and the commonness of clutch size in nidicolous species have been made with hole-nesting species. According to the above, however, these are not quite comparable with open-nesting species in all respects. In these analyses the non-productiviness of large broods has not always been evident.

LACK (1948b) found that in the Swiss Starling the brood size of five (the most common clutch size) gave as many survivors as larger clutches. We thus find, therefore, that the commonest clutch is the smallest giving a large number of surviving nestlings. This situation accords well with views presented earlier in this paper, especially when we take into consideration the low decline in clutch size frequency distribution (Fig. 3, Table 20). In British Starlings the situation may be the same but productivity may also be smaller in large broods (LACK 1948b).

CURIO's (1960) data on the productivity of the Pied Flycatcher in relation to brood size gave no support to the non-productiveness of large broods. LACK (1966), when analysing English data for the same species, found that common clutch sizes produce most survivors but the situation was by no means clear (see v. HAARTMAN 1967a). Using Finnish material the latter author calculated that there were no noteworthy differences in survival in relation to brood size. However, if in this material we consider as broods of normal size those with seven eggs (about 15 % of broods) hatched from clutches commenced between May 26 and June 4, the results are quite different. The situation seems, therefore, not to have been explored enough in the Pied Flycatcher.

In the Great Tit the situation is perhaps a clearer one. LACK *et al.* (1957) found the most productive clutch size was the most common in this species as well as in the Blue Tit. Using more material the most productive clutch size for the Great Tit was 9 (LACK 1966), which is near the commonest clutch size of the population studied. The annual variation was, however, large. This is what might be expected on the basis of rather symmetrical clutch size distribution and with individual selection in operation determining the clutch size.

Based on the ideas presented earlier in this paper, it is assumed that the non-productiveness of large broods is more clear-cut in open-nesting species because the after-fledging period is probably on an average more critical for these than for hole-nesting species.

LACK's (1949) attempts to show this for certain thrushes gave variable results and there was no clear tendency, if, indeed, there was any tendency at all, for large broods to be non-productive. The material presented in this paper for the Reed Bunting is the only one, as far as I know, where it has been shown for an open-nesting species.

I think there is no reason to treat thoroughly those investigations based on productiveness during the nestling period only, although they may give certain ± valid results for hole-nesting species.

In all the above cases the survivors from certain brood sizes have been treated by combining females and males together, which may be a source of error. It is also possible that the genetic factors determining the clutch size have pleiotropic effects on other features which may be favoured by selection differently from clutch size. Until we know more about the heredity of the clutch size we are on rather uncertain ground in comparing the productivities of different clutch sizes. The possible sources of errors may be so numerous that I think that even the fact that in some species the most common clutch size has been shown to be the most productive is a rather good result.

The most thorough investigations into the population dynamics of nidicolous birds have been conducted on hole-nesting species. This has allowed much data to be collected, but we also need the same kind of data for species building open nests although they are more laborious to study. These species, however, form the bulk of all passerines. It may be mentioned that the Great Tit, which is one of the most thoroughly investigated species in this respect, has the second largest clutch size of all passerines (LACK 1968). This naturally allows many aspects to be studied very thoroughly but such an extreme species is not necessarily a good study object in all respects.

Future research into the whole subject of clutch size will depend to a large degree on forthcoming knowledge of the genetics of clutch size. This, however, demands experimental work or perhaps thorough analyses of large materials of colour-ringed parents and their descendants as proposed by BIRCH & EHRLICH (1967). Both methods are rather laborious and difficult to put into operation in practice.

Acknowledgements

I wish to express my gratitude to my teacher, Professor Paavo Voipio, for valuable advice, including positive criticism of the manuscript, and for providing pleasant working facilities. My thanks are also due to Dr. Martti Soikkeli for encouraging me to begin a population study and for criticism of the manuscript, Prof. Tarvo Oksala, Mr. Risto Lemmetyinen, lic. phil., and Mr. Markku Haukioja for many helpful discussions, and Mr. Pertti Kalinainen and Mr. Raimo Hakila for help in field work. Mr. Arvi Laaksonen, Mr. Ilkka Stén, M. A. and Prof. Rauno Tenovuo have in various ways helped me. Mr. Christopher Grapes, B. A. has checked my English. My parents deserve thanks for their support during the field work. I also want to thank my wife, Mrs. Kaija Haukioja, B. A. for her patient attitude during my long field work periods.

This paper forms part of a larger study supported financially by the Satakunta Fund of the Finnish Cultural Foundation, the Leo and Regina Weinstein Foundation and the Emil Aaltonen Foundation.

Summary

This paper deals with the clutch size determination of passerine birds by analyzing clutch size material mainly of the Reed Bunting.

The field work concerning the Reed Bunting has been conducted while studying a colour-ringed population in south-western Finland in 1966—1969. 323 nests of Reed Bunting were found and over 1000 nestlings were ringed during the study. Survival of the young was studied by means of intensive netting.

The mean clutch size for completed clutches was 5.14 ± 0.05. Fig. 2 gives the change in mean clutch size during summer.

Clutches laid by an individual female are less variable in the same phase of the breeding cycle than those of the whole population, which indicates at least partial genetic determination of the clutch size. Environmental factors, however, also have an effect on the size of clutches laid.

Second or replacement clutches are of the same size as or smaller than the first clutch (Table 1). Year-old females lay on average smaller clutches than older females (Table 2). Mean clutch size differs significantly in different years (Table 3), probably as a result of weather conditions at the time of laying (Table 4). The start of laying of the population evidently does not affect the mean clutch size.

The clutch size of the population studied was significantly larger than in Switzerland and smaller than in a population studied in Swedish Lapland. Populations studied in Estonia and Finnish Lapland did not differ significantly from the population studied.

The productivity of different clutch sizes was studied in order to throw light upon the determination of clutch size. In ”early” broods (hatched not later than the 15th of June) neither the proportion of nests destroyed (Table 5), the hatchability of eggs (Table 6), the mortality of nestlings (Tables 7 and 10) nor the weights of young (Tables 8 and 9) were significantly correlated to the brood size. The nestling period could therefore not be shown to be a critical period from the point of view of productivity.

Young recovered after leaving the nest were used as a measurement of the productivity of the brood size. Table 11 gives the numbers of young recaught after the beginning of July in relation to brood size. Percentagewise small broods produced more recovered birds than large ones. The same phenomenon was observed for both sexes (Table 12). Thus the time between leaving the nest and the beginning of July was shown to be a critical period for the production of young.

The most efficient brood size was five, which was also the most common. The production of females was very small in broods with six young. Table 14 gives the probable brood sizes for clutches of different size and the mean productivity for each clutch size. The order of productiveness of the clutches was the same as that of their natural occurrence.

Young recovered and productivities for

brood sizes for broods hatched after the middle of June are given in Tables 15 and 16.

Parents over one year old proved to be more efficient in raising broods than younger parents (Tables 17 and 18).

The following conclusions about the genetics of the clutch size can be made according to the nesting material presented: The clutch size is genetically determined more probably as norms of reaction to certain environmental stimuli than as mere numbers of eggs, the clutch size inheritance can theoretically be passed on by both parents or by females only, and the heritability of the clutch size is evidently low. Imperfect knowledge about the genetics of the clutch size makes it difficult to interpret study results.

Because in the Reed Bunting the commonest clutch size proved to be the most productive, the survival of females did not decrease although they produced large broods (Table 19), and the productivity of clutches larger than found naturally would evidently have been low, the clutch size was supposed to be determined by individual selection. In order to get more knowledge about this fact data concerning the clutch size of some other passerine species were analyzed. Some predictions based on what might be expected in individual selection were made as to the breeding of hole- and open-nesting passerines. Because these predictions (more symmetrical clutch size distribution, and weight development more influenced by brood size in hole-nesting species) proved to be right, determination of clutch size on the basis of individual selection seems to be normal for temperate zone passerines. Thus the observations made of the Reed Bunting would seem to support a more general explanation for clutch size determination.

It is therefore possible to explain general features of clutch size of hole- and open-nesting species (the former have larger clutches and more symmetrical clutch size distributions) as results of individual selection. Studies of both groups are needed for a further examination of the problem of clutch size. It is very important to determine the genetic basis of the clutch size.

Selostus: **Pajusirkun pesyekoko**

Kirjoitus valottaa varpuslintujen pesyekoon määräytymistä pääasiassa pajusirkun pesyekokoaineiston pohjalla.

Pajusirkkua koskevat maastotyöt on suoritettu tutkittaessa vuosina 1966—1969 värirengastettua populaatiota Porissa, Kokemäenjoen suistoalueella. Kyseisenä aikana löytyi 323 pajusirkun pesää, joista rengastettiin yli 1000 pesäpoikasta. Poikasten myöhempiä vaiheita pyrittiin selvittelemään tehokkaalla syyskesäisellä verkkopyynnillä.

Täysilukuisten pajusirkkupesyeiden munamäärä on ollut keskimäärin 5.14 ± 0.05. Keskimääräisessä pesyekoossa tapahtuu vuodenaikaisia vaihteluja (kuva 2).

Saman naaraan munimat pesyeet ovat samassa pesimäkierron vaiheessa eri vuosina kooltaan vähemmän vaihtelevia kuin koko populaation pesyeet, mikä osoittaa pesyekoon olevan ainakin osittain geneettisesti määräytynyt. Kuitenkin myös ympäristötekijät vaikuttavat munittavan pesyeen suuruuteen.

Toisen tai uusintapesyeen koko on yleensä sama tai pienempi kuin ensimmäisen pesyeen (taulukko 1). Yksivuotiaat naaraat munivat keskimäärin pienempiä pesyeitä kuin vanhemmat naaraat (taulukko 2). Eri vuosien välillä on merkitseviä eroja keskimääräisessä pesyekoossa (taulukko 3), mikä liittynee muninta-ajan säätilaan (taulukko 4). Populaation muninnan keskimääräinen alkamisajankohta keväällä ei ilmeisesti vaikuta keskimääräiseen pesyekokoon.

Tutkitun populaation pesyekoko on merkitsevästi suurempi kuin sveitsiläisessä vertailuaineistossa ja merkitsevästi pienempi kuin eräässä Ruotsin Lapin populaatiossa. Sen sijaan Virosta ja Suomen Lapista ilmoitetut pajusirkun pesyekoot eivät poikenneet merkitsevästi tutkitun populaation pesyekoosta.

Pesyekoon määräytymisen selvittämiseksi tutkittiin eri kokoisten pesyeiden tuottoisuutta. "Aikaisissa" pesyeissä (ennen 16.6. kuoriutuneissa) eivät kokonaan tuhoutuneiden pesien osuus (taulukko 5), munien kuoriutumisprosentti (taulukko 6), poikaskuolevuus (taulukot 7 ja 10) eivätkä poikasten painot (taulukot 8 ja 9) olleet merkitsevästi riippuvaisia pesyekoosta. Pesäpoikaskausi ei täten osoittautunut kriittiseksi poikasten selviämisen kannalta.

Pesästälähdön jälkeen kontrolloituja poikasia käytettiin poikuekoon tuottoisuuden mittana. Taulukossa 11 esitetään heinäkuun alun jälkeen kontrolloidut poikaset suhteessa pesyekokoon. Pienet poikueet tuottivat prosentuaalisesti merkitsevästi enemmän kontrolloituja poikasia kuin suuret. Sama ilmiö havaittiin molemmilla sukupuolilla (taulukko 12). Kriittiseksi kaudeksi poikasten selviämisen kannalta osoittautui täten pesästälähdön ja heinäkuun alun välinen aika.

Absoluuttisesti tuottoisin poikuekoko oli viisi, mikä oli myös tavallisin. Kuuden poikasen poikueissa oli naaraiden tuotto jo hyvin vähäistä. Taulukossa 14 on esitettynä eri kokoisista munapesyeistä todennäköisesti tulevat poikuekokojakautumat sekä kunkin pesyekoon keskimääräinen tuottavuus. Pesyeiden tuottoisuusjärjestys oli sama kuin niiden runsausjärjestys luonnossa.

Kesäkuun puolivälin jälkeen kuoriutuneiden poikueiden kontrolloidut poikaset ja poikueiden tuottoisuudet on esitettynä taulukoissa 15 ja 16.

Yli yksivuotiaat emot osoittautuivat tehokkaammiksi poikasten kasvattajiksi kuin yksivuotiaat (taulukot 17 ja 18).

Maastotutkimuksen perusteella voidaan pesyekoon genetiikasta tehdä seuraavat päätelmät: Pesyekoko määräytynee geneettisesti todennäköisimmin reaktionormeina tiettyihin ympäristöärsykkeisiin eikä varsinaisina munamäärinä, pesyekoko voi teoriassa periytyä jälkeläisille joko molempien vanhempien kautta tai pelkästään naaraan kautta ja pesyekoon heritabiliteetti on ilmeisesti alhainen. Puutteellinen tietämys pesyekoon periytymisestä vaikeuttaa tutkimustulosten tulkintaa.

Koska yleisin pesyekoko osoittautui pajusirkulla tuottoisimmaksi, emojen oma selviäminen ei alentunut, vaikka ne tuottivat suuriakin poikueita (taulukko 19) ja lisäksi todettuja suurempien pesyeiden tuottoisuus olisi ilmeisesti ollut alhainen, oletettiin pesyekoon määräytyvän yksilöllisen valinnan perusteella. Asian lisäselvitykseksi tutkittiin eräiden muiden varpuslintulajien pesyekokotietoja. Näistä tehtiin eräitä yksilöllisen valinnan vallitessa todennäköisiä ennusteita avo- ja kolopesijöiden pesimisestä. Koska nämä ennusteet (kolopesijöiden symmetrisempi pesyekokojakautuma ja poikuekoosta riippuvaisempi painonkehitys) osoittautuivat suunnaltaan oikeiksi, näyttää pesyekoon määräytyminen yksilöllisen valinnan perusteella lauhkean ja viileän vyöhykkeen varpuslinnuilla normaalitapaukselta. Täten pajusirkulla havaitut seikat täydentävät ja tukevat yleisempää selitystä pesyekoon määräytymisessä.

Avo- ja kolopesijöiden pesyekoon yleispiirteet (jälkimmäisillä suurempi pesyekoko ja lähempänä normaalijakautumaa oleva pesyekokojakautuma) ovat seikkoja, jotka siis ovat ymmärrettävissä yksilöllisen valinnan perusteella. Molempien ryhmien tutkiminen, mikä avopesijöillä on yleensä työläämpää, on tarpeen pesyekoko-ongelman ratkomisessa. Erityisen tärkeää on pesyekoon geneettisen puolen selvittäminen.

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