The Determination of Clutch-Size in Birds a Review

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THE DETERMINATION OF CLUTCH-SIZE IN BIRDS A REVIEW

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1. INTRODUCTION

The full clutch of a bird varies from species to species. Sometimes it is constant: condors, albatrosses, shearwaters, and the King and Emperor Penguins lay one egg; most pigeons, many of the nightjars and other species of penguins have two; the Lapwing and the Golden Plover always have four eggs. In other species the full clutch varies within limits: the Swift has 2-4, the Starling 3-7 and the Partridge 14-20 eggs.

The question of why a bird lays a specific number of eggs can be approached in two different ways. One approach is concerned with the analysis of the mechanism controlling follicle growth and ovulation in the ovary, and the modification of this control by internal and external factors. This is an approach to the problem of the proximate determination of clutch-size.

The other approach to the problem is concerned with the evolutionary development of the size of the clutch. This feature of a bird species is part of its total organization, which came into being in the course of its evolution through the operation of natural selection on genetic variability in populations. The question can be raised as to what factors have played a part in this process of selection. Hypotheses concerning this question can be tested by manipulating the size of the clutch, and by comparing in related species clutch-size with other organizational features. This is an approach to the problem of the ultimate determination of clutch-size.

2. THE PROXIMATE DETERMINATION OF CLUTCH-SIZE

2.1. THE CONTROL OF OVARIAN ACTIVITY

We already know for many years that the growth and development of the follicles in the ovary are stimulated by gonadotrophic hormones secreted by the pituitary gland into the blood-vascular system. In some species the number of follicles responding to the stimulating hormones equals the number of eggs laid, and this number is definitely determined when laying begins. The number of eggs laid cannot be affected by the removal of eggs during the laying period, nor by the addition of eggs

TABLE 1

BIRD SPECIES WITH A VARIABLE CLUTCH-SIZE, WHICH HAVE BEEN RECORDED IN THE LITERATURE AS DETERMINATE LAYERS

Species	Clutch-size	References
Blue Snow Goose	3-5 (6)	VAN TIENHOVEN 1961
Brent Goose	(2) 3-5 (6)	VAN TIENHOVEN 1961
Pheasant	(7) 8-15 (16, 17)	POULSEN 1953
Lovebird	?	TIENHOVEN 1961
Budgerigar	4-7	TIENHOVEN 1961
Sky-lark	3-5	DELIUS 1965
Barn Swallow	(3) 4-5 (6, 7)	DAVIS 1955a
Black-billed Magpie	(4) 5-7 (8, 9)	DAVIS 1955a
Wren	(3, 4) 5-7 (8, 9)	ARMSTRONG 1955
Long-billed Marsh Wren	(3) 4-6 (7)	VERNER 1965
American Robin	(2) 3-4 (5)	HOWELL 1942
Song Thrush	(3) 4-5 (6)	CHAPPELL 1948
Nightingale	(3) 4-5 (6)	HILPRECHT 1954
Pied Flycatcher	(4) 5-8 (9)	BERNDT 1943; VON HAARTMAN 1967a
Tricolored Red-wing	(2) 3-4 (5)	EMLEN 1941
Starling	(3) 4-5 (6)	DAVIS 1958
Yellowhammer	(2) 3-4 (5)	CHAPPELL 1948
House Sparrow	3-5 (6, 7)	COLE 1917; BRACKBILL 1960
Tree Sparrow	4-6 (7)	EISENHUT & LUTZ 1936
European Goldfinch	(3) 5-6 (7)	CHAPPELL 1948
Canary	3-5	DUNHAM & CLAPP 1962

NOTE: Clutch-sizes in brackets are rare.

during or shortly before this period. These species have been indicated by COLE (1917) as determinate layers.

Probably, all the species with a single egg in the clutch belong to this category, but this has not yet been investigated. Further, pigeons, doves and many of the Laro-Limicolae have been classified as such (CRAIG 1913; STRESEMANN 1927-34). Later work has shown that this is incorrect for waders and gulls, though the size of their clutch is generally small and very constant (see below). For this reason, POULSEN (1953) re-examined the Domestic Pigeon, always having two eggs in the clutch. He made the following experiments.

1. In ten nests the first egg was taken as laid; the second was laid in normal time, and the bird incubated one egg.
2. In five nests one egg was added after the laying of the first; the second was laid in normal time, and the bird incubated three eggs.
3. In ten nests two eggs were added shortly before the first was laid; in five of these, two eggs were normally laid, and the bird incubated four eggs. In five others the whole clutch was suppressed, and the bird incubated the two supposititious eggs.

From these experiments POULSEN concluded that the Pigeon is a determinate layer, but in my opinion, the results are not conclusive in all respects (p. 8).

From the species with a larger and more variable clutch, those listed in Table 1 have been recorded to be determinate layers. There is, however, some doubt as to the correctness of the classification. Thus, both species of sparrows have been reported as indeterminate layers by PUHLMANN (1914), the House Sparrow also by WITSCHI (1935). In an experiment reported by CHAPPELL (1948), a Sky-lark laid ten eggs when the third and each subsequent egg laid was taken from the nest. The Pheasant may be another doubtful case, because gallinaceous birds proved to be indeterminate layers (see below and WESTERSKOV 1956). Further, there is some doubt about the Budgerigar (ANONYMOUS 1968), and in my opinion, the experiments of EMLEN (1941) with the Tricolored Red-wing are inconclusive. The evidence indicates that addition of eggs early during the laying period may suppress the production of some eggs. The classification of several other species listed in the table needs further confirmation, being based on too small a number of experiments, either on addition or removal of eggs only.

There seems to be no doubt about the Pied Flycatcher, as shown by the experiments of VON HAARTMAN (1967a), which are given here in full, because complete series of experiments concerning this question are rare (Fig. 1). It is shown, that the number of eggs produced is not affected, when the first three, or even the first five eggs are taken as laid, nor when some eggs are added to the nest one day before or on the day of the start of laying.

The mechanism controlling the specific number of follicles responding to the stimulating hormones is entirely unknown. In most determinate layers more small follicles are present in the ovary than the number responding, as appears from the fact that both Pigeons and Pied Flycatchers produce a repeat clutch within some days after the first one has been taken (POULSEN 1953; VON HAARTMAN 1954).

In a great many other species the number of follicles responding to the stimulating hormones is greater than the number of eggs laid. The follicles do not respond to the hormones synchronously, but constitute a series of increasing size, the cause of which is still unknown (STIEVE 1919; HARRIS 1964). The largest of the series ovulates first, and the released ovum passes into the oviduct. Shortly before this ovum is laid as an egg, the next follicle, which in the meantime reached its full size, ruptures, and so forth. This implies, that the development of some

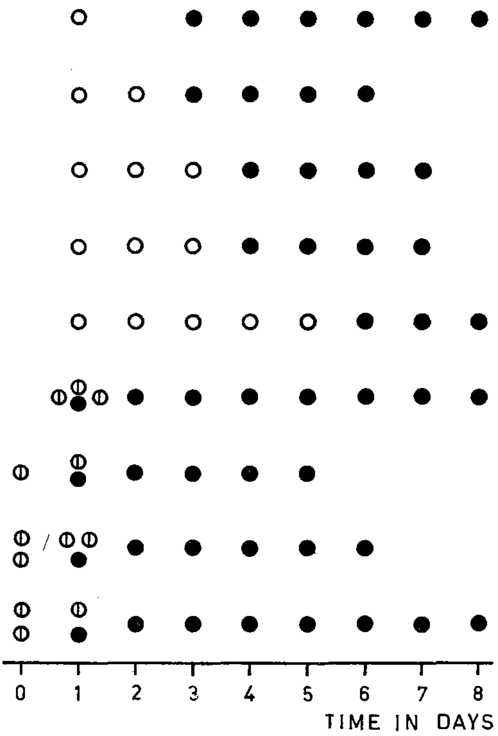

FIGURE 1. Number of eggs laid by nine Pied Flycatchers after removal (open circles) or addition (striped circles) of eggs. Day 1 is day of first laying. Eggs laid and incubated (dots). The normal clutch-size of this species in Finland is (5) 6-7 (8) eggs. After VON HAARTMAN (1967a).

follicles is inhibited in a later stage, and it has been shown that the stimulus involved originates from the contact with the eggs in the nest. As a consequence, if the eggs are removed as laid, the stimulus does not occur and laying continues beyond the normal clutch to an indefinite number. These species have been indicated by COLE (1917) as indeterminate layers.

If the eggs are taken when laid in such species (one or two eggs are usually left to prevent desertion), great numbers of eggs may be produced. This is shown in Table 2 for a variety of species. In some cases the eggs are produced with the normal frequency. Thus, the Flicker laid 71 eggs in 72 days, and the Wryneck 33 eggs in 33 days. In others the eggs seem to be produced in cycles separated by pauses of some days. Thus, the Kingfisher laid 20 eggs in four cycles of 7, 6, 4, and 3 eggs. As to the Wryneck the opinions differ in this respect, but this may result from the fact that in some experiments the eggs were immediately taken when laid, whereas in others they were removed in batches of four or five.

This cyclic laying, as in the Kingfisher, might be interpreted to mean that the hen produces some determinate repeat layings in succession, instead of laying indeterminately (DAVIS 1955a; LEHRMAN 1959). This supposition is supported by the fact that repeat clutches nearly always decrease in size with time progressing (p. 22). The phenomenon of cyclic laying has been studied in detail in the House Wren, which was classified as an indeterminate layer by COLE (1917). The clutches of this double or triple brooded species are characterized in having the first two or three eggs darker than the rest, and the last two eggs heavier than the first ones laid.

TABLE 2

NUMBER OF EGGS PRODUCED BY INDETERMINATE LAYERS WHEN THE EGGS ARE TAKEN AS LAID

Species	Eggs laid	References
Mallard	80-100	AUSTIN 1908 (in DAVIS 1955a)
Shelduck	18	HORI 1964
Scaled Quail	?	WAGNER 1957
Pheasant	?	WESTERSKOV 1956
Golden Pheasant	40	GOODWIN 1948
Moorhen	36	MILLER 1910
Herring Gull	12-16	SALOMONSEN 1939
Herring Gull	9-13	PALUDAN 1952
Kingfisher	20	SALOMONSEN 1939
Green Woodpecker	17	ALTUM 1906
Yellow-shafted Flicker	71	PHILLIPS 1887
Yellow-shafted Flicker	48	BURNS 1900 (in DAVIS 1955a)
Wryneck	62	ALDERSON 1897
Wryneck	33	WARGA 1925-26
Jackdaw	18	STIEVE 1919
Dipper	28	GRABHAM 1897
House Sparrow	10	PUHLMANN 1914
House Sparrow	50	WITSCHI 1935
Tree Sparrow	12-16	PUHLMANN 1914

When the eggs, starting from the second, are taken when laid, fairly large numbers of eggs (maximum 32 from one female) can be collected. These eggs are laid in cycles, separated by intervals of three to four days on the average in which no eggs are laid. The first and last eggs of a set are characterized by being, respectively, darker and heavier than the others, and this suggests indeed that successive repeat layings are laid in the same nest. This nest is not deserted presumably due to the fact that one egg is always present.

Although these experiments seem to suggest that the House Wren is a determinate rather than an indeterminate layer, one result does not fit in with this assumption. The number of eggs produced in the first cycle proved to be significantly higher (2.2 eggs on the average) than the size of the normal undisturbed first clutch, so that there is at least some protracted laying at the beginning of the breeding season. The number of eggs of the second and later cycles, however, fit in with the normal seasonal decline of clutch-size characteristic for this species, and protracted laying, therefore, is absent later in the season (COLE 1930; KENDEIGH *et al.* 1956).

One other experiment supports the view that the House Wren is a determinate layer. COLE (1930) added six eggs to a nest some hours after the laying of the first one, but this did not suppress the normal laying of the bird.

The question of determinateness or indeterminateness should be studied both by the removal and the addition of eggs, but the latter has never been a subject of systematic study in any of the species listed in Table 2, except the Herring Gull. Some authors report that parasitic egg laying or dump nesting—occurring when two females of the same or of different species deposit their eggs in the same nest—suppressed the number of eggs laid by the host, when the parasite's eggs are added during the host's laying period. This has been observed in the Partridge (BLANK & ASH 1960) and in some species of ducks (BENNETT 1938; WELLER 1959; HILDÉN 1964). The effect is only small, and it will be evident that the addition of eggs needs more study.

Research concerning this point should comprise both experiments with eggs in the nest and studies of ovarian development. Work of this type has been carried out with gulls, which like other Laro-Limicolae, formerly have been classified as determinate layers. This misconception was based on the small and constant clutch-size of these species and, especially, on the fact that—as was thought—the number of eggs laid could not be affected by the removal or addition of eggs. The Herring Gull, for instance, nearly always lays three eggs, and when the second and third egg are taken as laid, the gull starts incubating the first egg only. Again, when two eggs are added after the first has been laid, the second and third are laid as normal, and the gull starts incubating five eggs (DAVIS 1942; PALUDAN 1952). The same has been found in the Black-headed Gull (WEIDMANN 1956; YTREBERG 1956), and in two plovers: the Lapwing (LAVEN 1940; RINKEL 1940; KLOMP 1951), and the Ringed Plover (LAVEN 1940), laying always four eggs.

PALUDAN (1952) studied ovarian development of Herring Gulls killed in various stages of the reproductive cycle. He showed that prior to laying many more than three follicles increase in volume, and that shortly before the first ovulation takes place, four follicles have entered the final phase of rapid growth. Further, he showed that shortly after laying the first egg, the smallest of the four largest oöcytes (the one already laid included) degenerates, whereas the second, which already ruptured, and the third, then still in the ovary, develop to mature ova. PALUDAN deduced from this result that the degeneration of the fourth follicle is induced by the contact with the first egg in the nest during the 48 hours interval between the laying of the first and the second egg. During that time the bird regularly stays on the nest, though it is not brooding, because the broodpatches have not yet fully developed.

PALUDAN could provide more support for his view by removing the first egg from a number of nests shortly after laying. A small part of the birds desert upon this, but the others continue laying in the same nest. With the normal intervals these birds lay the second and the third egg, plus a fourth one, and this proves that the fourth follicle is not suppressed in this case. Again, when the first two eggs are taken as laid, two extra eggs are produced, and PALUDAN even has been successful in getting 13 eggs from one female by taking successively all the eggs as laid (Fig. 2).

SALOMONSEN (1939) has even been more successful and collected in the same way 16 eggs from one Herring Gull. These, however, were laid over a period of 40 days and, like in the House Wren, periods of laying with the normal intervals were interrupted by longer resting periods. Once again, this suggests that the ripening of the follicles is cyclic with some protracted laying at the start of the season.

The production of one extra egg, when the first one is removed shortly after laying, has also been observed in the Glaucous-winged Gull (VERMEER 1963), and in the Herring Gull and Lesser Black-backed Gull by HARRIS (1964).

On the grounds of these experiments, it could be expected that the contact of the bird with eggs before the first laying might suppress one or more of the three follicles which, if undisturbed, develop to ripe eggs. This could be tested, because Herring Gulls spend a great part of the days preceding laying on their nests. Indeed, when PALUDAN laid three eggs in such empty but occupied nests, the birds laid two instead of three eggs (Fig. 2). This happened independently of whether the eggs were added two or four days before the first laying, and this was inter-

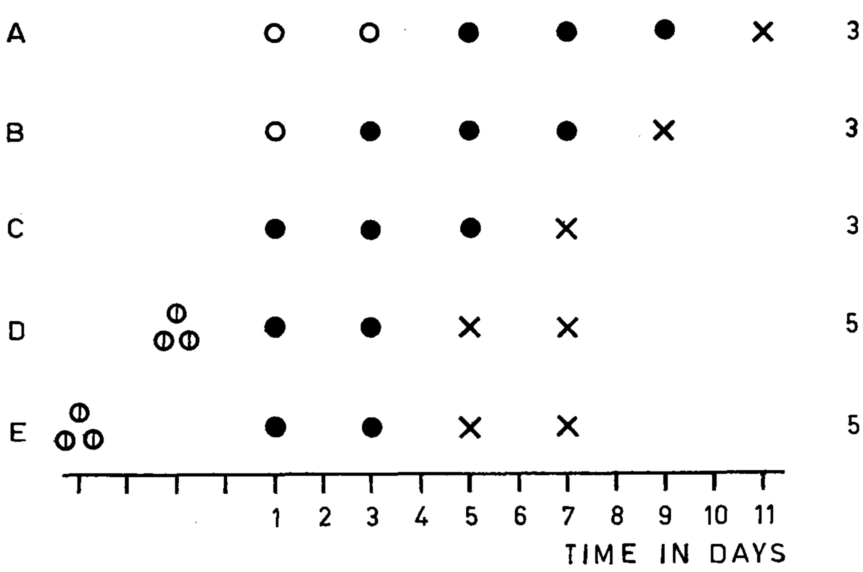

FIGURE 2. Experiments with eggs of Herring Gulls. **A.** The first and second, and (**B**) the first egg taken as laid. **C.** Normal egg laying. **D** and **E.** Three eggs added two and four days, respectively, before laying started. Eggs taken indicated by ○, eggs laid and incubated by ●, and suppressed follicles by ×. The last column gives the number of eggs incubated. Day 1 is day of first laying. After PALUDAN (1952).

preted by PALUDAN to show that the bird's physiological response to eggs in the nest changes in that period, otherwise in the latter case more than one egg of the bird's normal clutch would have been suppressed.

The Black-headed Gull, which has three eggs in the clutch too, responds to the presence of eggs in a similar way (WEIDMANN 1956). In this species the fourth follicle also starts to degenerate under the influence of the contact with the first egg in the nest. This occurs, like in the Herring Gull, while the follicle of the third ovum is still present in the ovary, and WEIDMANN rightly stated that the sitting on eggs affects the follicles differently. There seems to be a stage in follicle development before which they degenerate when the gull is sitting on eggs, and after which they ripen and ovulate whatever the gull's behaviour.

The Lapwing with four eggs in the clutch also has protracted laying after removal of the first or the first two eggs. This plover always deserts the empty nest in these cases, but completes the clutch with the normal laying frequency in another nest nearby. However, when three eggs are removed shortly after the third one has been laid, only the fourth is laid in another nest and this is abandoned. Obviously then, at the moment of egg removal, the degenaration of the fifth follicle has already begun and the ripening process cannot be restored again. After about seven days the bird starts with a repeat clutch of four eggs once more (KLOMP 1951).

Another wader, the Oystercatcher, presumably behaves in a different way. HARRIS (1967) reports that this species leaves the nest when the first egg is taken as laid, whence the rest of the clutch is laid in a new nest without the addition of an extra egg.

There is one example from another order of birds, the penguins, in which clutch-size is probably influenced by the contact of the bird with the first egg. The Adelie Penguin of Antarctica has a clutch of 1 (19 %) or 2 (81 %) eggs. In 19 nests the first egg was taken shortly after laying. Four birds deserted upon this, 3 laid a second egg, and 12 produced a second and third egg (TAYLOR 1962).

The experiments on gulls and waders have shown that the ripening of the follicles is inhibited by the contact of the bird with the first egg. In other indeterminate layers the number of eggs releasing follicle degeneration must be greater, because they continue laying beyond the normal clutch, when the eggs—the first one excepted—are removed as laid. In each species the degeneration is presumably released by a specific number of eggs depending on clutch-size, but so far this has not yet been investigated. STRESEMANN (1927-34) has suggested that laying might stop as soon as all the brood patches are in contact with eggs, but as shown earlier, this does not hold for the Laro-Limicolae. In other indeterminate layers it is also to be expected that degeneration will start before the clutch is full, because by then one or more of the follicles would have passed "the point of no return" and would develop two eggs anyway (p. 9).

So much for the experiments on removal and addition of eggs. Finally, we are faced with the question of the physiological mechanism of the control of the end of laying. This mechanism may be quite distinct for determinate and indeterminate layers. It has been suggested by EISNER (1960) that in the former the end of laying is either fixed by a predetermined number of follicles entering the final phase of rapid growth, or by reaching a certain level of progesterone or prolactin, accumulated after each ovulation during the laying period.

As to indeterminate layers, it has been stated by WITSCHI (1950) that the stimulus released from the eggs in the nest is perceived through tactile papillae in the skin of the bird's belly, without referring to experiments concerning this question. Although it is probable that tactile stimuli are involved, visual ones have never been excluded, and again more research is wanted.

The internal pathway of the sensory information is still very much of an open question as well. Most probably the information is conducted by the nervous system to the neurosecretory cells in the hypothalamus. These cells control the synthesis and secretion of hormones by the pituitary, and an induced change of neurosecretory activity should result in less gonadotrophins and more prolactin being produced by this gland. This should result in follicle degeneration in the ovary, and in a release of broodiness in the bird (EISNER 1958; LEHRMAN 1959).

2.2. MODIFICATIONS OF CLUTCH-SIZE BY INTERNAL FACTORS: THE AGE OF THE FEMALE

The proximate mechanism of clutch-size determination is affected by the age of the female in a variety of species. There is, of course, no effect of age in species laying one egg, though in many of them the juveniles have deferred maturation and do not lay any egg in their first year(s) of life (ASHMOLE 1963; AMADON 1964; LACK 1968). An effect of age also appears to be absent in the Woodpigeon, laying two eggs, and in the Lapwing, always laying four eggs. Further, the difference proved to be extremely small, if any, in the Bluebird (LASKEY 1943), the Velvet Scoter (KOSKIMIES 1957), and the Sky-lark (DELIUS 1965).

In many other species, the birds breeding for the first time, be it in the first or in a later year of life, tend to have a slightly smaller clutch. As shown in Table 3, the differences are small: in most species less than half an egg on the average. Effects of age on clutch-size, without indication of the size of the difference, have been found in the Black-headed Gull (NOLL 1931; GROEBBELS 1937), in the Trumpeter Swan, the Lesser Spotted Eagle, the Capercaillie and the Starling (GROEBBELS 1937), in the Caspian Tern (BERGMAN 1939), and in the Common Gull (HILDÉN 1964).

In a number of Passerines no further change in clutch-size occurred with further increase of age (KLUYVER 1935; CREUTZ 1955). In the Kittiwake, on the other hand, those breeding for the first time had an average clutch of 1.8 eggs, those breeding for the second or third time 1.9 eggs, and those breeding for at least the fourth time 2.4 eggs (COULSON & WHITE 1961). Further, three marked females of the Common Eider had mean clutches of 3.7, 4.7 and 5.7 eggs in three consecutive

TABLE 3

MEAN CLUTCH-SIZE OF DIFFERENTLY AGED BIRDS

Species and References ¹)	Locality	Age ²)	Mean clutch-size		Difference
			First breeding	Later breedings	
Yellow-eyed Penguin (1)	New Zealand	2 (3)	1.68	1.97	0.29
Kittiwake (2)	England	3 (4)	1.78	2.39	0.61
Swift (3)	Switzerland	2	2.33	2.77	0.44
Great Tit (4)	Netherlands	1	8.43	9.02	0.59
Great Tit (5)	England	1	8.28	8.76	0.48
Blackbird (6)	England	1	3.38	3.81	0.43
Redstart (7)	Netherlands	1	6.04	6.51	0.47
Pied Flycatcher (8)	Finland	1 (2)	5.65	6.33	0.68
Pied Flycatcher (9)	E. Germany	1 (2)	5.7	6.5	0.8
Pied Flycatcher (10)	C. Germany	1 (2)	5.96	6.54	0.58
Collared Flycatcher (11)	S. Germany	1	5.9	6.0	0.1
Starling (12)	Netherlands	1 (2)	4.45	5.60	1.15

¹) REFERENCES: (1) RICHDALE 1949, (2) COULSON & WHITE 1961, (3) WEITNAUER 1947, (4) KLUYVER 1951, (5) PERRINS 1965, (6) SNOW 1958, (7) RUITER 1941, (8) VON HAARTMAN 1967a, (9) CREUTZ 1955, (10) BERNDT & WINKEL 1967, (11) LÖHRL 1957, (12) KLUYVER 1935.

²) Age of first breeding in years, bracketed when part of the population deferres breeding to age shown.

years (GROSS 1938). In the Red-breasted Merganser birds breeding for the first time laid 6-8, those of the second breeding year 8-10, and the older birds laid 10-13 eggs (WILHJELM 1938). Similar results were reported for the Canada Goose by KOSSACK (1950).

In general, birds breeding for the first time start laying slightly later than older birds. In many species later layings tend to be smaller than early ones, but where studied the small mean difference in laying date could not account for all of the difference in clutch-size, as in the Pied Flycatcher (VON HAARTMAN 1967a), the Great Tit (KLUYVER 1951; PERRINS 1965), and the Kittiwake (COULSON & WHITE 1961).

DAVIS (1955b, 1958) has stated that the number of post-ovulatory follicles in the ovaries often exceeds the number of eggs in the nest, and he suggested that the slightly smaller clutch of yearlings might be due to the fact that they have to learn to get the eggs into the nest.

As shown by BLANK & ASH (1960), the Partridge is clearly an exception to the above rule. In an English population, the clutches of some individual females had 15.5 (eight nests), 15.3 (eight nests), 14.5 (four nests), and 11.0 eggs (one nest) in the first, second, third and fourth breeding season, respectively. Moreover, 61 females breeding for the first time had an average clutch of 15.75 eggs, and 39 females breeding for the second time had an average of 14.95 eggs, the difference being statistically significant.

It has been suggested by GROEBBELS (1937) and STRESEMANN (1927-34) that in some birds of prey, like the Buzzard and the Goshawk, and also in the Raven, very old females produce a slightly smaller clutch, but this needs further confirmation.

2.3. MODIFICATIONS OF CLUTCH-SIZE BY EXTERNAL FACTORS

2.3.1. THE INFLUENCE OF FOOD, WEATHER AND ALTITUDE

Positive relations between food abundance and clutch-size have been ascertained for several species. A good example is that given by MEBS (1964) between the population density of the Field Vole and the clutch-size of one of its predators, the Buzzard, in southern Germany (Table 4). Other examples are given by SCHENK (1912, 1914) for the White Stork, by SCHNEIDER (1928) for the Barn Owl, by SCHMAUS (1938) for the Buzzard, the Tawny Owl and the Barn Owl, by SOUTHERN (1959) for the Tawny Owl, and by MACARTHUR (1958) for the Bay-brested Warbler. For the last species it was shown that it had a slightly larger clutch when its prey, the spruce budworm, reached outbreak densities than in years when it was at endemic levels.

TABLE 4

RELATION BETWEEN FOOD QUANTITY AND CLUTCH-SIZE IN THE BUZZARD (MEBS 1964)

Density of voles (*Microtus arvalis*)	Years	Mean clutch-size
Crash, one year after peak	1956 and 1960	2.13
Start of increase	1957	2.25
Rising of plague	1958	2.41
Peak density of plague	1950 and 1959	3.17

The effect of food quantity on clutch-size can be studied profitably under conditions of short-term shortages. It is true, the disadvantage of the latter is that they are often directly caused by extreme weather situations, and as a consequence, food shortage and weather factors cannot be separated in their effect. Thus, it was shown by WEITNAUER (1947) and LACK (1956a) that, if there is an unusual cold spell in the main laying period of the Swift, the individuals that have started the clutch may postpone the laying of the second or third egg, or do not lay the third egg at all.

Another species which postpones laying with sudden cold weather is the Great Tit, at least when laying has not yet started. The Blue Tit, on the other hand, behaves like the Swift, and postpones the start of laying and interrupts once it has started (KLUYVER 1951). It is not known whether—like in the Swift—this results in a smaller clutch, but in connection with the general seasonal decline of clutch-size it is likely to be the case (p. 18).

A fine example of the influence of extreme weather on clutch-size is given by SNOW (1958) for the Blackbird. This species was studied from 1950 to 1955 at Oxford. In 1954 April was extremely dry, and during the dry spell there was an abnormally cold period. In this period mean clutch-size was remarkably lower than the mean over the six years of study, but returned to normal values as soon as the cold spell was over, though the drought persisted for another five-day period.

These results indicate that in temperate regions the food supply is not plentiful when laying starts. This is further supported by the evidence collected by PERRINS (1965) suggesting that the female Great Tit does not start laying before it can find enough food to produce an egg. This does not imply, however, that the number of eggs is also directly determined by food quantity. In general, the tits' food is rapidly increasing during springtime, whereas clutch-size decreases over this period, proving that other factors must be involved (Fig. 3). Therefore, in this species once laying has started the food supply will generally suffice for continued laying, unless exceptionally cold weather reduces the amount of food considerably. This continued laying does not occur, however, and is most likely to be prevented by one of the mechanisms discussed in section 2.1. Though several nesting studies of this titmouse have been performed, this mechanism has never been investigated.

Similar observations have been made on the Kestrel in The Netherlands by CAVÉ (1968). Firstly, he showed that the start of laying in this species is postponed in years when the density of the voles is low during the preceding winter and spring. Secondly, it was shown in experiments during winter that the growth rate of the ovarian follicles of caged birds was inhibited in the poorly fed ones. On these grounds CAVÉ suggested that the Kestrel does not start laying before it can find enough food to produce an egg. The size of the clutch is most probably not directly determined by food quantity because vole density generally increases after early spring, while clutch-size decreases (p. 26).

In many species significant annual differences in clutch-size occur, part of which have been attributed to variations in food supply. These cases will be discussed later (Section 2.3.5).

There is some evidence showing that clutch-size may vary with altitude, and this variation might be linked with climate. Thus, COULSON (1956) has shown that in England the clutch-size of the Meadow Pipit decreases with increasing altitude: at sea level it is 4.52 and at 1000 feet it is 4.07. This is the more remarkable because there is no variation with latitude. Breeding starts about 10 days later at thousand feet than at sea level, but this cannot account for the difference in clutch-size because in this pipit there is an initial rise of mean clutch-size in the course of the breeding season (Section 2.3.4).

The Pied Flycatcher in Switzerland has an average clutch of 5.70 eggs at altitudes lower than 700 m, but lays 5.45 eggs on the average at higher altitudes (GLUTZ VON BLOTZHEIM 1962). Again, in a Norwegian mountain area this flycatcher lays a mean clutch of 5.95 eggs, and has 6.31 eggs on the average in the Swedish lowlands (MEIDELL 1961). In both regions breeding starts later at the higher altitudes, and this may account for the differences, because this species has a decreasing seasonal trend of clutch-size right from the start of the breeding season (Fig. 3).

In another Passerine, the Song Sparrow of western North America, it is just the other way round. The clutch of this species increases with a rise of altitude (JOHNSTON 1954). However, in this case different subspecies are involved, and the differences between the size of the clutches may be hereditary; if so, they need an ultimate explanation.

JENKINS *et al.* (1963) found smaller clutches at higher altitudes in Red Grouse in Scotland, but these differences proved to be correlated with laying date (Section 2.3.4).

2.3.2. THE INFLUENCE OF THE HABITAT

Differences in mean clutch-size between geographically separated populations of the same species, inhabiting various habitats in most cases, have been found regularly. It is generally assumed that such differences have a genetic basis instead of being modificatory in nature. If this assumption is correct, they need an ultimate rather than a proximate explanation, and therefore, will be considered in Section 3.5.

In some species habitat-linked differences of clutch-size have been found between less remote localities, so that hereditary differences between the populations are unlikely. Thus, KLUYVER (1951, 1963) found differences in mean clutch-size of the Great Tit between different types of habitats in The Netherlands, which only partly depended on variations in population density (Section 2.3.3). In general, the largest clutches were found in rich oak wood and the smallest in gardens and open parkland. The same trend has been found for this species in England by LACK (1955). Both KLUYVER (1951) and LACK (1955) found relatively large clutches of the Great Tit in Scots pine forests, which they partly attributed to low population density. Moreover, the size of genuine second clutches shows—as compared with first ones—a less steep drop in Scots pine than in broad-leaved, and KLUYVER's figures suggest that second clutches in the latter are actually smaller than in conifers.

In England the Blue Tit has about the same trend as its congener (LACK 1955). For this species the following mean values were found in southern England: oakwood 11.5, mixed 10.6, Scots pine 10.4, small gardens 9.6 and Corsican pine 9.0 eggs.

In the Great Tit variations of mean clutch-size even occurred between adjacent habitats in the same forest, which had a regular interchange of individuals, so that genetic differences could be excluded with certainty. Areas with tall oaks or elms had larger mean clutches (9.99-10.21) than areas with lower and denser trees (8.97-9.28), and these differences could not be attributed to variations in laying date or density. Moreover, consistent differences in age composition between the breeding birds of the various habitats appeared to be unlikely (PERRINS 1965).

Further, there is some evidence for habitat-linked differences in two other species, the Blackbird and the Pied Flycatcher. SNOW (1958) found a slightly smaller clutch in populations of the former species in gardens in Oxford than in broad-leaved wood in the surroundings of this town. In April and May the layings in gardens had respectively 2.8 and 3.4 eggs, and in the wood 3.2 and 4.1. Though allowance was made for the possible influences of the age of the birds and of the time of laying (Sections 2.2 and 2.3.4), the effect of density could not be excluded. The wood had a much lower density, and the differences might, at least partly, be linked with this factor (LACK 1966).

CREUTZ (1955) found small differences in clutch-size between populations of the Pied Flycatcher inhabiting orchards (6.5 eggs), parkland (6.3) and mixed wood (6.1) in eastern Germany, but it is not known whether they are statistically significant. LÖHRL (1965) and BERNDT & WINKEL (1967) found smaller mean clutches of this Flycatcher in pine than in broad-leaved forest. In Finland this species has no habitat-linked differences in clutch-size (VON HAARTMAN 1954).

COULSON & WHITE (1961) found differences in mean clutch-size between colonies of the Kittiwake in northern England and Scotland, but these proved to be correlated with laying date (p. 23).

The variations in clutch-size with the habitat must be due to some form of reaction of the bird to the environment, but the proximate factors involved are not known. Measurements of the amount of food present (LACK 1955), or habitat-linked differences in the survival rates of the young (LACK 1955; SNOW 1958) strongly suggest that the habitats with the larger clutches have more suitable food at the time the young are reared, but this food is not available at the time of laying so that the birds cannot directly respond to this factor. Therefore, PERRINS (1965) considers it to be more likely that the birds respond to the general appearance of the vegetation.

2.3.3. THE INFLUENCE OF POPULATION DENSITY

The effect of density on clutch-size has been studied in a small number of species only. It seems to be absent in gallinaceous birds like the Partridge (BLANCK & ASH 1960), the Capercaillie and the Black Grouse (HELMINEN 1963) and the Red Grouse (JENKINS *et al.* 1963). As to ducks, an effect of density is most probably lacking in the Tufted Duck and the Scaup (HILDÉN 1964). In Finland the density of these diving ducks steadily increased from 1949 up to 1963, but the clutch-size did not decrease during this period. According to HILDÉN, this can be expected in nidifugous birds.

In Passerines an effect of density was first found in the Great Tit in Holland by KLUYVER (1951), and afterwards in England by LACK (1955) and PERRINS (1965). PERRINS calculated that in a population inhabiting broad-leaved forest, the clutch decreased by approximately two eggs, when the population doubled in density. In the Dutch populations this reduction was clearly less. The size of the first clutch decreased approximately from 10 to 8 eggs over the range from 0.3 to 10 pairs per 10 ha, including data of widely different habitats. This geographical difference might be connected with the fact that in Holland a much higher proportion of the breeding birds produced a second clutch, and this fraction proved to be affected by density considerably (KLUYVER 1951).

A similar effect of density on clutch-size has been found in two other species of tits, the Blue and the Coal Tit in England (LACK 1955, 1966). On the other hand, there seems to be no appreciable effect of density in the Pied Flycatcher in England (LACK 1966: Table 20), in Finland (TOMPA 1967), and in Germany (BERNDT & WINKEL 1967).

The elements of "density" to which the birds respond are not known. This may be either the smaller size of the territory or the more intense contact with their neighbours, or both.

2.3.4. SEASONAL VARIATIONS OF CLUTCH-SIZE

LACK (1947-48) reports that in some birds of prey and owls the clutch-size can increase in the course of the breeding season. This has been observed in species preying on small mammals, and only in years in which the abundance of the prey increased enormously (SCHNEIDER 1928). What happens in years without plagues of prey animals is uncertain, except for the Kestrel (Table 5, Fig. 3).

TABLE 5

LIST OF SPECIES IN WHICH A SEASONAL CHANGE OF CLUTCH-SIZE HAS BEEN ESTABLISHED

Species	Country	References
Species with a decline right from the start of the breeding season		
ANSERIFORMES		
Greater Snow Goose	Canada	LEMIEUX 1959
Blue Snow Goose	Canada	COOCH 1961
Blue-winged Teal	U.S.A., Canada	BENNETT 1938; SOWLS 1949; DANE 1966
Mallard	Netherlands	EYGENRAAM 1957
Mallard	Canada	SOWLS 1949
Mallard	Germany	DATHE & PROFFT 1936
Mallard	England	OGILVIE 1964
Gadwall	Canada	SOWLS 1949
Pintail	Canada	SOWLS 1949
Shoveller	Canada	SOWLS 1949
Redhead	U.S.A.	LOW 1945
Pochard	Czechoslovakia	HAVLIN 1966
Wood Duck	U.S.A.	LEOPOLD 1951
Velvet Scoter	Finland	KOSKIMIES & ROUTAMO 1953
Tufted Duck	Finland	HILDÉN 1964
Tufted Duck	Czechoslovakia	HAVLIN 1966
Scaup-duck	Finland	HILDÉN 1964
Red-breasted Merganser	Finland	HILDÉN 1964
FALCONIFORMES		
Sparrow Hawk	England	OWEN 1926-27
Kestrel	Netherlands	CAVÉ 1968
GALLIFORMES		
Red Grouse	Scotland	JENKINS *et al.* 1963
Prairie Chicken	U.S.A.	HAMERSTROM 1939
Bobwhite Quail	U.S.A.	ERRINGTON 1933; LEOPOLD 1933
Partridge	U.S.A.	YEATTER 1934

Table 5, continued

Partridge	England	Lack 1947*; Blank & Ash 1960; Jenkins 1961
Pheasant	U.S.A.	Errington & Hamerstrom 1937; Randall 1939; Leedy & Hicks 1945; Stokes 1954; Wagner *et al.* 1965.
	Gruiformes	
Coot	Germany	Kornowski 1957
	Charadriiformes	
Oystercatcher	England (Wales)	Harris 1967
Dotterel	Scotland	Nethersole-Thompson 1951
Greenshank	Scotland	Nethersole-Thompson 1951
Herring Gull	E. Canada	Paynter 1949
Herring Gull	Denmark	Paludan 1952
Herring Gull	England	Brown 1967
Lesser Black-backed Gull	Denmark	Paludan 1952
Glaucous-winged Gull	W. Canada	Vermeer 1963
Common Gull	Finland	Bergman 1939
Common Gull	Estonia	Onno 1967
Black-headed Gull	Switzerland	Noll 1931
Black-headed Gull	Finland	Bergman 1939
Kittiwake	England	Coulson & White 1961
Caspian Tern	Finland	Bergman 1953
Common Tern	Finland	Bergman 1939
	Caprimulgiformes	
Oilbird	Trinidad	Snow 1962b
	Apodiformes	
Swift	Switzerland	Weitnauer 1947; Weitnauer & Lack 1955
Swift	England	Lack & Lack 1951; Lack 1956a
Alpine Swift	Switzerland	Lack & Arn 1947
	Passeriformes	
Barn Swallow	E. Germany	Brinkmann 1938
Barn Swallow	U.S.A.	Mason 1953
Barn Swallow	Poland	Kuzniak 1967
Martin	E. Germany	Brinkmann 1938
Martin	Finland	Lind 1960
Tree Swallow	E. Canada	Paynter 1954
Bank Swallow	U.S.A.	Petersen 1955
Jackdaw	England	Lockie 1955
Magpie	Switzerland	Huber 1944
Rook	England	Lockie 1955
Great Tit	Netherlands	Tollenaar 1922; Kluyver 1951
Great Tit	England	Lack 1950*, 1956b, 1966
Great Tit	Finland	von Haartman 1967a*
Great Tit	Japan	Royama 1966
Blue Tit	Netherlands	Lack 1950*
Blue Tit	England	Lack 1950*, 1955, 1958
Coal Tit	England	Lack 1950*, 1955
Crested Tit	England	Lack 1950*

TABLE 5, continued

Black-capped Chickadee	U.S.A.	Kluyver 1961
House Wren	U.S.A.	Kendeigh 1941
Long-billed Marsh Wren	U.S.A.	Verner 1965
American Robin	U.S.A.	Howell 1942
Fieldfare	Finland	von Haartman 1967a*
Redstart	Netherlands	Ruiter 1941
Whinchat	Germany	Schmidt & Hantge 1954
Wood Warbler	England	E. Lack 1950*
Pied Flycatcher	Finland	von Haartman 1954, 1955, 1967a
Pied Flycatcher	Wales	Campbell 1950, 1955; Lack 1966
Pied Flycatcher	Germany	Creutz 1955; Curio 1959; Berndt & Winkel 1967
Collared Flycatcher	S. Germany	Löhrl 1957
Spotted Flycatcher	England	Summers-Smith 1952*
Spotted Flycatcher	Finland	von Haartman 1967a*, 1967b*
Cedar Waxwing	U.S.A.	Putnam 1949
Red-backed Shrike	S. Germany	Schreurs 1941
Red-backed Shrike	England	Owen & Lack 1946
Starling	Netherlands	Kluyver 1933; Lack 1948b
Starling	Scotland	Dunnet 1955
Starling	Finland	von Haartman 1967a*
Prothonotary Warbler	U.S.A.	Walkinshaw 1941
Chaffinch	England	Newton 1964*
Chaffinch	Finland	von Haartman 1967a*
American Goldfinch	U.S.A.	Stokes 1950; Holcomb 1969
Bullfinch	England	Lack 1966

Species with an initial rise and final decline of clutch-size

Crested Lark	Germany	Haun 1931
Crested Lark	Netherlands	Verwey 1931
Wood-lark	Germany	Haun 1931
Sky-lark	Germany	Haun 1931
Sky-lark	England	Delius 1965
Meadow Pipit	England	Coulson 1956
Coal Tit	Netherlands	Verwey 1931
Coal Tit	England	Lack 1958
Wren	England	Armstrong 1955
Blackbird	Netherlands	van 't Sant 1921
Blackbird	Germany	Mildenberger 1940
Blackbird	England	Lack 1949a*, 1954, 1956b Snow 1955*, 1958
Song Thrush	Netherlands	van 't Sant 1921
Song Thrush	England	Lack 1949a*, 1954; Snow 1955*
Song Thrush	Scotland	Snow 1955*
Song Thrush	Finland	Siivonen 1939; von Haartman 1967a*, 1967b*
Mistle Thrush	England	Snow 1955*
Redwing	Finland	von Haartman 1967a*; Tyrväinen 1969
Robin	England	Lack 1945, 1948a
Robin	Continental Europe	Lack 1945, 1948a
Yellowhammer	Germany	Haun 1931
Yellowhammer	Poland	Lack 1954
Yellowhammer	England	Parkhurst & Lack 1946; Peakall 1960*

TABLE 5, concluded

Song Sparrow	U.S.A.	JOHNSTON 1954
Tree Sparrow	England	SEEL 1964, 1968
House Sparrow	England	SUMMERS-SMITH 1963; SEEL 1968

NOTES: (1) Data from nest-record cards indicated by an asterisk (*).
(2) Some songbirds seem to have a constant clutch-size over the initial part of the breeding season, followed by a decline. This has been reported for the Coal Tit in English pine woods, for the Song Thrush in Finland by VON HAARTMAN (1967a), but not by SIIVONEN (1939), for the Spotted Flycatcher in England, and for the Chaffinch in England and Finland.
(3) There are two cases of double brooded species, in which the final decline of clutch-size is doubtful, namely the Meadow Pipit in England, and the Yellowhammer in Germany, though the latter has a clear decline in Poland and England.

There are some species which have a constant number of eggs in the clutch throughout the breeding season. The Lapwing, which is single brooded but produces repeat clutches after disturbance, always has four eggs (KLOMP 1951), and the Redshank apparently behaves in the same way (BANKES 1897). The Woodpigeon, which has several broods in a year, apparently has always two eggs (LACK 1947-48; MURTON 1958). In the Crested Grebe, the clutch of which varies from 2 to 5 eggs, there is no trend from April through June, and perhaps July. In Switzerland the averages over these months amount to 4.25, 4.12, 4.24, and 4.52 eggs (BAUER & GLUTZ 1966). In a "colony" in the central parts of The Netherlands, where the average size of the clutch appeared to be small as compared with other areas, the means are 3.7, 3.5, 3.6, and 2.6, respectively (LEYS *et al.* 1969). Finally, according to OWEN (1960), there is no seasonal change in the clutch of the Common Heron in England. This species lays three to five eggs, and is single brooded. Repeat clutches are regularly produced, sometimes three or four in succession, when the eggs are robbed by crows, but the size of these clutches does not decrease.

In most other species studied a seasonal change has been observed. In one group there is a decrease of clutch-size right from the start of the breeding season. In another there is an initial increase followed by a gradual decrease of the number of eggs in the clutch (Table 5, Fig. 3 and 4). It has been suggested by LACK (1954) and COULSON & WHITE (1961) that the species of the first group are single brooded, and those of the second double or triple brooded. Though this holds for most species, there are some exceptions in the first group. For instance, in the American Robin, which is double and partly triple brooded, the second clutch is smaller than the first, and the third smaller than the the second one (HOWELL 1942), and the same holds for the Barn Swallow and the Martin in Germany and Poland (BRINKMANN 1938; KUZNIAK 1967). In the Great Tit in Holland, the Fieldfare in Finland, the Starling in Holland and Scotland, and the Cedar Waxwing, the Goldfinch and the Prothonotary Warbler in the U.S.A. at least part of the females have two broods per year, though this part is usually small. In some species (see note to Table 5) the clutch is constant over the initial part of the breeding season and in these cases there is evidence that a considerable part of the population is double brooded.

From several species listed in Table 5 graphs as presented in the Figures 3 and 4 cannot be composed, because the relation between laying date and clutch-size is unknown. Then the authors have only indicated the mean difference between first and repeat layings, or between first and second layings. This holds for the ducks studied by SOWLS, the Coot, Sparrow-Hawk, Dotterel, Greenshank, most of the gulls, most of the swallows, Magpie, Whinchat and Red-backed Shrike.

For many of the others mean clutch-size has been given for layings started in successive intervals of time. These intervals have been taken quite differently by the various authors, with the result that the curves for some species are rather smooth, while others show a scattering of the interval-means. This scatter is partly due to chance, since some points in the graphs are based on less than five nests only; additionally, the scatter results from the fact that the graphs are composed of figures from different habitats and densities, differently aged birds and different years. This holds especially for the graphs derived from nest-record cards, marked in Table 5 by an asterisk(*).

As discussed earlier, young birds have smaller clutches, and as they tend to start laying slightly later than adults, they contribute to the decline of clutch-size later in the season. It has been suggested that the seasonal decline is (or might be) mainly due to this effect in the Black-headed Gull (NOLL 1931), the Common Gull (HILDÉN 1964), the Starling (KLUYVER 1933, 1935) and in the Greater Snow Goose (LEMIEUX 1959).

The last species was studied in 1957 on an island north of the Hudson Bay. The season suitable for breeding is very short in this northern area and the geese started laying within the extremely short interval of 10-14 June. Nevertheless there is a clear trend as shown in Table 6. LEMIEUX suggests that the decline of clutch-size may result from the slightly later nesting of young birds breeding for the first or second time.

TABLE 6

CLUTCH-SIZE AND LAYING DATE IN THE GREATER SNOW GOOSE

First egg of clutch laid on June	10	11	12	13	14
Mean clutch-size	6.5	5.5	4.9	3.9	4.0
Number of nests	4	2	6	6	4

In other species the effect of age is much less pronounced. The age-linked differences in the start of laying are only small and cannot account for the steady decrease of clutch-size over the whole breeding season. Moreover, where different age classes were treated separately, they showed a similar trend. This has been established for the Pied Flycatcher (BERNDT & WINKEL 1967; VON HAARTMAN 1967a), the Blackbird (SNOW 1958), and the Kittiwake (COULSON & WHITE 1961). See Figures 3 and 4.

The graphs given in the Figures 3 and 4 usually include first and repeat layings in single brooded species, and first, second, third, and repeat layings in double and triple brooded species. Most probably the size of the clutch is primarily determined by the laying date irrespective of its nature. This is, however, difficult to demonstrate, because the nature of the clutches can rarely be distinguished. In the single brooded Kittiwake, which rarely produces repeat layings, the trend results from the fact that birds starting early in the season tend to have a larger clutch (COULSON & WHITE 1961). The same holds for single brooded species which produce repeat layings, if the first clutch is destroyed. Where such replace clutches could be separated from the genuine first layings, there proved to be a seasonal trend within the latter. Thus, in the Great Tit early first layings are larger than late ones in the same season (LACK 1955, 1966; PERRINS 1965), and the same holds for the Blue Tit (LACK 1955, 1966), and the Pied Flycatcher (CURIO 1959-60), though probably not for the Whinchat (SCHMIDT & HANTGE 1954).

In species with a decreasing clutch right from the start of the breeding season, the repeat and second layings fit in with the seasonal decline of the first layings, resulting in an overall downward trend over the whole breeding season.

Double and triple brooded species usually have an initial rise of clutch-size (Fig. 4). It is not known, whether this rise is due to an increase of first layings with time or to larger repeat and second layings, or to both, but it is to be expected that also in this group of species the size of the clutch is primarily determined by the laying date irrespective of the nature of the clutch. This has been established for the Blackbird (SNOW 1958).

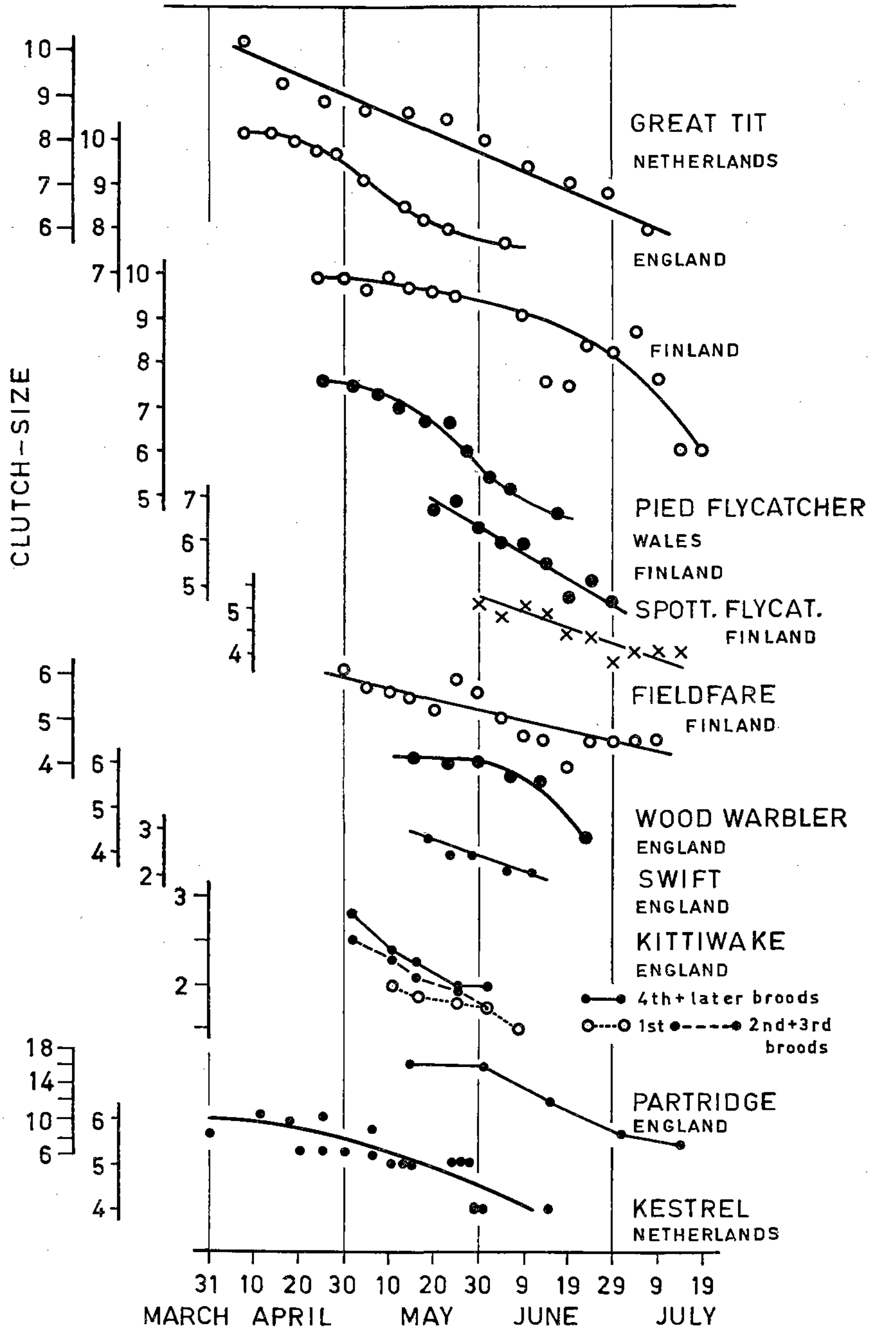

FIGURE 3. Seasonal changes of clutch-size in species with a decline right from the start of the breeding season.

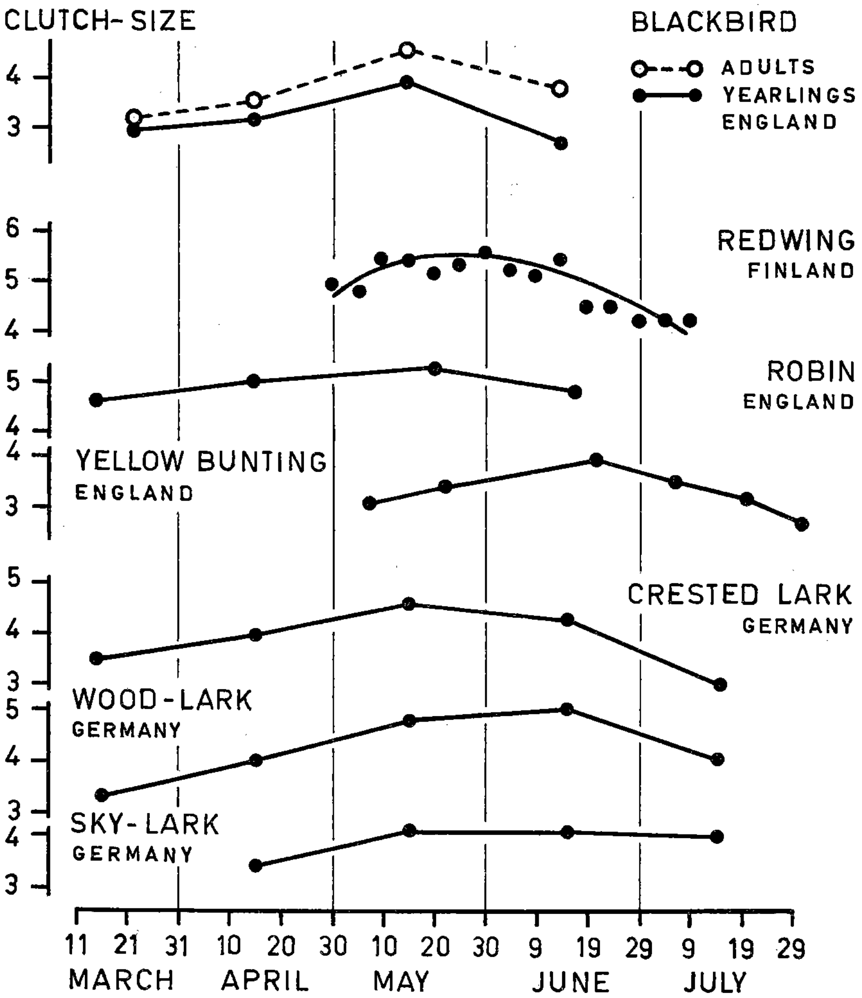

Figure 4. Seasonal changes of clutch-size in species with an initial rise followed by a decline.

When we now come to reviewing the proximate factors involved in the causation of the seasonal changes, we primarily have to consider the important question of whether the changes are in fact modificatory. This has been questioned for the Velvet Scoter by Koskimies (1957), who showed that the clutch-size within individual females is very constant in successive years, in spite of differences in the start of laying between years. Between females, however, the differences were remarkable and varied between 7.5 and 9.6 eggs irrespective of age. Koskimies assumes these differences to be hereditary, because they could not be attributed to environmental factors. Now the females (genotypes) with the largest and the smallest clutch, start laying respectively earliest and latest each year, resulting in a seasonal decline of clutch-size for the population as a whole. He further assumes that the tendency to start early is genetically fixed as well, and that the genes for a large clutch and early laying are linked.

When this interpretation is correct, the seasonal decline of clutch-size is indeed not influenced by environmental factors. The argument is, however, based on the observation that there is no correlation within females between clutch-size and laying date, but there may be too few observations to draw this conclusion (KOSKIMIES & ROUTAMO 1953).

In other species the seasonal trend is of a modificatory nature, since it has been established not only for the population, but also for successive layings of individual females, like in the Robin (LACK 1945, 1948a), the Pied Flycatcher (VON HAARTMAN 1967a), the Sparrow Hawk (OWEN 1926-27), the Red-backed Shrike (OWEN & LACK 1946), and others.

The proximate factors involved are very badly understood. One theory, originally put forward by TOLLENAAR (1922), and recently reformulated by WAGNER *et al.* (1965), states that the female bird has a certain amount of energy at its disposal at the start of the breeding season, which has to be distributed over the sequence of reproductive activities, such as egg production, brooding and feeding young. Hence, when the first clutch of a single brooded species is destroyed, the repeat clutch must be necessarily smaller, because the amount of energy left is insufficient to produce a clutch of equal size. However, this theory cannot account for the smaller first clutch of individuals starting late, unless the late birds have been less successful in the formation of their energy reserves. In addition, some single brooded species even produce repeat clutches after having fed young, and hence must have spent most of their reserves. Finally, the theory is difficult to maintain for species, the repeat clutches of which are greater than their first layings, like in the Blackbird (SNOW 1958).

It was previously discussed that clutch-size in some species might be directly controlled by the amount of food available for the laying female. It has been shown for the Great Tit in England, which has a declining clutch right from the start of the breeding season, that food density at the same time increases rapidly (LACK 1966), and this is likely to occur with the food supply of much more Passerines of temperate regions. Also in the Kestrel there is good evidence for the occurrence of opposite seasonal trends of clutch-size and food quantity, though food availability may decrease due to the growing vegetation. Kestrels clearly prefer a short vegetation for hunting (Cavé 1968). Snow (1955) has suggested that the initial rise of clutch-size of the Blackbird is unlikely to be the result of a direct response to food, because earthworms—the preferential food of the bird—are most numerous at the surface early in spring.

Another factor which might have a proximate effect on clutch-size is daylength, but as shown in the Figures 3 and 4, if there is a relation, it cannot be a simple one. Many of the species presented in Figure 3 have a declining clutch before the summer solstice and go on declining after 21 June. Those presented in Figure 4 initially increase their clutch, but all culminate before the longest day, except the Yellowhammer in England and the Wood-lark in Germany. Snow (1955) has shown that the clutch-size of the Song Thrush in England culminates one week earlier than that of its relative, the Blackbird.

The seasonal decline in the layings of the House Wren has been attributed to the rising trend of temperature in spring by Kendeigh (1934). These observations were later confirmed by some experimental results showing that high temperatures appear repressing and low temperatures stimulating for the laying of extra eggs in this species (Kendeigh 1941).

Summarizing, it may be concluded that in fact nothing is known about the proximate factors determining the seasonal trends of clutch-size. The most obvious environmental factors can at most be correlated with part of the trends observed, and it has therefore been suggested by Berndt & Winkel (1967) that the seasonal change of the clutch is controlled by an intrinsic physiological mechanism, the operation of which might be timed by daylength. Finally, it can be stated that there is a great need for experimental work in this field, but the total lack of this is a reflexion of its difficulties.

2.3.5. Annual variations of clutch-size

In a number of species the average size of the first clutch varies year by year. The range of variation is presented in Table 7 for populations the clutch-size of which has been determined for at least four successive years. In addition, annual differences have been found in the Canada Goose and the Pintail (quoted by Hildén 1964), the Kestrel (Cavé 1968), the Caspian Tern (Bergman 1953), the Alpine Swift (Lack & Arn 1947), the Tree Swallow (Paynter 1954), the Rook (Owen 1959), the Crested Tit (Lack 1950), the Coal Tit (Lack 1955), the Long-billed Marsh Wren (Verner 1965), the Blackbird and Song Thrush (Lack 1949a; Snow 1955), the Robin (Lack 1948a, 1949a), and the American Goldfinch (Holcomb 1969).

TABLE 7

THE MINIMUM AND MAXIMUM ANNUAL MEAN OF THE SIZE OF THE FIRST CLUTCH OF BIRD POPULATIONS STUDIED FOR AT LEAST FOUR SUCCESSIVE YEARS

Species and References [1]	Locality	Number of years	Mean clutch-size		
			Min.	Max.	Diff.
White Stork (1)	Hungary	4	2.85	3.37	0.5
Velvet Scoter (2)	Finland	5	8.30	9.25	1.0
Tufted Duck (3)	Finland	9	9.3	10.2	0.9
Tufted Duck (4)	Czechoslovacia	7	7.77	9.29	1.5
Pochard (4)	Czechoslovacia	7	8.29	8.47	0.2
Scaup Duck (3)	Czechoslovacia	9	9.6	9.9	0.3
Ring-necked Duck (5)	U.S.A., Maine	12	8.7	9.5	0.8
Common Eider (3)	Finland	9	4.5	5.0	0.5
Common Eider (6)	Finland	6	4.72	5.44	0.7
Buzzard (7)	S. Germany	6	2.13	3.17	1.1
Red Grouse (8)	Scotland	5	6.1	8.1	2.0
Hazelgrouse (9)	Finland	7	7.93	9.40	1.5
Black Grouse (9)	Finland	7	7.99	8.62	0.6
Capercaillie (9)	Finland	7	7.15	7.59	0.4
Partridge (10)	England	9	14.81	15.87	1.1
Swift (11)	C. England	5	2.0	2.5	0.5
Rook (12)	England	6	4.2	4.7	0.5
Great Tit (13)	Netherlands	14	8.98	10.17	1.2
Great Tit (14)	Netherlands	37	8.0	10.2	2.2
Great Tit (15)	England	6	7.8	12.3	4.5
Blue Tit (16)	England	6	10.2	13.4	3.2
Redstart (17)	Netherlands	4	6.07	6.46	0.4
Pied Flycatcher (18)	England	16	6.4	7.5	1.1
Pied Flycatcher (19)	Finland	22	5.7	6.7	1.0
Pied Flycatcher (20)	Berlin	5	6.0	6.8	0.8
Pied Flycatcher (21)	Dresden	22	5.3	6.6	1.3
Collared Flycatcher (22)	Stuttgart	7	5.5	6.2	0.7
Starling (23)	Netherlands	7	5.06	5.55	0.5
Tree Sparrow (24)	England	7	4.57	5.60	1.0

[1] REFERENCES: (1) SCHENK 1912, (2) KOSKIMIES & ROUTAMO 1953, (3) HILDÉN 1964, (4) HAVLIN 1966, (5) MENDALL 1958, (6) BERGMAN 1939, (7) MEBS 1964, (8) JENKINS *et al.* 1963, (9) SIIVONEN 1952, (10) BLANK & ASH 1960, (11) LACK & LACK 1951, (12) OWEN 1959, (13) LACK 1950, (14) KLUYVER 1951, (15) LACK 1955, (16) LACK, GIBB & OWEN 1957, (17) RUITER 1941, LACK 1949a, (18) CAMPBELL 1955, LACK 1966, (19) VON HAARTMAN 1967a, (20) CURIO 1959-60, (21) CREUTZ 1955, (22) LÖHRL 1957, (23) LACK 1948b, (24) SEEL 1968.

The differences between the maximum and minimum average clutches may vary considerably. In ducks, for instance, the maximum is 3-20 per cent higher than the minimum. In gallinaceous birds the maximum is only 5.6 per cent higher than the minimum in the Capercaillie, but as much as 33 per cent in the Red Grouse. In the Buzzard the greatest average clutch is 52 per cent higher than the smallest average, and a similar range has been reported for the Great Tit. In the well studied

Pied Flycatcher the range varies between 13 and 24 per cent of the minimum clutch for different breeding populations in Europe (Table 7).

It was shown in Section 2.2 that juvenile birds have smaller clutches than adults, the Partridge excepted. Therefore, in principle, the mean clutch may be expected to vary according to the proportion of juveniles in the population. However, KLUYVER (1951) is of the opinion that in the Great Tit the difference in clutch-size between yearlings and adults is too small to account for the substantial annual variations.

On the other hand, MENDALL (1958) has shown that there is a correlation between the mean clutch-size of the Ring-necked Duck in a given year and the breeding success of the preceding year. If the latter is poor the clutch tends to be large next year. Again, HILDÉN (1964) collected some evidence suggesting the same relations to occur in the Tufted Duck and the Scaup.

Unlike all other species studied so far the juveniles of the Partridge have a slightly larger clutch than the adults. BLANK & ASH (1960) were able to estimate the proportion of juveniles in a breeding population on an English estate from 1949 to 1957. In 1955 there were only 18 juveniles to 100 adults, and the mean clutch had a minimum value of 14.8 eggs, which was at least partly attributed to the abnormal age composition. Over the other years the proportion of juveniles varied from 100-254 to 100 adults, but in this range of age ratios there was no relation with clutch-size.

In the Great Tit the annual variation of clutch-size could partly be attributed to differences in population density, at least at densities higher than 4 pairs per 10 ha (KLUYVER 1951). A similar effect of density was found in the Great and the Blue Tit by LACK (1955, 1966). Also, when density is high, the population may be expected to be composed of a high proportion of juveniles, but even this effect is only small and cannot explain all of the annual variations (LACK 1966).

The annual differences in clutch-size proved not to be related to density in the Tufted Duck and the Scaup (HILDÉN 1964).

In several species the annual variation is related to laying date. Thus, in colonies of the Caspian Tern the proportion of clutches with 3 eggs decreases the later the start of egg laying (BERGMAN 1953). In the Kestrel the start of laying is postponed by food shortage and heavy rainfall in winter and spring, and by low temperatures in spring, and in such years the size of the clutch decreases to fit in with the seasonal decline (CAVÉ 1968). This point has been studied in much more detail in the Great and Blue Tits, and in the Collared and Pied Flycatchers. These birds tend to have a smaller average clutch in the years that breeding in the population starts later, fitting the trend in the course of each season (CREUTZ 1955; LACK 1955, 1966; LÖHRL 1957; VON HAARTMAN 1967a).

In the Pied Flycatcher in Finland the clutch decreased by 0.07 egg on the average for each day that laying started later (Fig. 5, small dots). This decline fits in with the overall relationship between laying date and clutch-size for this species given in the same figure (large dots). The same fit of annual variation and seasonal decline was found for the Pied Flycatcher in England (CAMPBELL 1955; LACK 1966) and in central Germany (BERNDT & WINKEL 1967), and for the Great Tit in England (LACK 1966). The clutch of the latter decreased by 0.09 egg for each day later that it was laid, both within one season and in different years.

The average date of first layings is highly correlated with the temperature in March and April each year. This might be a direct effect of temperature on the tits, but not on the flycatchers, which do not arrive at their breeding grounds until the second half of April. However, temperature in early spring is closely correlated with the appearance of fresh green vegetation and the birds' food, and LÖHRL (1957) therefore suggested that it is one of these factors to which the birds respond. Also in the Great Tit the amount of food available for the hens is likely to play a dominant part in the timing of the start of laying (PERRINS 1965).

Though the food supply may be of primary importance in this respect, it cannot be effective as a proximate factor in the determination of clutch-size. Both in early and late springs food rapidly increases during the period that the eggs are laid (p. 14). In fact, the proximate factor that connects clutch-size with the time of the year is unknown.

Not all of the annual variation of average clutch-size in Flycatchers is related to the mean laying date. This appears from the scatter of the small dots in Figure 5. Clutch-size in years with a late start can be significantly larger than in early years. This cannot be explained by differences in population density, which has no effect on clutch-size in this species (p. 17); nor can it be explained by differences in age composition, the effect of which is too small (p. 12). Therefore, there must be an additional factor affecting the size of the clutch, but this is unknown in the Pied Flycatcher (VON HAARTMAN 1967a).

This also applies to the Great Tit. As shown, in this species annual variations of clutch-size are due to effects of density and age-composition to a small extent, and they further depend on variations in laying date. Like in the Flycatcher there is, however, a rest-variation which must be due to an unknown factor. LACK (1955) and LACK, GIBB & OWEN

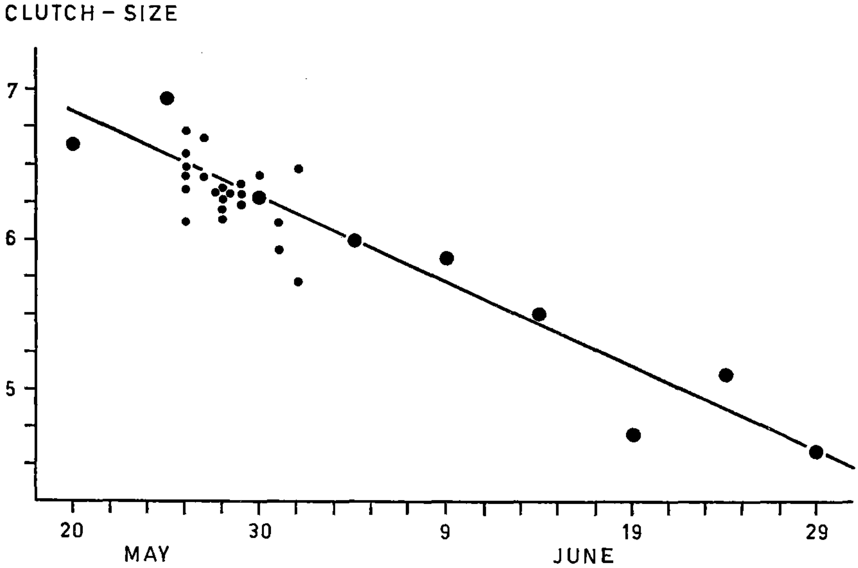

FIGURE 5. Mean size of clutches of the Pied Flycatcher in Finland started during 5-day periods, including all first and repeat layings over the years 1941-1965 (large dots). Mean size of first layings of different years (1943-1965; 1958 excluded), plotted over the date on which half of the females had started laying (small dots). After VON HAARTMAN (1967a).

(1957) have shown, that the average size of the first clutch of Great and Blue Tits varies in parallel, and that it is related to the amount of food present in mixed broad-leaved forest at the time the young are in the nest. The adult birds cannot respond to this factor at the time of egg-laying, however, since then the caterpillars are not yet available. Therefore, in April and early May the birds respond to some unknown factor, which is related in some way or other to the amount of food later available for the young.

A similar situation has been found in the Alpine Swift, in which the annual variations are not related to the mean laying date (see below). In a Swiss population of this species the proportion of clutches with three and four eggs varies between 50 and 90 per cent. This variation proved to be correlated with the mortality rate of the young in the larger broods: in years with a high proportion of large clutches the mortality rate of the nestlings was low. This strongly suggests, that the adults respond to some unknown factor during the laying time, which is correlated with the amount of food present some three weeks later when the young are fed (LACK & ARN 1947).

In the Kittiwake the annual variations of clutch-size could be studied in individual females (COULSON & WHITE 1961). Firstly, the clutch is significantly affected by the age of the female (p. 11). Secondly, when the clutch changed from one year to another it was additionally related to laying date: a large clutch was correlated with an early start (p. 23). Of 21 females both age and laying date were known over four successive years. The actual mean clutch of these individuals could be compared with an expected mean clutch, based on age and laying date each year. The former proved to deviate from the latter in a special way. There was an evident tendency to producing an average clutch greater than the expected value when the latter was high, and a smaller one than that expected when this was low. The authors concluded from this result, that clutch-size is affected by an unknown factor, additional to age and laying date.

In a number of species annual variations of clutch-size are not related to laying date, even though there is a significant trend within each season. This occurs in the Starling (KLUYVER 1933; LACK 1948b), the Swift (LACK 1956a), the Alpine Swift (LACK & ARN 1947), the Tufted and Scaup Duck (HILDÉN 1964), and in the Common Eider (BERGMAN 1939). Noticeable annual variations also occur in species without seasonal trends of clutch-size, or in which trends have not yet been demonstrated. In many of these cases the annual variations of the average clutch proved to be correlated with differences in food supply, or with variations of weather, which generally cause variations of food abundance. Several examples of this relation can be given. For instance, in 1947, 1948 and 1952 94 per cent of the clutches of the Swift in Oxford had 3 eggs. In these years the period immediately before the start of laying was warm and sunny. In 1953 and 1954 only 44 per cent of the clutches had 3 eggs, and in these years the period in question was cold and rainy (LACK 1956a).

In Africa and Australia many birds lay smaller clutches (or do not breed at all) in dry years when food is scarce, than in wet years with plenty of food (HOESCH 1936; MOREAU 1944a; LACK 1954).

In the Nutcracker in S. Sweden the annual differences are correlated with the crop of hazelnuts, their preferred food. When the crop is below average, the mean clutch is three eggs next spring. In years with a good crop the clutch has four eggs on the average (LACK 1954).

Another example of a relation between annual variations of clutch-size and food is given by SIIVONEN (1952, 1954, 1957). He showed from evidence collected by an inquiry, that in some nidifugous tetraonids in

Finland, the Capercaillie, the Black Grouse and the Hazel Grouse, years with low clutch-size were also characterized by low hatching success and low survival of the young. The low survival rate of eggs and young was evidently predetermined by the quality of the eggs, since the mortality occurred in an embryonic state or immediately after hatching in the nest. In his 1957 paper SIIVONEN explains these phenomena with variations of the food in the pre-laying period. In winter the hens of the three species gradually loose body weight as a result of their forcible feeding on trees when snow covers the ground. Consequently, winter food is ligneous and of high cellulose content, and is not easily digested. In the pre-laying period there is a sharp increase in weight parallel to a switch from feeding on trees to feeding on the ground when the first snow-free patches occur. Then they feed on budding leaves and blossoms, and on berries, which have wintered under the snow and are rich in nutritive content.

In some years these early growing green plants are not available due to exceedingly late spring arrival or to late periods of severe frost which interrupt plant growth. Then the spring rise of weight is poor and this results in small clutches and low survival of eggs and newly hatched young in the three species simultaneously. The mortality of the young seems to be directly related to the amount of yolk present in the yolk sac after hatching.

In other gallinaceous birds there is also evidence for a direct influence of food on the condition of the female. The Partridge population of Finland suffers high mortality in winters with heavy snow fall, and the surviving birds have smaller clutches than after winters with a lighter snow cover (SIIVONEN 1956). In the Red Grouse in Scotland clutch-size is correlated with the amount of winter die-back of heather, the main food of the birds. JENKINS *et al.* (1963) report that the heather was in a good condition in the spring of 1957, 1960 and 1961, as indicated by its green colour, and mean clutch-size varied from 7.8 to 8.1. In 1958 and 1959 the heather wintered badly and coloured brown in spring. In these years the adults suffered high mortality, and those surviving had significantly smaller clutches than in the other years, the means being 6.9 and 6.1, respectively.

It has been suggested by HILDÉN (1964) that the annual variation of clutch-size in ducks might be due to the availability of winter and spring food. "In winters with severe ice conditions, for instance, the survival of many ducks remains difficult long into the spring, and they may be in suboptimal nutritional condition at the time of onset of egg-laying". LACK (1967b) in discussing the effect of food on clutch-size in waterfowl, states that ducks do not usually lay a smaller clutch when food is sparse, nor produce more eggs when food is unusually plentiful. There is, to my knowledge, no direct evidence supporting this view.

Finally, an effect of food on the annual variation of clutch-size has been reported in owls and birds of prey (SCHMAUS 1938; LACK 1947-48). This has been clearly demonstrated for the Buzzard by MEBS (1964) (Table 4 and Section 2.3.1).

To sum up, annual variations of clutch-size are caused by variations of the age-composition, the density, and the mean laying date of the population. In some species, where the effect of these factors has been accounted for, there is a rest-variation due to an unknown proximate factor, which seems to be related to the food supply present some weeks later when the young are in the nest.

In some species annual variations of clutch-size are due to differences in the supply of food during the period immediately preceding laying. In the nidicolous owls and birds of prey, and in the Nutcracker, where the abundance of food is more or less indicative for its amount later in the season when the young are fed, the effect of food is presumably indirect. In the nidifugous tetraonids and ducks food quantity is likely to have a direct effect on the reproducing adults (p. 102).

The annual variations considered so far are likely to be modificatory in nature. However, as suggested by CHITTY (1960, 1967), the annual differences in prolificacy observed in the Field Vole are related to changes in the genetic composition of the cyclic fluctuating populations. At the higher densities it is the aggressive, less prolific genotypes, which should be selected for, thus changing the average prolificacy (litter-size) of the population.

There is no evidence suggesting similar phenomena to occur in birds. It is true, in tetraonids the variations in clutch-size are presumably related to cyclic fluctuations of density, but there is no evidence whatsoever for parallel changes in the genetic composition of the populations (SIIVONEN 1952).

3. THE ULTIMATE DETERMINATION OF CLUTCH-SIZE

All animal species have a long evolutionary history during which they evolved to what they are today. The hypothesis is now generally accepted, that the organization of each species came into being through the operation of natural selection on genetic variability in populations. During the evolutionary history this variability was enlarged again and again by mutation of genes already present in the populations. Only an extremely small fraction of these mutations was advantageous, i.e. affording their carriers a greater proportionate contribution to the gene pool of the next breeding population, with the final result that the mutants have spread through the population.

It is obvious that genes raising the reproductive capacities of their carriers afford a direct advantage, assuming that these genes have no disadvantageous effects on other characteristics determining the fitness of the phenotypes. Therefore, during the evolutionary history, natural selection will have maximized the reproductive rate of each species, naturally within the possibilities of their given organizational structure and within the limitations of the environment in which the species evolved. The factors that have played a part in this process are called ultimate factors.

If the reproductive rate of a bird has been evolved along the above lines, then its characteristic clutch-size has to be hereditary. This aspect will be considered firstly (Section 3.1). Further, it has to be shown that the average clutch of a population of birds produces the maximum number of offspring in the given environment. For that purpose one can study the contribution to the next breeding population of pairs with variable clutch-size. This can be done successfully by decreasing or increasing the clutch or brood experimentally beyond its natural range. In this part of the analysis special attention has to be given to factors, other than the size of the clutch itself, determining the number of offspring produced. Such factors are likely to have operated as ultimate factors during the evolutionary process (Sections 3.3.1-3.3.3).

Another way of gaining insight into the ultimate factors involved concerns the comparison of the average clutch-size of widely separated populations of one species, living under different conditions. Again, making a comparison of the clutch-size of species differing to a varying extent in their behavioural and structural organization may be profitable (Sections 3.3.4-3.3.5).

3.1. THE GENETIC BASIS OF CLUTCH-SIZE

The hereditability of clutch-size is extremely difficult to analyse. Straightforward selection experiments have been successfully conducted in the domestic fowl, but not in wild birds (HUTT 1949). Crossing experiments have the disadvantage that nothing is known about the male's contribution to clutch-size. Moreover, many of the wild birds are unsuitable for such experiments, since they do not breed readily in captivity.

Consequently we have to rely on the study of the intra- and inter-individual variation of clutch-size in natural populations. If the variability of successive first layings within females is smaller than the variation between females, the latter may be assumed to have a hereditary component, if there are no consistent differences between other factors affecting the size of the clutch of these females.

This has been found, for instance, in the Velvet Scoter by KOSKIMIES (1957). In this species the variation of successive layings of one female is small compared with the differences between females. Thus, in one female the clutch was either 9 or 10 eggs in seven different years, whereas another produced invariably clutches of 8 eggs in five successive years. These individual differences could not be attributed to age, density or habitat, though there were small differences in laying date (p. 26).

KLUYVER (1951) studied the size of first layings of 22 individual Great Tits recorded in three or more successive years. Out of these only one had the same clutch each year. Nevertheless, the differences in clutch-size between one year and another of 104 individual females tended to be smaller than those to be expected according to the assumption that they had no tendency towards consistency in clutch-size. KLUYVER remarks that this tendency not necessarily has an innate basis, but may merely reflect the fact that individual females tend to breed in the same habitat in successive years.

Later he studied clutch-size variability in this species along similar lines, but he then concluded that intra- and inter-individual variation is of about the same magnitude, and the latter, therefore, may be wholly phenotypic (KLUYVER 1963).

The variation of clutch-size within females proved to be smaller than that between females in the Kittiwake (COULSON & WHITE 1961), the Swift (WEITNAUER 1947; LACK & LACK 1951), the Alpine Swift (LACK & ARN 1947), the Sky-lark (DELIUS 1965), the Collared Flycatcher (LÖHRL 1957), the Great Tit (LACK 1950), and the Starling (LACK 1948b).

Out of 76 females of the Collared Flycatcher 40 had the same clutch in two or more years, including the first breeding year. Of 17 others clutch-size increased from the first to the second breeding year, and was constant thereafter. In those remaining there were only small differences in successive years, which could partly be explained with variations in laying date. In addition to the small variation within individuals, there was a tendency for daughters to produce clutches of the same size as their mothers. Therefore, the more pronounced differences between females may be assumed to be hereditary (LÖHRL 1957).

Summarizing, it may be stated that our knowledge about the hereditability of clutch-size is negligibly small. Moreover, there are only some indications that the inter-individual variations of clutch-size in populations have a genetic basis.

3.2. THE BROODING CAPACITY AS ULTIMATE FACTOR

It has been postulated above that clutch-size will be maximized by the operation of natural selection, but logically, this cannot proceed indefinitely. At first sight it seems obvious to suppose that the clutch is limited by the maximum number of eggs that the sitting bird can cover effectively. If the number of eggs in the nest would surpass this maximum, it can be expected that the average number hatching successfully is smaller than the maximum, since during incubation one egg will be in an unfavourable position at one time, and another egg at another time. Then, genotypes with such an oversized clutch would be at a disadvantage as compared with those having a clutch that can effectively be covered.

This principle has been demonstrated by RICE & KENYON (1962) for the Laysan Albatross. This species lays one egg, and if an extra egg is added, one of the two is often rolled out of the nest by the bird. In the rare cases that it is not removed only one egg hatches, or more often, neither of the eggs produces a young.

However, this result should not be interpreted to demonstrate that clutch-size in this species has evolved in relation to the maximum number of eggs that the bird can cover. In fact, only one egg can be brooded successfully, because the bird has one small broodpatch. The number of the broodpatches and the size of the clutch will have been evolved in parallel, and consequently, if a small clutch has been evolved under the influence of another ultimate factor than the maximum number that can be covered, the broodpatches will have been adapted to the small size of the clutch.

Birds with a greater and more variable number of eggs often have one large broodpatch, and this is less strictly related to the normal size of the clutch. If clutch-size in such species would have been evolved in relation to the maximum number of eggs that the bird can cover, then hatching success would be maximum for the most frequent layings. It has been shown for a number of species that this is not so.

Thus, in the Partridge in England the most frequent clutch is 15, but hatching success is the same up to at least 20 eggs (LACK 1947, 1954; JENKINS 1961). In the American Coot oversized clutches of 15-21 eggs hatch as successfully as those of natural size, though the broodpatch is too small to cover all eggs. However, the eggs are regularly rolled by the incubating bird so as to receive sufficient heat to complete development (FREDRICKSON 1969). Again, the Wood-duck usually has 11-14 eggs in the clutch, and the eggs hatch with the same rate up to layings of 20 (LEOPOLD 1951). Similar results were obtained for the Alpine

Swift (Lack & Arn 1947), the Swift (Lack & Lack 1951), the Tree Swallow (Paynter 1954), Great, Blue and Coal Tits (Lack 1955), Robin (Lack 1958), Blackbird (Snow 1958), and the Collared Flycatcher (Löhrl 1957).

It has been reported by Paynter (1949) and Harris (1964) that in Herring and Lesser Black-backed Gulls hatching success increases up to and including the most frequent clutch of 3 eggs. This proved to be the result of differential predation by other gulls, perhaps because three eggs stimulate the female to incubate more steadily than do smaller clutches. However, it has not been tried to find out experimentally through the addition of eggs what happens in clutches larger than 3, which is of course necessary to get an answer to the question raised in this section.

On the other hand, Hildén (1964) has reported that in the Tufted Duck and the Scaup in Finland the proportion of unhatched eggs increases with clutch-size as follows:

clutch-size	6-7	8-9	10-11	12-13	14-15	16-19
percentage unhatched	2.5	2.4	3.8	8.2	8.7	22.9

Similar results have been obtained in the Ring-necked Duck (Mendall 1958) and in the Redhead (Weller 1959) in North America.

These data have to be considered critically, since they all refer to species with dump nesting. In the Tufted and Scaup Ducks the most frequent clutch is 8-9 eggs, and Hildén considers all layings of 15 and more to be the result of parasitic egg laying by other females. Nevertheless, Hildén is of the opinion that the smaller hatching success of the larger clutches of a single female is the result of the fact that the female is unable to cover them effectively. The contrast with the Wood-duck is explained by its nesting in tree-holes, where the eggs are more easily kept together and, in addition, heat is more efficiently retained than in a ground nest.

However, the data presented by Hildén show that, although the rate of hatching decreases with increasing clutch-size, the absolute number of young hatching increases up to layings of 15 eggs. This suggests that it is not the maximum number that can be covered, which is responsible for the fact that layings of 8-9 are the most frequent.

Among songbirds an effect of brooding capacity on hatching success has been reported for the Pied Flycatcher in Germany (Creutz 1955). This species, in which layings of 6-7 eggs are most frequent, has a constant hatching rate of about 75 per cent up to 8 eggs included. The rate declines sharply to 52 per cent for clutches of 9 eggs. According to

CREUTZ, one or more eggs of such large clutches are insufficiently covered and are disregarded by the female after most eggs have hatched.

Finally, the experiments of NELSON (1964) with the Gannet are worth mentioning. This species has always one egg, which is incubated by placing one foot over one side of the egg, and the other over the other side. NELSON added one egg to each of 17 nests, and found the hatching success the same as in the controls (87 and 85 per cent, respectively), notwithstanding the unique brooding habit.

Taking all evidence together, it can be stated that clutch-size is unlikely to have evolved in relation to the maximum number of eggs that the sitting bird can cover in songbirds, ducks, gallinaceous birds, and some other species. More evidence is needed from other groups, especially waders. As pointed out by LACK (1947-48) and AMADON (1949) these birds have large eggs in relation to their body weight, and in many of them the clutch is invariably four eggs. This might indicate that the females meet difficulties in covering larger clutches, though it has once been observed that the Spotted Sandpiper can successfully incubate five eggs (BOND 1950). Recently it has been shown by HARRIS (1967) that the most frequent clutch of the Oystercatcher on Skokholm is three, whereas the hatching success of c./4 is at least as good as of c./3. Moreover, as pointed out by LACK (1947-48) with reference to the decreasing seasonal trend of clutch-size, other ultimate factors must have been involved in the determination of the size of the clutch later in the season, assuming that the trend has adaptive significance. Such decreasing trends have indeed been found in some waders, like the Greenshank and the Dotterel (NETHERSOLE THOMPSON 1951), and the Oystercatcher (HARRIS 1967), but not in the Lapwing, which produces layings of four eggs throughout the season (KLOMP 1951).

3.3. THE EVOLUTION OF CLUTCH-SIZE IN NIDICOLOUS BIRDS

LACK (1947-48, 1954) has formulated the hypothesis that the clutch-size of nidicolous bird species has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food. Under this hypothesis the young in broods larger than the most frequent ones should, on the average, suffer undernourishment, with the result that fewer young survive from these than from broods of smaller size. Therefore, when clutch-size is hereditary, genotypes with over-sized clutches will be selected against, with the ultimate result that the most frequent clutch in the population will also be the most productive one. Several aspects of this hypothesis will be considered in the following sections.

3.3.1. STARVATION OF YOUNG IN THE NEST

On LACK's hypothesis starvation of young should not only occur in broods of extraordinarily large size, but also in broods of normal size when the supply of food in the environment is below average. This aspect of the thesis will be briefly reviewed.

A relation between brood-size and starvation has been observed in some species. In the Alpine Swift in Switzerland the proportion of young fledged in nests with 1, 2, 3 and 4 eggs was 98, 86, 78 and c.60 per cent, respectively, over the years 1932-1947 (LACK & ARN 1947). Similarly, in the Swift in Switzerland the respective values were 86, 91, 82 and 62 per cent, and in England 92, 80, 70 and 50 per cent (WEITNAUER & LACK 1955). The food supply for swifts (air-borne insects) is highly dependent on the weather, and as a result, the survival rate of the young is positively correlated with the amount of sunshine, especially during the early nestling period when the young have not yet formed reserves. Consequently, in wet and cold seasons the survival rate of the young in the larger broods was 31 per cent only, as compared with c.80 per cent in fine seasons (LACK & LACK 1951). Moreover, in wet seasons the nestling period is longer, and the growth of the feathers slower, especially in the larger broods (LACK 1956a).

In other well-studied birds, the tits, nestling mortality is generally low (c.5 per cent) in broad-leaved forests in England, and independent of brood-size, though there are some exceptions (LACK 1950, 1955, 1958, 1966). However, the weight of the nestlings when 15 days old proved to be related to brood-size, being significantly lower in the larger broods, especially in years with a low food supply (LACK, GIBB & OWEN 1957; PERRINS 1965).

In The Netherlands, on the other hand, nestling survival proved to be correlated with brood-size in the Great, Blue, Crested, and Coal Tit. In the Great Tit, for instance, the survival rate of the young in nests started in the period of 10-29 May was 84, 84, 83, 76 and 50 per cent in broods of 1-6, 7-9, 10-12, 13-15, and 16-21 nestlings respectively (LACK 1950). See Table 8.

Pine forests proved to be unfavourable for tits in both countries. Thus, in the Breck pines in England in 1949 the survival of young Great Tits was highly dependent on brood-size (LACK 1950). Also, KLUYVER (1963)

TABLE 8

FLEDGING RATES OF THE GREAT TIT IN HOLLAND IN RELATION TO CLUTCH-SIZE

Clutch-size	Proportions of young flying from number of eggs laid			
	April 1-29	April 30-May 9	May 10-29	May 30 onwards
1-6	83	83	84	86
7-9	83	87	84	84
10-12	81	84	83	81
13-15	79	77	76	68
16-21	63	72	50	—

NOTE: The dates given are those on which the first egg of the clutch was laid. After LACK (1950).

reports that reduction of the number of young in nests of the Great Tit in pine forests in The Netherlands resulted in a higher growth rate and better survival of those left in the nest.

Mortality of nestlings has also regularly been observed in owls and birds of prey. These birds start incubating well before the last egg has been laid, with the result that the young hatch asynchronously. In species with a relatively large clutch like the Snowy Owl, there may elapse a fortnight between the hatching of the first and the last chick (INGRAM 1959). In the Buzzard and Rough-legged Buzzard all the chicks born are raised in some cases only. In broods of three, one or two of the young may die within about ten days, and their bodies are fed to the surviving chick(s) by the parents (WENDLAND 1958; INGRAM 1959; MEBS 1964). The mortality rate of the chicks proved to depend on the food supply. In broods of two young SCHMAUS (1938) observed a 29 per cent mortality in years with vole plagues, and 40 per cent in years after the crash of the prey. In broods of three young the corresponding values were 26 and 42 per cent in another part of Germany (MEBS 1964).

In eagles, which often have two young, the last born chick is regularly killed by the other within some weeks after hatching, during which the chicks are aggressive (INGRAM 1959; AMADON 1964; BROWN 1966). In the Lesser Spotted Eagle, for instance, the second chick hatches three to four days after the first, and the former is invariably killed by the latter within three to five days, because it is prevented from taking any food (WENDLAND 1958). Similar observations have been made on the chicks of Verreaux's Eagle in southern Africa, and SIEGFRIED (1968) summarizes considerable evidence showing that the persecution of the second-hatched chick by the larger nest-mate occurs while the supply of food is seemingly adequate. The early death of the youngest chick before the food supply is short has also been observed in the White Pelican by VESEY-FITZGERALD (1957), and in the Blue-faced and Brown Boobies by DORWARD (1962). In all three species the two young hatch asynchronously and the younger is always bullied to death by the older, in the boobies normally within three days after hatching. DORWARD experimentally twinned several nests of the boobies with young of about the same age, and then the parents are clearly able to supply enough food for longer than the few days that normally elapsed before the younger chick died. Nevertheless, one of the twins ultimately established a supremacy over the other, which gradually lost weight and finally died in all cases (DORWARD 1962; ASHMOLE 1963; NELSON 1966).

Asynchronous hatching has also been observed in the White Stork (SCHÜZ 1957), and in the Common Heron (OWEN 1960). In the Stork the smallest chick is sometimes attacked by the parents, especially by young males. In some cases the victim falls out of the nest, in others it is swallowed. SCHÜZ suggests that this should occur in years with a poor food supply. Also in the Heron the smallest young die in bad food years only.

The phenomenon has also been observed in songbirds. The Great Tit starts incubating late layings before the last eggs have been laid (ZINK 1959), with the result that one or more of the young die when food is scarce (GIBB 1950; LACK 1966). The same occurs in the Jackdaw and the Rook (LOCKIE 1955), the Blackbird (SNOW 1958), the Redwing (TYRVÄINEN 1969), the Starling (DUNNET 1955), and the Black-faced Quelea (WARD 1965).

The biological significance of the phenomenon has been discussed at some length by LACK (1954) and LÖHRL (1968). LACK suggests that the habit of starting incubation before the clutch is complete is an adaptation for adjusting the family-size to the food supply, which may be expected to have survival value in species with long nestling periods and a more or less erratic food supply.

To sum up, there is evidence from several species that nestlings suffer from starvation in the larger broods and under conditions of a lower than average food supply. These findings support LACK's theory and make it worth studying nestling and fledgling survival in relation to brood-size in more detail.

3.3.2. BROOD-SIZE, FEEDING RATES, AND THE GROWTH AND SURVIVAL OF THE YOUNG

According to LACK's hypothesis the nestlings of broods greater than the most frequent ones would on average be undernourished. The first approach to this question concerns the measurement of the number of feeds brought to the young in broods of different size.

Brood-size and the number of feeds per nestling. In a number of species, mostly Passerines, the amount of food brought to the nestlings by their parents has been estimated by counting, or automatically recording, the number of visits to the nest. Thus, MOREAU (1947) counted the feeding frequency of several species of swallows and swifts in tropical Africa, the clutch-size of which varies from 1 to 2, or 1 to 3. In all species studied the feeding rate increased with the number of young in the nest but, with some exceptions, less than proportionately. Since the nestling period was independent of brood-size, MOREAU concluded that the young of the larger broods will fledge at a lower mean weight, though this was not measured. This conclusion is probably incorrect in the light of later knowledge (Section 3.7).

The feeding rate of the Swift in southern England has been studied by LACK & LACK (1951) and LACK & OWEN (1955). Under good weather conditions the frequency of the visits to the nest was considerably higher in broods of two and three young than in those with one nestling, but nevertheless the number of feeds per young decreased, and amounted to 8.4, 7.8 and 6.4 per 10 hours in broods of 1, 2 and 3 respectively. In bad weather, single nestlings were fed reasonably well, but broods of 2 and 3 were heavily starved.

A less than proportionate increase of the feeding rate with increasing brood-size has further been established in the Starling in Holland as shown in Figure 6A, B (KLUYVER 1933), the Starling in NW. Germany (HAARHAUS 1968), the Robin in England (LACK & SILVA 1949), the Great Tit in England (GIBB 1950, 1955), the House Wren in N. America (KENDEIGH 1952), the Bank Swallow in N. America (PETERSEN 1955), the Pied Flycatcher in Finland (VON HAARTMAN 1954) and Germany (CURIO 1959), the Grey Starling in Japan (KURODA 1963), the House Martin in Finland (LIND 1960), the House Sparrow in England (SEEL 1969),and in the Manx Shearwater in England (HARRIS 1966).

The data of the House Martin are of special interest, because the range of the brood-size was artificially extended from 3-6 to 1-10. On warm days the feeding rate gradually increased from 11.3 feeds per hour in broods of one to 66.5 feeds per hour in broods of ten, but the number of feeds per nestling decreased. On cold days this decline was much more pronounced, and fell from 13.0 feeds per nestling per hour in broods of one to about 2 feeds per nestling per hour in broods of 8-10 young.

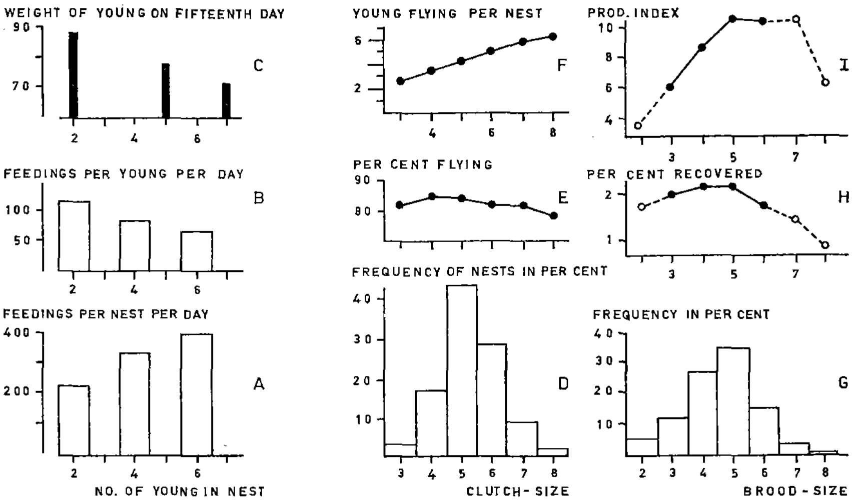

FIGURE 6. Feeding rates (**A**, **B**), weight of nestlings (**C**), frequencies of clutch- and brood-size (**D**, **G**), survival of nestlings (**E**), productivity at fledging (**F**), recovery rates of young more than three months after fledging (**H**), and productivity indices (**I**) for the Starling. A, B and D, E, F refer to Dutch birds laying in April (KLUYVER 1933); C to English birds (LACK 1948b), and G, H, I to early breeding Swiss Starlings (LACK 1948b). The open circles in H and I refer to small numbers of broods. Further explanation in the text.

In the Manx Shearwater the feeding rate of parents with artificial twins was higher, but less than twice that of parents with a normal brood of one. Moreover, the gain in weight after feeding was less in a twin than in a singly reared young, which was attributed to the contents of feeds being smaller in the former than in the latter case (HARRIS 1966).

As is well known, the foraging activity of the parents is stimulated by the begging intensity of the young (VON HAARTMAN 1953). If this were the only factor determining the feeding frequency, the latter could be expected to increase about proportionately with the number of nestlings, assuming that the energy content of the feeds is independent of brood-size. In most species studied, however, the feeding rate increases less than proportionately with increasing brood-size, and this may suggest that the parents are unable to find the required amount of food for the larger broods, which should support LACK's hypothesis. However, it has been suggested by ROYAMA (1966) that the need for food of a nestling decreases with increasing brood-size as a result of a smaller heat loss per nestling in the larger broods (p. 46; Section 3.7).

There are some exceptions to the rule. Firstly, in two out of nine species studied by MOREAU (1947) the feeding rate increased proportionately, with the result that the number of feeds per nestling per hour was independent of the size of the brood.

Secondly, Kluyver (1950) reported similar observations for the Great Tit in Holland, and he suggests that in this species the parents change their feeding frequency according to the begging activity of their young. Consequently, Kluyver's evidence is not in accordance with that of Gibb for the same species in England, and the latter author suggests (1955) that this might result from Kluyver's data being taken from five separate localities and in six different years. In a study of the Japanese subspecies of the Great Tit the feeding rate increased less than proportionately in 1958 and 1959, but in 1960 the increase proved to be about proportional with brood-size (Royama 1966).

Thirdly, Kluyver (1961) collected some evidence suggesting that in the Black-capped Chickadee in North America, the number of feeds per young was the same in broods of three and six on their eleventh day of life. He is of the opinion that even the parents of the larger broods do not forage at their maximum capacity. Again, in the Redwing in Finland the number of feeds per young on the nestlings' eighth day was independent of the size of the brood (Tyrväinen 1969).

Finally, Skutch (1949) measured the feeding frequency of the Song Tanager in Central America to be 7.5 feeds per young per hour in a brood of two, and this was maintained at the same level when—on the next day—one young of the same age was added, or—again one day later—two of the three young then present were removed. Like Kluyver, he concluded that the parents can readily modify their activity according to the needs of the young.

These partly contradicting results should be considered critically, however, because feeding rates are affected by many factors. Firstly, to have a measure of their variability, they should be studied under different weather conditions, and in years with different available food amounts. If Kluyver's and Skutch's data happened to be obtained under very favourable conditions, it could be expected that even the largest broods could be raised readily; also, annual variations in food conditions might explain the opposite results of Royama for the Great Tit (p. 45).

Further, feeding rates should be measured on different days and over large parts of the day, because there are considerable variations in intensity of foraging both within and between days, as found in the African swallows and swifts (Moreau 1947), in the Robin and the Starling in Denmark (Boëtius 1949), in the Swift in England (Lack &

LACK 1951), the Great Tit in Holland (KLUYVER 1950), and the Starling in Scotland (DUNNET 1955).

Part of these variations proved to be correlated with the size of the feeds. In the Great Tit in Holland, for instance, the first brood of a pair was fed 1068 feeds per young during the whole nestling period with a mean weight of 45-50 mg, whereas the second brood of the same pair received 577 feeds per young with a mean weight of 240 mg. This shows the feeding rate to be a misleading index for the amount of food brought to the young. Similar inverse relationships between feeding rate and size of the feeds were found in the Great Tit in Japan (ROYAMA 1966) and in England (GIBB & BETTS 1963), in the Robin (BOËTIUS 1949), the Starling (DUNNET 1955), the Black-capped Chickadee (KLUYVER 1961), and the Nuthatch (LÖHRL 1966).

In the Starling in Scotland the weight of food brought per visit varied from 0.15 to 4.5 g, depending on the number of items per feed; moreover, the daily mean weight per feed varied from 0.48 to 1.59 g. DUNNET (1955) concluded from his extensive observations that the feeding rate in the Starling cannot be stated to be proportional to the amount of food brought to the nest, not even under similar conditions of size and age of the brood.

These observations show that feeding rates cannot inform us satisfactorily about the possible relationship between the amount of food brought to the nest and the size of the brood. To be of value, they should be combined with observations on the size or weight of the feeds, and the total amount of food brought should be compared with the growth and the survival of the young in broods of different size.

A study of this sort has been carried out by ROYAMA (1966) in Japan with the Great Tit. He measured both the feeding rate and the size of the feeds brought, and from relationships between prey size and dry weight established for different categories of prey he could determine the total amount of food in dry weight brought to the nestlings per day over the whole nestling period. These total amounts of food appeared to be remarkably similar for broods of different size, though there were great differences in feeding rate and prey size, suggesting that the food requirements of the total broods (though being of different size) were about the same.

On the other hand, food consumption per day per nestling proved to be noticeably higher in small than large broods, though on the 13th day of life the body-weights per nestling were about equal up to broods of eight young. ROYAMA concluded that these phenomena have to be attributed to the fact that heat loss per young is much higher in a small than large brood, because the proportion of the exposed surface area per unit volume of the body mass of a brood as a whole will be much higher in the former than in the latter. Therefore, in a small brood much of the greater amount of food digested per young is used for temperature maintenance (Section 3.7).

These observations support the view of KLUYVER (1961) that—at least up to broods of a certain size—the parents' foraging activities are primarily controlled by the chicks' begging intensities, his opinion being based on a decline of the activity in the afternoon in Starlings and Great Tits, and a much higher than normal feeding rate in Black-capped Chickadees when foraging has been slackened for a long period by unfavourable weather. The afternoon decline of the activities of the parent Great Tits has also been observed by GIBB (1955), especially in large and late broods, and therefore he interpreted the phenomenon to mean that the parents were tired and could not keep up their initial feeding rates all day.

The observations of ROYAMA also provide an explanation for the fact that the feeding rate per young already decreases with an increase of brood-size in an abnormally low range, as in the Pied Flycatcher (VON HAARTMAN 1954) and in the House Martin (LIND 1960). In the latter species the number of feeds per nestling decreased on favourable, warm days from 11.3 to 8.3 per hour in artificial broods of one and two young, respectively. Where the mean brood-size is about four, it can hardly be expected that the decline results from the limited foraging abilities of the parents.

Brood-size and the growth and survival of the young. In ROYAMA's study, the weight of the nestling Great Tits on the 13th day of life in broods of nine and more decreased with an increase of brood-size, and this suggests that the food requirements of such large broods are beyond the parents' foraging capacities. This fact supports LACK's thesis that clutch-size has been adapted by natural selection to correspond with the largest number of young the parents can feed. Therefore, the relationships between brood-size on the one hand and weight and survival of the young on the other hand will be considered in more detail.

One of the first reports dealing with this relation is that on the *Starling* presented by LACK (1948b). The weights of nestlings in broods of 2, 5 and 7 young were 48.3, 45.1 and 38.2 g on the sixth day, and 88.0, 77.6

and 71.4 g on the fifteenth day of life, respectively (Fig. 6C). The percentage of young fledging proved to be independent of brood-size in Dutch Starlings, resulting in a steady increase of the number of young flying with increasing clutch-size (Fig. 6E, F). However, as suggested by LACK the light young of large broods may survive less well than the heavier young of small broods later in the season. After fledging the young still depend on their parents for food, and when the former have a higher death rate during this period than the latter, more of the young of the smaller than of the larger broods will survive to an—arbitrarily chosen—age of three months and more. LACK checked this using the ringing material of Swiss Starlings. He showed that, of fledglings ringed in the first broods, the percentage recovered more than three months after fledging was higher for broods of 3-5 than 6-8 young (Fig. 6H). Similar results were obtained for late broods of Swiss Starlings, where the percentages recovered after three months and more were 2.2, 1.8 and 1.4 for broods of 4, 5 and 6 young, respectively.

During the first two months after fledging the recovery rates of English and Swiss Starlings proved to be higher for young from large than small broods, and this supports the above findings.

The breeding of the Starling has also been analysed by DUNNET (1955). He studied a colony in nesting boxes in a cultivated area in Scotland, where the young were fed earthworms and, above all, leatherjackets. In 1951 and 1952, the latter made up 86 and 82 per cent of the weight of the food, respectively. In the first two years of the study, the maximum weights of the young were independent of brood-size, but in 1952 the weight per nestling decreased from 85.0 g in one brood of two, to 74.0 g in some broods of six young, but the differences were statistically insignificant. In agreement with these small variations of weight, there was no relation between brood-size and the survival rate of the nestlings. The occurrence of a differential post-fledging mortality was not studied.

Based on these facts, DUNNET did not consider brood-size to be limited by the amount of food brought in by the parents; his opinion being further supported by the fact that the breeding rates were similar in 1951 and 1952, though the density of leatherjackets in the latter year was 17 per cent of that in the former only. However, as compared with KLUYVER's study area, the density of these larvae was extremely high: in 1951 it amounted to 500-1000 larvae per m^2 on most plots, whereas KLUYVER (1933) recorded 10-30 larvae per m^2 as normal. This might indicate that the feeding conditions happened to be very favourable in DUNNET's study area.

Much more detailed data have been collected for tits. GIBB (1950) studied the growth of young *Great Tits* in nesting boxes in England, and obtained some evidence for a lower weight of young in the larger broods. Later (1955) he could corroborate these preliminary results both for the young of early and late broods. In the former the survival rate of nestlings was still the same for all broods. In the latter—mostly repeat layings—the differences in weight between young of small and large broods were more pronounced, and many of the lighter young died of starvation when about 15 days old.

LACK (1950), analysing the data of Dutch tits from very different areas collected by KLUYVER, has shown that there is a significant decrease of the survival rate with increasing clutch-size in Great, Blue, Crested and Coal Tits. The data for the Great Tit are most complete, and the means over many years are summarized in Table 8. It is shown that the proportion of young flying drops distinctly in nests initially containing more than 12 eggs, both in early and late broods.

Combining the data from several years collected in a well-defined study plot (the O.N.O. area), KLUYVER (1951) did not find a relation between the proportion of birds flying from first broods of the Great Tit and the size of the family, initially ranging from 6-13 eggs. Larger clutches were not present. In second broods, initially ranging from 3-12 eggs, the nesting success clearly decreased in broods of more than 10. Hence, these data are in agreement with those of GIBB and LACK given earlier.

In English Great and Blue Tits nestling survival was independent of brood-size over the years 1947-1949 in deciduous forest, but declined significantly with increasing brood-size in the Breck pines. Such habitat-linked effects have also been shown to occur in Holland by KLUYVER (1963). Reduction of the number of young caused a more rapid growth of the remaining ones and increased their survival in pine, but hardly so in broad-leaved forest.

As shown by LACK, GIBB & OWEN (1957), the relation between brood-size and growth and survival of the young can be modified by the amount of food present. The authors made a long-term study of the reproduction of the Great Tit in broad-leaved forest in England, where the tits feed their young mainly on oak caterpillars. The density of these larvae was estimated by measuring the amount of fecal droppings. In years with an abundance of food (e.g. 1947 and 1948) the weight of the young on the 15th day hardly differed in small and large broods. When food density was normal or low (e.g. 1949-1951 and 1953-1955) the differences in weight were considerable, but even then the mortality rate of the nestlings appeared to be independent of brood-size. There was, however, an apparent effect on the post-fledging mortality in these years. In winter, the recovery rate of ringed nestlings from broods of 9 and 10 young was about 7 per cent, but from broods of 11 it was only 3 per cent. In 1947 and 1948 the survival rate of fledglings was very high and independent of brood-size, even though the mean brood-size was above average in these years. KLUYVER (1951), on the other hand, did not find a relationship between the size of the clutch and the proportion of young recovered after 1 November of the first year. From clutches of 8-10, and 11 and more, all studied in the O.N.O.-area, 5.5 and 5.8 per cent were recovered, respectively.

This question has been studied elaborately by PERRINS (1965), who made use of the data of the above English workers and of details collected in later years in the same area. Taking all data together, there was a clear relation between brood-size and weight of the young when 15 days old (see also LACK 1966, Fig. 10). Additionally, in years with an extremely low food abundance, the mortality of the nestlings proved to be highly dependent on brood-size. Thus, in 1961 the mortality rate rose from 3 per cent in broods of 2-4 young to 24 per cent in broods of 11-13 young. Finally, he studied post-fledging mortality of ringed young, which were caught in great numbers during the next winter. In all years studied, the recovery rate proved to be higher in young with a high than in young with a low nestling weight, though there were considerable differences between years (Fig. 7).

Based on these facts, LACK (1966) hypothesized that post-fledging mortality of tits will depend both on the amount of food taken during the nestling period, and on the food conditions after fledging. If the former is of significance, the differential mortality can be expected to occur during the first weeks after fledging, and in fact during this period more young were observed belonging to the heavy than to the light weight-classes, these being recognizable by coloured rings (PERRINS 1965).

Another species worth mentioning is the *Pied Flycatcher*, studied by VON HAARTMAN (1954) in Finland. Also in this species the weight of the young—measured when eleven days old—proved to be dependent on brood-size. VON HAARTMAN extended the normal range of the broods to 2-10 by removal and addition of young, and he found a gradual decrease of weight from 15.5 g per nestling in broods of two, to 12.4 g in broods of ten. Nevertheless, the mortality of the nestlings was not significantly affected by the size of the brood. Later (1967a) he compared the recovery rates of ringed young, and he concluded that there were no significant differences in survival between fledglings of different broods either. However, when the data for the largest broods are grouped together, it is clearly indicated that the survival of young is higher from broods of 6-7 than from broods of 8-10 (Table 9, column 4).

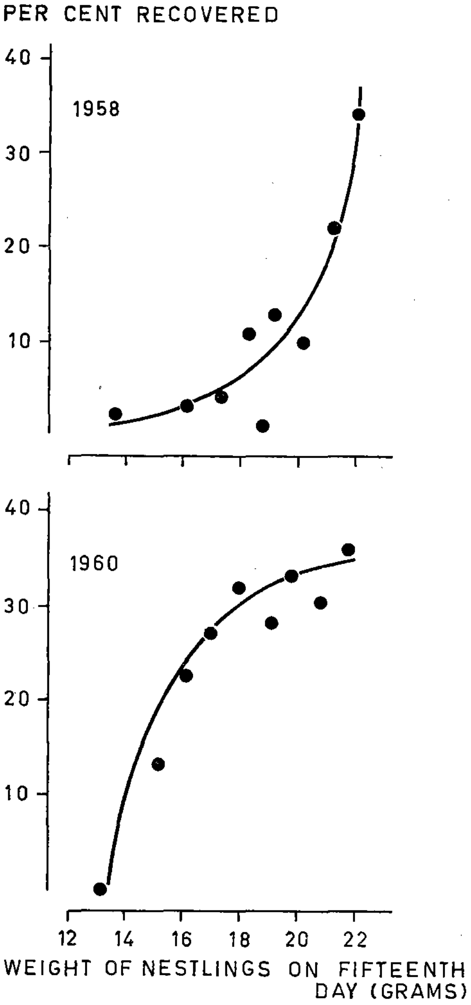

FIGURE 7. Relation between the weight of Great Tit nestlings shortly before fledging and their chances of subsequent recapture when at least three months old. In both years the heavier chicks survive better to the winter than the lighter young, but those with an intermediate weight had a much better chance to survive in 1960 than 1958. After PERRINS (1965).

TABLE 9

SURVIVAL OF YOUNG PIED FLYCATCHERS AFTER LEAVING NEST
After VON HAARTMAN (1967a)

Brood-size	Frequency in percent	Number of young ringed	Recoveries per 100 young ringed	Productivity index
5	10.4	700	2.6	0.13
6	40.5	1644	2.6	0.16
7	37.8	1036	2.4	0.17
8-10	6.5	242	1.7	c. 0.15

TOMPA (1967) working with the same species in Finland in 1964 and 1965 found the mean weight of nestlings from broods of 7 to be significantly lower than those from broods of 6 young, and from the rare broods of 8 to be remarkably lower than those from broods of 7. The mortality rate of the nestlings was independent of brood-size up to broods of 7 inclusive, but a much higher proportion died in broods of 8 young.

The same species has been studied in central Germany by CURIO (1958, 1960). He marked all young from a population during the years 1950-1954 and studied their return to the breeding area in later seasons. The proportions of young recovered varied between 7.6 and 11.0 per cent, but were not related to brood size.

In contrast to the results of VON HAARTMAN and TOMPA, the mortality rates of nestlings of the closely related *Collared Flycatcher* are negatively correlated with brood-size. LÖHRL (1957) studied this species during seven successive years in southern Germany, where the commonest brood had six young. In broods of five, six and seven, the proportions of young flying of those hatched were 79, 85 and 94 per cent respectively, the differences being statistically significant. This phenomenon has been attributed by LÖHRL to a phenotypic adaptation of clutch-size to the season: in early spring the normal clutch is seven, decreasing to five later in the season, and the young of the early broods are raised in the most favourable part of the season. To obtain unbiased results, simultaneously raised broods of different size should be compared. The other studies referred to in this section certainly do not completely fulfil this condition as well, and this may have influenced the results more or less unfavourably.

The mortality rate of nestlings seems to be independent of brood-size in the *Blackbird*, the *Song Thrush*, the *Robin* and the *Redstart* (LACK 1949 a), and in the *Redwing* (TYRVÄINEN 1969), or the dependency is only slightly indicated (LACK 1948a). In agreement, the maximum weight of nestling Robins was found to be independent of brood-size, though the feeding rate per nestling decreased in the larger broods (LACK & SILVA 1949). In the Blackbird the weight of the nestlings even proved to be highest in the largest broods, and this was attributed by SNOW (1958) to the fact that the more efficient parents, usually the older birds, had larger clutches. Moreover, the young hatched from the largest clutches were reared in the most favourable time of the year.

The mortality of nestling Blackbirds was independent of brood-size in broad-leaved forest near Oxford, but tended to decrease with increasing brood-size in the Botanic Garden of this town.

As to the post-fledging mortality in this thrush, the evidence from literature is contradictory. According to LACK (1949a) the fraction of ringed young recovered more than three months after fledging is smaller from broods of 4-6 than from broods of 2-3. On the other hand, SNOW (1958) found that young of very different weight at fledging have an equal chance to survive to the 15-20th day.

Deviating results have been obtained from the *Tree Swallow*. This species, the commonest clutch of which is six eggs, was studied by PAYNTER (1954) in southern Canada. The weight of the young was not related to brood-size over the range of 4-7 young, and only slightly higher in broods of three. Moreover, the fraction of young fledged increased with increasing brood-size both in 1947 and 1948, but the number of nests studied was low.

The *Swift* is another species which has carefully been studied with respect to the problem discussed in this section. In England it normally has two or three eggs, rarely one and only exceptionally four, those of one being partly due to losses of eggs from clutches of two (Fig. 8A). The weight of the nestlings on the thirtyfifth day has been determined by LACK (1956a) in years with fine, moderate, and wet and cold summers. In the first category of years the weights of young from broods of different size are about the same, but in less favourable years the weights decrease from broods of one to broods of three young (Table 10). In contrast to the species discussed above, which have mainly a differential mortality of fledglings, in the Swift the proportion of nestlings dying of starvation is dependent on brood-size (LACK & LACK 1951; LACK 1954; LACK 1956a; LACK 1966). This is shown for all years (1946-1952) in

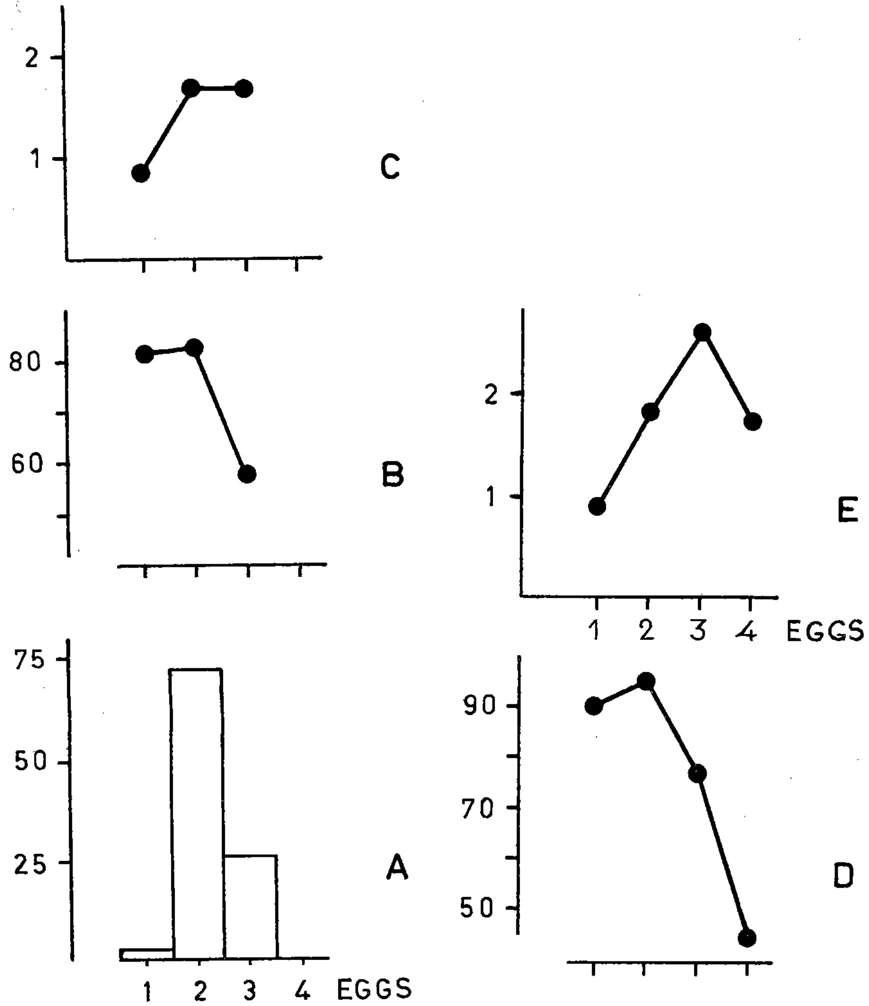

FIGURE 8. **A**. Brood-size of the Swift in England based on 170 nests (the frequency of c./4 is less than 1 per cent). **B**. Survival rate of nestlings, and **C**. Number of young fledged per brood, 1946-1952 (LACK 1954). **D**. Survival rate of nestlings, and **E**. Number of young fledged per brood, 1958-1961 (PERRINS 1964). Further explanation in the text.

Figure 8B. In wet and cold summers the dependency is much more pronounced. Thus, in 1946-1948, only 50 per cent fledged of the broods of two, and 31 per cent of the broods of three.

Later, PERRINS (1964) studied the relation between brood-size and nestling mortality over a wider range by increasing the number of broods of four artificially. He added one young to broods of three at

TABLE 10

WEIGHT (grams) ON 35TH DAY (A), SURVIVAL RATE OF NESTLINGS (B), AND NUMBER OF YOUNG FLEDGED PER BROOD (C) IN THE SWIFT IN ENGLAND, 1948-1956
From LACK (1956a)

		Brood-size			
		1	2	3	4
Fine	A	49.1	47.7	47.4	—
summers	B	92	92	92	—
	C	0.9	1.8	2.8	—
Moderate	A	51.1	47.8	44.6	37.3
summers	B	(100)	100	(50)	?
	C	(1.0)	2.0	(1.5)	?
Bad	A	40.4	35.2	34.2	—
summers	B	(100)	33	(50)	—
	C	(1.0)	0.7	(1.5)	—

NOTE: Numbers in brackets refer to low numbers of nests.

the moment that the fourth egg would have hatched if naturally present. Though these experiments were carried out in favourable years, the young in these large broods were heavily starved, and survived for 45 per cent only (Fig. 8D).

In Switzerland, where the Swift has a slightly larger clutch (WEITNAUER 1947), similar results were obtained. From 1948-1954, 91, 82 and 62 per cent of the nestlings of early clutches survived in broods of two, three and four, respectively (WEITNAUER & LACK 1955).

In the *Alpine Swift* the most frequent clutch is three, but nests with four eggs seem to be as exceptional as in the common Swift. LACK & ARN (1947) studied more than thousand broods of this species, and found nestling survival to decrease as 97, 87, 79 and 60 per cent in broods of one, two, three and four, respectively. Ringing recoveries showed post-fledging mortality to be independent of brood-size.

Little is known about birds from other orders. NELSON (1964) artificially twinned twentyfive nests of the *Gannet*, which always lays one egg. Twins of the same age both survive, but have a retarded growth as compared with single chicks. When the age of the twins differs one or more days, the youngest is finally killed by the eldest. Of fifty experimentally twinned young 70 per cent fledged, compared with 94 per cent of solitary chicks.

OWEN (1960) studied the survival of young *Common Herons* in three colonies in England during 1953-1957. From broods with an initial number of 2, 3, 4 and 5 young, the proportions fledging were 100, 90, 78 and 62 per cent, respectively. The chicks dying were always the smallest, and the meagre contents of their gizzards showed that they died of starvation. Moreover, the death rate after fledging proved to be higher among young from larger broods. The proportions of young recovered after 1 September of the first year were 24.5, 14.4 and 12.9 per cent for fledglings from broods of 2, 3 and 4, respectively.

HARRIS (1964) has shown that in the *Herring Gull*, which normally lays three eggs, the initial growth of the young in broods of one, two and three is equal, but shortly before fledging the weight of triplets is lower than of young in smaller broods. Mortality rates in relation to brood-size have not been studied.

Finally, MEBS (1964) has presented some data on differential mortality of chicks in the *Buzzard* in relation to brood-size. In 1959, 36.4 per cent of the nestlings died of starvation in six broods of four, and 24.3 per cent starved in twelve broods of three and one brood of two young, even though the main prey, the vole, reached plague densities that year.

To sum up, in songbirds the weights of the young tend to decrease with increasing brood-size, but in rich food years they may be independent of the size of the brood. The proportion of young fledged appears to be independent of brood-size, except in unfavourable seasons and habitats. After fledging, light young may survive less well than heavy ones. In the swifts, the growth rate and maximum weight of the young are highly dependent on brood-size, especially in wet and cold summers. The proportion of young fledged decreases in the larger broods, but post-fledging mortality is not clearly related to brood-size.

Though these findings support LACK's hypothesis, this can be accepted only when the phenomena described above result in the production of a lower number of reproducing offspring from broods larger than the most frequent ones. This question will be discussed in the next section.

3.3.3. THE MOST FREQUENT AND THE MOST PRODUCTIVE CLUTCH-SIZE

As shown in the foregoing section, in most of the nidicolous species studied so far, there is a differential mortality between broods of different size, viz. the young of the larger broods survive less well than those of the smaller. On LACK's hypothesis, the differential mortality has to be such that, on the average, broods larger than the commonest ones produce fewer, not more, young per brood. If the differential mortality occurs in the nest, this question can simply be studied by determining the number of young flying from broods of different size. In several species, however, the differential mortality does not, or does not only, occur in the nest, but after fledging. Then differences in productivity between broods can be determined from the recovery rates of ringed young. If the differential mortality occurs, for instance, during the first three months after flying, then the proportions of young recovered when more than three months old are measures for the differential mortality rates. It can simply be verified that for broods of n to be the most productive, the recovery rate (q) of young from broods of m, has to be smaller than n/m times the recovery rate (p) of young from broods of n. To assess this, it is simplest to calculate the product of the size of each brood at fledging and the corresponding proportion of young recovered. If $m.q$ is smaller than $n.p$, then n is the most productive brood-size. Such products, named *productivity indices*, have repeatedly been calculated in the following discussion.

In the *Starling*, the survival of nestlings is independent of brood-size, though their weight is negatively correlated with the size of the brood in some years (p. 47, Fig. 6C). However, after fledging the young of large broods survive less well than those of small broods. In early breeding Swiss Starlings the recovery rate of ringed young is about equal from broods of 3-5, but it decreases for young from larger broods (Fig. 6H). As a result, the productivity indices of broods of 5-6, and possibly 7, are about equal, whereas the index is probably much lower for broods of 8 (Fig. 6I). For a definite conclusion more data are needed, especially for the larger broods.

Comparing broods of 4 with those of 6 shows that the former are much commoner than the latter, though the productivity index of broods of 6 is higher (Fig. 6G, I). This might result from the population possibly being composed of two categories of birds: those breeding for the first time having mainly clutches of 4, and older birds having on the average a larger clutch.

In late broods of Swiss Starlings, mainly composed of relayings of older birds and first layings of young birds, the productivity indices are about equal for the most frequent broods of 4 and 5 young, and the index is slightly lower in the less frequent broods of 6 young. In this case more data are needed also.

Similar results were obtained for English and Dutch Starlings (LACK 1948b).

KURODA (1963) artificially increased the size of some broods of the *Japanese Grey Starling*, the most frequent broods of which have 5-6 young.

He concluded from his observations that the maximum number of young that the parents can raise is 6 in some pairs and 7 in others, and he considers broods of 5-6 to be the most productive. In my opinion, however, his conclusion is based on far too few experiments.

Productivity in relation to brood-size has amply been studied in the *Great Tit.* The first report concerning this species has been presented by LACK (1950). He studied the recovery rates of young over three months old in Dutch, English and Swiss populations of the Great Tit, and found a consistent lower rate of recovery for young of the larger clutches. The differences were not statistically significant, however, and what is even more important, the decrease in the survival rate with increasing brood-size was insufficient to offset the greater initial number of young in the larger broods. Hence, based on this limited material, it could tentatively be concluded that the less common larger clutches were the most productive. As stated by LACK, this leaves the problem of why so many females produce small clutches.

One year later KLUYVER (1951) reached the same conclusion based on his extensive data of the breeding of the Great Tit on the O.N.O.-estate of mixed pine forest in The Netherlands. The recovery rates of young from clutches of 4-7, 8-10, and 11 on, were 6.0, 5.5 and 5.9, respectively, and he concluded that the survival of fledglings was independent of brood-size.

Several years later LACK, GIBB & OWEN (1957) re-analysed KLUYVER's ringing results, to which several new recoveries were added. As many nestlings starved, it was argued that survival had to be studied from the time of hatching, not fledging as was done by KLUYVER. The recovery rates of young from broods of 7, 8, 9 and 10 were found to be 7.7, 7.1, 4.3 and 4.2, respectively and this resulted in the following respective productivity indices: 0.54, 0.57, 0.39 and 0.42. This strongly suggests that clutches of 7 and 8 are more productive than those of 9 and 10. This result is not in accordance with LACK's hypothesis, because in KLUYVER's O.N.O.-area 9 is the most frequent clutch-size. LACK (1966) has suggested that this might be due to an insufficient isolation of the O.N.O-population from populations inhabiting broad-leaved forests nearby, where the commonest clutch may be 9, like in English deciduous forests.

However, the fact that LACK *c.s.* studied the survival from the time of hatching cannot explain the discrepancy with KLUYVER's analysis, since KLUYVER (1951) showed that the mortality rate of nestlings in the

O.N.O.-area was independent of brood-size (p. 49). Therefore, the inclusion of the mortality in the nest cannot contribute to making the overall mortality rate of young tits to be dependent on the size of the brood.

In 1958, LACK has presented an analysis of the breeding results of the Great Tit in Marley wood, a mixed broad-leaved forest near Oxford. He determined the recovery rates of young fledged from first broods over 1947-1956. The productivity indices derived from these rates showed that the commonest brood-size (8-10) was, on the average, also the most productive (Table 11).

TABLE 11

RECOVERY RATES OF YOUNG GREAT TITS OVER THREE MONTHS OLD, AND PRODUCTIVITY INDICES IN RELATION TO BROOD-SIZE; 1947-1956, MARLEY WOOD, NEAR OXFORD, ENGLAND
From LACK (1958)

Brood-size	3-7	8	9	10	11	12-14
Per cent recovered	6.8	6.6	8.4	6.4	2.5	1.3
Productivity index	c. 0.3	0.53	0.76	0.64	0.28	c. 0.15

In the studies quoted so far, the data of several years have been taken together. Where there are great differences between years with respect to weather and food supply, it could be expected that the most productive brood-size varies between years. This was shown by LACK, GIBB & OWEN (1957), who studied the survival of young from first broods in Marley wood. In normal food years the productivity indices for broods of 7 up to 11 inclusive, were 0.41, 0.52, 0.66, 0.65 and 0.30, respectively. This showed that broods of 9-10 were the most productive, and these were also the most frequent in those years. In years with an abundance of food, like 1947 and 1948, the recovery rates for broods of 5-10, 11-12 and 13-15 were 11.8, 11.4 and 11.7 per cent, respectively. Hence, the largest clutches were the most productive under these conditions, even though the mean size of the clutch tended to be larger than in normal and bad food years.

From 1958 onwards, PERRINS (1965) has extended the investigations on the Great Tit in Marley wood, firstly by studying a greater number of pairs over a larger area, including all Wytham, and secondly by increasing the number of large broods by transferring newly hatched young from one brood to another. The post-fledging survival of young could be studied intensively by catching many of them during the following winter. Therefore, Perrins was able to calculate productivity indices in relation to brood-size for separate years (Table 12). It is shown that broods of 9-11, which on the average are the most frequent, are the most productive in three years, whereas broods of 6-8 produce most survivors in two other seasons, and broods of larger than average size do so in two other years. Consequently, these figures indicate that selection for the commonest clutch-size will at most be slight.

Table 12

Productivity indices in relation to brood-size for the Great Tit at Wytham, incl. Marley, Oxford, England
From Perrins (1965)

Brood-size	1958	1959	1960	1961 1)	1961 2)	1962	1963
(1) 2-5	0.50	0.63	1.03	0.39	0.30	0.61	0.88
6-8	0.87	0.90	1.83	0.60	0.43	1.14	1.89
9-11	0.85	1.36	2.81	1.25	0.33	1.26	1.52
12	—	—	—	—	—	—	2.57
12-14 (16)	0.83	0.95	3.83	1.00	0.23	1.25	1.86

Notes: (1) All Wytham, except Marley.
(2) Marley, which had an exceptionally high population density and a low food abundance this year.

Perrins's analysis was based on the years 1958-1963. The Great Tit has been studied in Marley from 1947 onwards, and the results obtained in the earlier years have been analysed by Lack, Gibb & Owen (1957) and Lack (1958). These authors have grouped several years, thus including the disturbing effect of adaptive modifications of clutch-size, and moreover they did not take into account the losses of young in the nest, which in some years also vary with the size of the family (p. 50). Therefore, Lack (1966) re-analysed all years separately, and his assessments of the most productive brood-size can be summarized briefly as follows. The most productive family-size was 5-6 in two years, 8 in two years, 9-10 in eight years, and 11-12 or yet higher in five years. Hence, in most years the most productive brood-size coincides with the most frequent one, being 9-10 young. In some years, however, it is considerably higher, but Lack considers this possibly to result partly from adaptive modifications. The most important modification is that related to date: the young of the earliest broods, which tend to be larger, have the highest survival.

One other study of the Great Tit is worth reviewing, because the results are a seeming contradiction to those discussed earlier. Kluyver

(1963) classified the female tits on three study areas according to the total number of fledged young they produced per season, i.e. the number of young of the first and the possible second brood together. Over many years the production per female ranged from 0 to 17-21 young, females producing 7-8 young being the most frequent. Further, KLUYVER measured the rate of recruitment for all classes of females, i.e. the proportion of young recovered after a year in the breeding area. From this he showed that the number recovered steadily increased with an increasing number of fledglings produced per female. Thus, of females producing 1-4, 5-6, 7-8, 9-10, 11-12 and 13-14 fledglings, 0.30, 0.37, 0.53, 0.66, 0.75 and 0.80 yearlings were later recovered. KLUYVER concluded from this result that the variability in the number of fledglings produced per female is not likely to be determined by genetic factors. Indeed, adaptive modifications of clutch-size, and of the number of broods per female per year may have influenced the results to such an extent that they, in my opinion, cannot be used as an argument to invalidate LACK's hypothesis.

PERRINS (1965) also studied the recoveries of ringed *Blue Tits* in relation to brood-size. In two out of six years the category of the largest broods (12-16) was most productive, but in the other years the smaller broods of 9-11, or 12 young had the highest number recovered per brood. The most frequent brood-size in this species at Wytham was 10-12 young, and this shows that in most years the most productive size is near to the commonest size of the brood.

Another species which seems to support the thesis of LACK concerning the evolution of clutch-size in nidicolous birds, is the *Bullfinch*. This finch has been studied by I. NEWTON in England (see LACK 1966). It normally has 4-5 eggs, occasionally 3 or 6. NEWTON made up four artificial broods of 6 and 7 young and studied the mortality of young in natural and artificial families both in the nest and after flying.

All the hatched young flew successfully in the natural broods of 3-5, but the proportion flying in the four artificial families was 58 per cent only. Many of the ringed young could later be recovered by capturing winter birds. This yielded a remarkable difference between the recovery rates of young from the two types of broods, these being 62 per cent of the young hatched in broods of 3-5, and only 15 per cent in broods of 6-7. Rough estimates of the productivity indices for the commonest broods ($4.5 \times 0.62 = 2.8$), and for the large unnatural broods ($6.5 \times 0.15 = 1.0$) indicate that the latter produce fewer offspring than the former. As shown, this results from a differential mortality both in the nest and after flying.

Another group of Passerines to be discussed is that of the old-world flycatchers. Survival in relation to family-size in the *Pied Flycatcher* has been studied in three different parts of its range. Firstly, CURIO (1958) determined the proportions of marked young returning to the breeding area in later seasons (p. 52). The recovery rates were not related to brood-size, and the largest broods of 7 young had the highest index of productivity. The most frequent family had 6 young.

Secondly, VON HAARTMAN (1954, 1967a) showed that the mortality of nestlings was independent of the size of the brood, whereas post-fledging mortality was probably highest for young from broods larger than the most frequent one (p. 51). As a result the productivity index was maximum for the latter (Table 9).

Finally, LACK (1966) analysed CAMPBELL's data collected in a population in England. To exclude, at least partly, the disturbing effect of modifications with laying date, the available data were grouped into four categories: early period, early and late middle period, and late period. In none of these groups the proportions of young recovered, when at least three months old, were related to the size of the brood, and there was a tendency for the largest broods to be the most productive.

In the closely related *Collared Flycatcher* studied by LÖHRL (1957), the largest broods of 8 young produced most fledglings, whereas broods of 6 were the most frequent. Post-fledging mortality has not been studied in this species.

The breeding data of the *Spotted Flycatcher* collected on nest-record cards in Britain, analysed by SUMMERS-SMITH (1952), indicate that the breeding success is somewhat lower in broods of 5 than 3 and 4, but the difference does not offset the greater initial number of young in the former. Hence, broods of 5 produce most flying young. These broods are the most frequent in northern England and Scotland, but in the other parts of England and in Wales families of 4 are commonest.

Production in relation to brood-size has also been studied in some thrushes. In general, the survival of nestlings seems not to be related to the size of the brood (p. 52). Post-fledging survival was found to be independent of brood-size in the *Song Thrush*. In the *Blackbird* the recovery rate of yearlings when at least three months old was lower from broods of 4-6 than 2-3, but the difference was too small to offset the higher initial number of young in the larger broods (LACK 1949a). The productivity indices for broods of 2, 3, 4 and 5/6 were 0.03, 0.05, 0.04 and 0.06, respectively. Where the commonest brood is 4, the indices do not suggest that the most frequent and most productive family-size coincide. However, from the findings of SNOW (1958) it can be inferred that such overall figures may be influenced to a large extent by phenotypic modifications. Therefore, there is a great need for data in which such variations have been allowed for. In the *Redwing* in Finland the mean numbers of young flying from broods of 1-4, 5, and 6 are 1.9, 3.3, and 4.5, respectively, whereas the commonest brood has an initial number of 5 young. Post-fledging mortality has not been studied in this species (TYRVÄINEN 1969).

In a colony of the *Boat-tailed Grackle* studied by TUTOR (1962) in Texas, the brood-size varied from 2-5 young. Those of 3 were the most frequent, but those of 5 produced most fledglings (Table 13). The growth of the young and their post-fledging mortality were not studied.

TABLE 13

NESTING SUCCESS OF 517 NESTS OF THE BOAT-TAILED GRACKLE IN TEXAS, 1959
After TUTOR (1962)

Clutch-size	2	3	4	5
Frequency in per cent	7.4	53.0	36.9	1.2
Per cent hatched	73.7	71.5	76.7	76.7
Per cent fledged of those hatched	96.7	98.3	92.5	78.3
No. of young fledged per nest	1.4	2.1	2.8	3.0

In 211 nests of the *Black-faced Quelea* studied by WARD (1965) in Nigeria, the clutch ranged from 1-5 eggs. In 157 nests of 3 eggs, 92 per cent of the initial number of young fledged, i.e. 2.8 young per nest. In 4 nests of 4 eggs, 81 per cent of the young fledged, giving 3.2 young at fledging. WARD measured the growth and survival of the nestlings in three artificial broods of 4, and three of 5 young, made up by adding eggs to the clutch. In these broods 33 and 47 per cent of the young died respectively, as compared with 5 per cent in six control broods of 3. The experimental broods of 4 survived considerably less well than natural broods of that size, and therefore the results are inconclusive.

In the *Swift* in England the number of young flying per brood increases up to broods of 3 in fine summers, whereas in cold and wet summers broods of 2 young produce most fledglings (LACK & LACK 1951; LACK 1954, 1956a; Table 10). When the results of all years (1946-1952) are summarized, families of 2 and 3 at hatching produce an equal number of fledglings, and where a brood of 3 requires the production of an extra egg, it can be expected that broods of 2 will be commoner than those of 3 (Fig. 8A-C).

PERRINS (1964) studied this species at the same locality from 1958-1961. He transferred a number of young from broods of 2 to broods of 3, thus artificially increasing the number of families with 4 young. The mortality rate of nestlings in such abnormally large broods was so high, that broods of 3 produced more fledglings than those of 4; the number flying from families of 1, 2, 3, and 4 young being 0.9, 1.9, 2.6 and 1.8, respectively (Fig. 8D, E). Broods of 2 and 4 were about equally productive, but where a brood of 4 involves the production of two extra eggs, it is understandable that clutches of 4 are rare. Because the years of study had fine summers, PERRINS's data confirm the earlier results of LACK: broods of 3 produce more young than those of 2 under favourable conditions.

Over fifteen years of study, broods of 1 were the most productive only once (1954); broods of 2 were so in five years (1946-1948, 1953, 1956); in one season (1950) families of 2 and 3 had about the same productivity, and in eight years those of 3 were the most productive (LACK 1956a, 1966). Therefore, the results indicate that the most productive and the most frequent brood-size do not correspond: like in the Starling, the former seems to be larger than the latter.

Similar results were obtained for the Swift in Switzerland. Though the mean clutch is slightly larger than in England, among layings started up to the eighth of June, those of 2 are yet commoner than those of 3, but over the years 1948-1954, the latter were the more productive (WEITNAUER & LACK 1955).

In the *Alpine Swift* in Switzerland 3-layings are the most frequent, and these proved to be also the most productive. From a study of 1060 nests, LACK & ARN (1947) determined the following numbers of young raised per brood: 1.0, 1.8, 2.4 and 2.4 for broods of 1, 2, 3 and 4, respectively. The productivity of the infrequent broods of 4 appears to be high as compared with the much more frequent broods of 2 and 3. This might be explained by two facts. Firstly, the population studied is composed of two categories of birds: those breeding for the first time, roughly 20 per cent of the population mainly producing clutches of 2, and older birds, the most frequent clutch of which is

3 eggs. Secondly, clutches of 4 are laid in very favourable years, and therefore have a high survival. For a fair comparison to be made, clutches of 4 should be studied under all conditions.

Like in the Swift, post-fledging survival seems to be independent of brood-size.

There is one bird of prey, the *Kestrel*, the breeding success of which has been studied in relation to brood-size (Cavé 1968). In the reclaimed polder of the former Zuiderzee in the central part of Holland, this species was studied in nesting-boxes, 1960-1964. Among early broods, the eggs of which were laid before 1 May, those of 6 chicks were commonest. Broods of 6 and 7 produced significantly more fledglings than broods of 5, and those of 7 slightly more than those of 6, though the latter difference was insignificant. Among late broods, the eggs of which were laid after 30 April, those of 5 were most frequent, but those of 6 produced slightly, though insignificantly, more fledglings (Table 14).

Table 14

Fledging in relation to brood-size in the Kestrel in Holland
After Cavé (1968)

	Early broods					Late broods			
Brood-size	1-3	4	5	6	7	1-3	4	5	6
Frequency	9	14	47	53	11	25	44	61	34
Per cent fledged	71	89	90	83	75	82	85	85	75
No. fledged per brood	1.7	3.6	4.5	5.0	5.3	2.1	3.4	4.2	4.5

In addition to these data, Cavé gives some more arguments in favour of the view that brood-size in the Kestrel is not limited by the amount of food the parents are able to provide for the young. Thus, the mortality rate of the young was highest in the first week after hatching, when their food demands are comparatively small. The maximum weights of the chicks, reached some days before fledging, were independent of the size of the brood. Moreover, the parents proved to be able to raise the feeding frequency considerably during dry periods on rainy days, thus compensating for the slow feeding rate during periods of rain.

There are, however, several findings in Cavé's study which point to an effect of food shortage on breeding success. Firstly, in early broods the survival rate of broods of 6 and 7 is significantly lower than those of 5 young. Also, in late broods those of 6 have a significantly lower survival rate than those of 5 (Table 14). Secondly, though most of the young die in their first week of life, food shortage cannot be excluded as a causative agent. CAVÉ has shown that a considerable proportion of the clutches is deserted during incubation, when the females are fed by the males. This proportion was negatively correlated with the density of the Common Vole, the main food in that period, and CAVÉ has suggested that desertion is mainly due to the failure of the male to bring the female enough food. Therefore, it seems plausible to suppose that food shortage may still be operative some weeks later when the chicks have hatched, especially because food is collected by the male only during the first week after hatching (TINBERGEN 1940). Thirdly, though Kestrels are clearly able to raise the feeding frequency over short periods which interchange with periods of relative inactivity, it is an open question whether they could do so continuously over longer periods.

Finally, the question may be raised as to whether modificatory variations have sufficiently been eliminated from the data in Table 14. Variations with laying date have partly been allowed for, but annual variations are included; moreover, nothing is known about the influence of age on clutch-size, and all ages have been included in the material.

As to the other orders of birds, there is evidence from three species of tube-nosed swimmers, all laying a single egg, showing that addition of young to the normal brood results in fewer young surviving per brood. RICE & KENYON (1962), working on one of the Hawaiian islands, made up 18 artificial twins in the *Laysan Albatross* when the young were nine days old. In 15 nests both young died prior to fledging, and only one pair raised both chicks. From the initial number of 36 young 3 left the breeding area, i.e. 0.17 fledglings per pair. From 18 nests with the normal single young 12 survived to fledging, i.e. 0.67 per pair. This shows that a pair cannot normally raise two young.

HARRIS (1966), working on Skokholm off Wales, has provided nine nests of the *Manx Shearwater* with twins, the young being added immediately after hatching of the single egg. The twins had a slower growth, and those surviving had a considerably lower weight than single chicks at fledging. From the initial number of 18 young only 3 fledged, i.e. 0.3 per pair, whereas 44 control pairs with single chicks raised 42 young to fledging age, or 0.95 per pair.

LACK (1966) has reviewed work of C. E. HUNTINGTON on the breeding of *Leach's Petrel*. Twentythree pairs of this species were given two chicks. At a control after ten days, the second nestling had died or disappeared in 14 nests, in 7 it was underweight, and in only 2 nests it was in a good condition. Again, this suggests that also this species cannot normally raise more than a single chick.

These experiments show that in the Procellariiformes the parents cannot provide enough food for more than a single chick, and this strongly supports LACK's hypothesis.

In view of the conclusion reached above it is remarkable that similar experiments in the *Gannet*, performed by NELSON (1964) on the Bass Rock, Scotland, gave opposite results. Addition of eggs or chicks resulted in 25 nests with twins, and from the initial number of 50 young, 35 were raised to fledging age, i.e. 1.4 per pair. In control nests with single chicks 0.9 young fledged per pair. The weight of the twins at fledging was about 0-10 per cent lower than that of single chicks, but NELSON is of the opinion that these differences are unlikely to give rise to differential post-fledging mortality. The experiments were carried out in 1962, a less favourable year for fishing, and therefore it may be stated that, in general, the normal brood is less productive than an artificial brood of two young.

On the contrary, in the related tropical *Red-footed Booby*, also laying a single egg, all experimentally twinned nests failed completely (NELSON 1966).

Finally, experiments on adding eggs or young to make up broods of above the normal size have been carried out with three species of gulls, though only in the Glaucous-winged Gull on an extensive scale.

The *Kittiwake* has been studied by COULSON & WHITE in north-eastern England (see LACK 1966). From broods of 1, 2 and 3 chicks 0.9, 1.8 and 2.2 young fledged, respectively. This suggests, that the commonest broods of 2 are less productive than broods of 3, but this may well be due to phenotypic modifications: broods of 2 were mainly the product of unexperienced and late breeders, whereas broods of 3 were mainly produced by the more efficient and experienced early breeders. In one year, 1959, COULSON made up 4 broods of 4 young each, from which all chicks flew, but the fledglings were most probably underweight. This may have led to differential mortality after fledging, but this was not studied.

The experiments with the *Glaucous-winged Gull* have been carried out by VERMEER (1963) on Mandarte Island, British Columbia. He made up broods of 4, 5 and 6 young, and showed that the proportions of young raised were similar to that in normal broods of 3. This suggests that the parents can feed considerably more young than the normal number of 3. However, nothing has been reported about the weight at which the young fledged, nor about the occurrence of differential mortality after fledging, and therefore, the results cannot be satisfactorily evaluated.

HARRIS & PLUMP (1965) made up two broods of 5, and two broods of 4 chicks in the *Lesser Black-backed Gull* on Skokholm in 1964, immediately after hatching of the normal clutch of 3. As compared with one brood of 2, the young in the over-sized broods had a normal growth and reached the same maximum weight at fledging. Clearly, the parents could feed more than the normal number of three young, though they obtained most of their food "naturally", i.e. from the shore and from arable land, and not from nearby fish-docks, like most of the Glaucous-winged Gulls did.

Of all species studied, the preliminary results obtained in only one suggest that the most productive brood-size is smaller than the most frequent family. In the *Common Heron* studied by OWEN (1960) in England both the mortality in the nest and after fledging proved to be related to the size of the brood (p. 56). As a result of this, broods with an initial number of 2, 3 and 4 young had productivity indices of 0.49, 0.39 and 0.40, respectively. (Broods of 5 young were too rare for an index to be calculated.) This suggests that broods of 2 are the most productive, whereas broods of 4 are by far the most frequent.

Summarizing, we can make up the following survey.

1. The most productive brood-size is, or is near to, the most frequent brood in the Great Tit, Blue Tit, Starling, Bullfinch, Swift, Alpine Swift, Laysan Albatross, Manx Shearwater, Leach's Petrel, and the Red-footed Booby. When small discrepancies are present, like in the Starling and the Swift, the most productive size tends to be larger than the size of the commonest brood.
2. The most productive brood-size is larger than the most frequent family in the Pied and Collared Flycatchers, Redwing, Song Thrush, Blackbird, Boat-tailed Grackle, Kestrel, Gannet, Kittiwake, Glaucous-winged Gull, and Lesser Black-backed Gull.
3. The most productive brood seems to be smaller than the commonest family-size in the Common Heron only.

If we now look back on the evidence these findings are based upon, it seems to be sufficiently detailed and comprehensive in the Great Tit, the Swift, the tube-nosed swimmers, the Red-footed Booby and the Gannet. In several other species, like the Blue Tit, the Starling, and the Bullfinch more data are needed for statistical reasons. In the flycatchers, the thrushes and the Kestrel more allowance should be made for the disturbing effect of phenotypic variations, though the important modifications with laying date have been eliminated for the Pied Flycatcher in England, and partly so for the Kestrel in Holland. In the Boat-tailed Grackle, the Gannet, and the gulls the occurrence of a differential post-fledging mortality has not been studied. An effect of this seems to be unlikely in the Gannet and the Lesser Black-backed Gull, but may well be responsible for a seemingly high most productive family-size in the other species.

Consequently, the available information on the well-studied species supports LACK's hypothesis, except that on the Pied Flycatcher in England and Germany, the Lesser Black-backed Gull, and the Gannet. As to the Flycatcher, LACK (1966) is of the opinion that this species should be studied in yet more detail with respect to phenotypic variations. As to the Gannet, he believes that it can raise twins because its numbers are at present far below the carrying capacity of the feeding grounds due to persecution in the past (LACK 1966, 1968; see also NELSON 1966).

As discussed above, the available information suggests that in some species the most productive brood-size is larger than the commonest one. This discrepancy has recently been considered by MOUNTFORD (1968). He argues, like other selectionists, that natural selection will favour the genotype producing the greatest number of surviving descendants. However, as demonstrated in a numerical example, this does not imply that the most productive brood-size necessarily occurs most frequently in the population. According to MOUNTFORD, it should be taken into account that the size of the clutch, and hence of the brood, varies between individuals of the same genotype. Therefore, the number of surviving descendants of the genotype has to be computed as the sum of the separate contributions from all the brood-sizes characteristic for that genotype. In this way, a genotype with an average production of, say, 5 descendants per brood may be the most frequent type in the population, whereas a brood of 7 (or any other size, be it smaller, equal to, or larger than 5, depending on the frequency distributions of the brood-sizes of the genotypes) produces most surviving offspring.

The argument is based on the assumption that individuals of the same genotype have different brood-sizes. In my opinion, this will occur only, when they live under dissimilar environmental conditions, giving rise to non-adaptive or adaptive modifications of brood-size. Adaptive variations frequently occur in birds (Section 4), and when the size of the brood is always modified perfectly to the prevailing situation, then the largest brood will be the most productive, though not necessarily the most frequent. Therefore, these modifications should be excluded from the information as much as possible. This has been effectuated in some species by studying the survival in relation to brood-size under as similar conditions as possible, i.e. within one population, within one year and among clutches produced in a short time-interval. In so doing, the possible non-adaptive modifications are excluded likewise to a large extent. This means that the remaining variations of clutch-size are mainly hereditary, and then the most productive size of the clutch can be expected to equal the commonest one. Nevertheless, in some species the former was found to be larger than the latter, and I am inclined to attribute this to an insufficient exclusion of adaptive modifications rather than to an effect as postulated by MOUNTFORD.

3.3.4. RELATIONS BETWEEN CLUTCH-SIZE AND OTHER FEATURES IN RELATED SPECIES

As shown in the last section, the theory of LACK on the evolution of clutch-size in nidicolous birds has won support from the study of survival of young in relation to brood-size. Further supporting evidence, though circumstantial, might be obtained from intra- and interspecific comparisons between clutch-size on the one hand, and on the other hand, factors determining the want of food of the young and the amount of food the parents are able to collect. Such factors may be both intrinsic and extrinsic.

The want of food of the young will depend on such factors as the size of the bird, their rate of growth, and the heat isolating properties of the nest. The food amount collected by the parents will depend on the size of the bird, the kind, the density, and the availability of the food, the time available for searching, and the pair-bond.

To gain insight in the extent to which these factors have played a part in the evolution of the size of the clutch, one should compare populations of birds with different mean clutch-sizes, but differing in as few of the other factors as possible. Thus, comparisons of geographically isolated populations of one species, which generally show only minor structural differences, can inform us about the effect of the extrinsic factors as the density and the availability of the food and the time available for searching. Differences between populations with respect to the intrinsic factors mentioned above in fact occur on the species level only, but even comparisons of related species nearly always involve more than one or two factors, which may be supposed to have affected clutch-size ultimately. To obviate this difficulty the comparison should not be limited to one pair of species, but should be extended to other pairs, showing a similar difference with respect to the factor under study, but which may differ as to other features possibly affecting clutch-size. If enough related species can be compared in this way, general trends can be established, which make an ultimate effect of the factor in the evolution of clutch-size appear likely.

If not enough closely related species are available, the comparisons can be made between species of different genera, families, or even orders, but then, especially in the last two cases, so many features with a possible effect on clutch-size may be involved that the trends found can in most cases be regarded as suggestive only.

As to the regional differences in clutch-size and the ultimate factors involved in their causation, the discussion has been postponed to

Section 3.5, because several of its implications also refer to nidifugous birds, which are discussed in Section 3.4.

The ultimate effects of other factors will be treated in this section. They have amply been discussed by LACK (1947-48, 1954, 1967a, 1968), and will therefore be considered here only concisely.

The first factor to be considered is the growth rate of the young. If the clutch of a species has been evolved to correspond with the largest brood for which the parents can provide enough food, then the growth rate of the young might have influenced the evolution of clutch-size, because with the same quantity of food per day few young can be raised rapidly and more young slowly. To check this, LACK (1947-48) grouped the central European small passerine birds into those with 6 eggs or more (24 species) and with 5 eggs or less (60 species), and found the nestling periods to be 16.6 and 13.5 days, respectively.

Now, long nestling periods are disadvantageous, because the longer the young are in the nest, the more vulnerable to predation they will be. Therefore, short nestling periods will be selected for, unless predation is so low, that a higher number of slowly growing young results in a higher number of survivors per pair. It is therefore interesting that such a slow growth rate has especially been found among hole-nesters, the young of which run a lower risk to predation (LACK 1954). In 1968 LACK showed that the nestling time and the clutch-size decrease in parallel among small Passerines having their nests respectively in holes, roofed, in a niche, or quite open. It is true, these data are based on comparisons of species in different subfamilies, and hence may be regarded as suggestive only, but similar trends were found within the subfamilies of the thrushes and the tropical tanagers.

When the comparisons are extended to other orders, several exceptions come in. Thus, the swifts though all breeding in holes and having slowly growing young, have a small to very small clutch, but this is presumably related to such factors as the kind and availability of the food (LACK & LACK 1951). The significance of these factors has especially been studied in marine aquatic birds by LACK (1967a, 1968). He showed that clutch-sizes tended to be smaller, and nestling periods to be longer in offshore than inshore feeding seabirds. This not only holds for broad comparisons between different orders or families, but the same trend is found within families and subfamilies. Thus, among the boobies and gannets, the North Atlantic Gannet and the tropical Red-footed Booby are offshore-feeders with a single egg in the clutch, whereas the Blue-footed and Brown Boobies are inshore-feeders having

2-3 and 2 eggs, respectively. Again, the Galapagos Fork-tailed Gull and the Kittiwake, which feed offshore, have a clutch of one and two respectively, and long fledging periods, as compared with inshore-feeding other gulls, which normally have three eggs. Similar trends occur within the terns and the auks.

In contrast with hole-nesting landbirds, where large clutches and long nestling periods go hand in hand, the offshore-feeding seabirds, and also the swifts, have small clutches combined with long nestling periods. Hole-nesting Passerines as compared with free-nesters differ in their vulnerability to predation, whereas the density and availability of the food are, on the average, assumed to be similar in both categories. However, among seabirds, offshore-feeders as compared with inshore-feeders have less accessible food resources due to the longer distance to their feeding grounds, and a consequent lower feeding rate. Moreover, in offshore-feeders the food supply is erratic, because most of the prey moves down to lower levels in stormy weather. Swifts meet similar situations under rainy and windy weather conditions. In both groups of birds, the chicks can survive such bad weather periods when they have fat reserves, and these can be built up owing to their slow growth rates. These slow rates may be supposed to have evolved owing to a comparatively low vulnerability to predation: offshore feeding seabirds breed on islands where predators are rare or absent, and swifts breed in holes.

An inverse relation between the size of the bird and the size of the clutch is well demonstrated by the birds of prey. The smallest representatives in this group, like the Merlin and the Kestrel, lay 4-5, sometimes 6 or 7 eggs; those of medium size, like the Goshawk, the Kite and the Peregrine, have mostly 2-4 eggs, and the largest species, the condors and the larger vultures and eagles, have only 1 egg in the clutch. The significance of the small clutch of large raptors has been discussed by AMADON (1964). He is of the opinion that they can raise only one chick, because their special kind of food is scarce. Eagles are strongly territorial in the breeding season, and therefore forage in a relatively small area only. AMADON observed that eagles find it hard to carry large prey over long distances, and regularly interrupt their homeward flight to rest a while. As a result, they have a very low feeding rate and the chick, having a slow growth, seems to be well adapted to this situation. The scarcity of the food is also demonstrated by the fact discussed earlier, that the last hatched chick is often killed by its nest mate in species with two eggs in the clutch (p. 41).

One other important organizational feature ought to be discussed in relation to brood-size: the share of the sexes in feeding young. For this the reader is referred to the next section.

3.3.5. CLUTCH-SIZE IN POLYGYNOUS SPECIES

It has been pointed out by SKUTCH (1949) that the clutch-size in polygynous species in which the young are fed by the female only, is the same as that in species where the young are raised by both parents. He compared the polygynous hummingbirds and manakins with the monogamous antbirds, finches and tanagers, and found that in Central America all these birds lay two, rarely three eggs. Also, within the family of the American flycatchers, including some polygynous species, the size of the clutch did not vary according to the share of the parents in feeding the young. It is true, the young of the polygynous species had slightly longer nestling periods, but these could not compensate for the absence of a second feeding parent.

SKUTCH stated that these findings, in addition to those concerning the feeding rate in relation to brood-size (p. 45), do not support LACK's hypothesis on the evolution of clutch-size in nidicolous birds, and he is of the opinion that other factors than the amount of food collected by the parents have ultimately affected the size of the clutch (Section 3.6).

The question has been amply discussed by VON HAARTMAN (1954, 1955). Like SKUTCH, he compared clutch-sizes of related monogamous and polygynous species, but the differences proved to be very small, if any. Thus, there was no significant difference in the size of the clutch between the mostly polygynous Corn and Cirl Buntings, and the monogamous Yellow, Reed, and Ortolan Buntings. Again, the difference was very small, if any, between the Chiffchaff, the male of which is said to neglect its offspring, and the Willow and Wood Warblers, in which both sexes feed the young. Further, no correlation could be established between clutch-size and the share of the male in feeding the young within the (sub)families of the wrens, icterids, and penduline tits. VON HAARTMAN calls special attention to the last group, in which the highly polygynous palaearctic Penduline Tit has 7 eggs, and the monogamous nearctic Verdin has only 4, or less often 5 eggs. However, according to LACK (1968) there is some doubt about the taxonomic relationship of these tits, though they show a remarkable resemblance in morphology and habits. This may be due to convergence, and if so, the comparison looses much of its significance.

LACK (1968) has quoted several examples of related monogamous and promiscuous species, in which the former have clutches twice, or more than twice, as large as the latter, but in all cases there are, or there may be, clear parallel differences in the kind of food of the young.

To sum up, some of the comparisons have provided evidence apparently not supporting LACK's hypothesis. Therefore, the relevant cases should be studied in more detail with respect to feeding frequencies, kinds of food of the young, and nestling periods. The feeding frequency has been studied by KENDEIGH (1952) in the House Wren, and by VON HAARTMAN (1955) in the Pied Flycatcher. They showed that solitary females speed up there feeding rates considerably, thus compensating for the loss of the male's contribution to a large extent. Nevertheless, in the latter species nestling mortality appeared to be higher in broods fed only by the female than in broods of comparable size fed by both parents (TOMPA 1967). More knowledge concerning these questions is needed, before a final conclusion can be drawn.

3.4. THE EVOLUTION OF CLUTCH-SIZE IN NIDIFUGOUS BIRDS

Nidifugous birds form an extremely heterogeneous group. They agree in having young which leave the nest shortly after hatching, and brooding them during the night and under unfavourable weather conditions normally outside the nest. Their clutch-sizes vary enormously, and hence the number of young they produce. Moreover, they differ to the extent in which they feed their young after leaving the nest. In some species the parents do not feed their young at all, like many of the waders, most of the gallinaceous birds and the ducks. Some make the food available to the young by scratching, like the Partridge, whereas others really feed the young for several days, as in the bustards, cranes, rails, grebes and oystercatchers.

It is therefore understandable that very different theories have been put forward to explain the evolution of the size of the clutch. One of these theories postulates that the size of the clutch has been evolved to correspond with the maximum number of eggs that the sitting bird can effectively cover. This theory has amply been discussed in Section 3.2, and it was shown that clutch-size is unlikely to have evolved in this way, though more evidence is needed for the waders.

Another theory states that clutch-size has ultimately been limited by predation pressure. In general, nidifugous birds start incubating when the last egg has been laid, and consequently, the more eggs are laid, the longer they are unguarded, and hence more vulnerable to predation. The possible ultimate effect of this factor will be discussed in Section 3.6, and as will be enunciated, it seems unlikely that it has affected the size of the clutch.

The third theory postulates that, like in nidicolous birds, over-sized broods will produce less surviving offspring than broods of normal size, because the mortality rate of the young is higher in the former than in the latter. This has been attributed to different possible causes. Firstly, it has been suggested that predators are more attracted to larger than smaller broods (Section 3.6). Secondly, in some species of geese and ducks, where the young hatch slightly asynchronously, the female leaves the nest immediately after the last young have hatched, and these being not yet prepared to leave straggle and are unable to compete for brooding space under the guarding bird. The larger the clutch, the more differently aged the young are, and the higher the mortality rate will be on the average. This has been reported for the Blue Snow Goose (COOCH 1961), and the Tufted Duck and the Scaup (HILDÉN 1964). Thirdly, it has been suggested by LACK (1947-48) that in species which feed their young, the size of the clutch might have been evolved to correspond with the number of young for which the parents on the average can provide enough food. If so, several features of clutch-size observed in these species could be understood, such as the south-north trend (Section 3.5), the seasonal trend (Section 4.3), and the influence of rain on clutch-size in African cursorial birds. However, such trends have also been observed in ducks, which do not feed their young (Section 3.5), and rain may have a direct effect on the laying female (Section 2.3.1.).

The last theory on the evolution of clutch-size in nidifugous species to be discussed has been formulated by LACK (1964a, 1967b, 1968). He has suggested that the size of the clutch may have been evolved in relation to the average amount of food available to the laying hen. LACK has not illucidated this view more fully, but it can be visualized as follows. As already stated (p. 35), natural selection will have maximized the reproductive rate of a bird species within the possibilities of its organizational structure and within the limitations of its environment. In several nidicolous birds the evidence supports the view that the size of the clutch is ultimately limited by the amount of food the parents are able to collect for the nestlings. In nidifugous species which do not feed their young, this factor cannot have had an influence on the evolution of the size of the clutch. Here the number of eggs may have ultimately been limited by the amount of material the female is able to collect for yolk and albumin deposition, and this amount directly depends on the quantity of food available to the female, both before and during the period of laying.

If the clutch of nidifugous birds has been evolved in this way, then food shortages can be expected to have proximate suppressive effects on clutch-size. Several examples of this have been given in Section 2.3.5 for gallinaceous birds and ducks. Nevertheless, as stated by LACK (1968), the size of the clutch is not proportionately more variable in these birds than in other groups, and this is attributed to the ability of the female to postpone breeding until she has formed enough reserves to produce a clutch of about normal size. More evidence about this possible response of the female is wanted.

LACK's hypothesis on the evolution of clutch-size in nidifugous birds cannot be tested by manipulating clutch or brood-size, as has been done in nidicolous birds. Artificial addition of eggs or young will, within certain limits, result in an increase of the number of offspring, because the limiting factor has ultimately played a part in an earlier phase of the reproductive cycle, viz. in limiting the number of maturing oocytes in the ovaries. Therefore, it can be expected that the number of young produced increases parallel with the size of the clutch, and this has in fact been found.

JENKINS *et al.* (1963) have measured the survival of broods of the Red Grouse in Scotland up to the second week of August. They found a steady increase of the number of young produced up to the largest clutches of 10 and 11 eggs, whereas the commonest clutches had 6-8 eggs. Again, HARRIS (1967) studied the Oystercatcher on Skokholm off Wales, where clutches of 3 are the most frequent, but those of 4 not uncommon. HARRIS showed that broods initially having 4 young produce more survivors up to the age of thirty days than those of 3 young. The Oystercatcher is, however, exceptional among the nidifugous species, because the chicks are fed by the parents for a considerable period after leaving the nest.

Circumstantial evidence supporting LACK's hypothesis originates from comparisons of the size of the clutch with the size of the eggs in related species. This point has been considered in detail by LACK (1967b, 1968). As already stated by HEINROTH (1922) there is a clear positive relation between the size of the bird and the size of its eggs. Therefore, for comparisons to be made, the weight of the egg has to be expressed as a percentage of body-weight. When this proportionate egg-weight is plotted against body-weight for different families, it shows firstly, that proportionate egg-weight varies inversily with body-weight, and secondly, that this inverse relationship is characteristic for each family (Fig. 9). When the different families of gallinaceous birds are treated this way, there proves to be an inverse relation between the proportionate size or weight of the egg characteristic for each family, and the mean clutch-size for that family: Megapodidae, having the largest proportionate egg-size, lay their eggs singly, Cracidae have 2-3 eggs, Numididae about 7, Phasianidae average about 10, and the Tetraonidae, having proportionately the smallest eggs, lay the largest numbers of eggs on the average. This also holds good within the Phasianidae, where the species with 2-4 eggs have proportionately larger eggs than the species with 10 or more eggs in the clutch (Fig. 9).

Similar relationships are found in the waterfowl, Anatidae. LACK (1968) grouped the species of this family into five categories with decreasing proportionate egg-size, and he found that the average clutch-size of these groups increased. The same inverse relation was found within the species of the genus *Anas*, and even within four subspecies of the Mallard.

The inverse relationship between clutch-size and proportionate egg-size suggests that larger eggs have been evolved, so to speak, at the expense of clutch-size. Logically, this will have occurred only when large eggs are advantageous. From large eggs the young hatch in a more advanced stage of development, or they carry more reserves when leaving the nest, and this will be of significance in birds which do not feed their young. This is shown by the fact that in general the proportionate size of the egg is noticeably larger in nidifugous than nidicolous birds, but also within the former the conditions under which the chicks live vary considerably. Thus, the northern ducks, such as the Goldeneye, have proportionately large eggs as compared with species from temperate regions, and the chicks hatch with large fat stores which are mobilized and metabolized while feeding in cold water. Many more examples are given by LACK *l.c.*

The relationships between clutch-size and proportionate egg-size are only broad. This is, for instance, illustrated by the fact that in the category of waterfowl, considered above, with proportionately the largest eggs, the average specific clutch varies from 2.5-8 eggs, and in the category with proportionately the smallest eggs, from 6-11 eggs (LACK, 1968). This is most probably due to a rather great variation in the kind and availability of the food in different species. In extreme cases this may obscure any

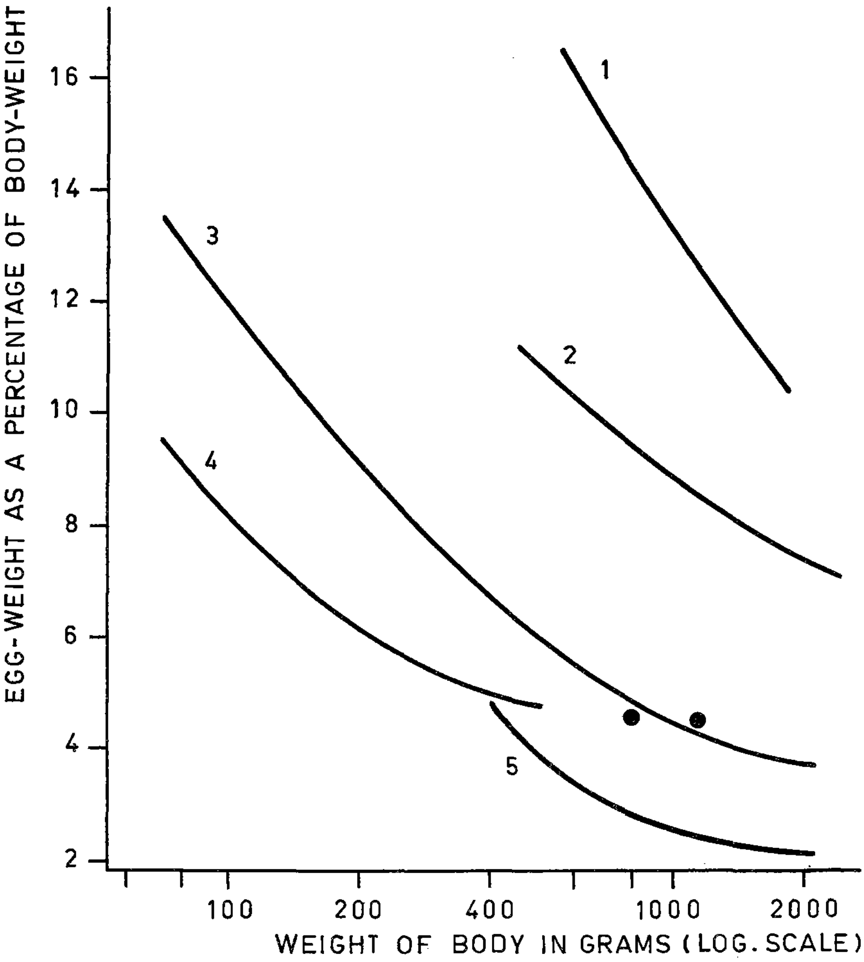

FIGURE 9. Relations between proportionate egg-weight and body-weight in different families of gallinaceous birds. 1. Megapodidae. 2. Cracidae. 3. Phasianidae with clutches of 2-4 eggs. 4. Phasianidae with clutches of 10 and more eggs. 5. Tetraonidae. Two species of Numididae indicated by ●. After LACK (1968).

possible relation between clutch-size and proportionate egg-size, as seems to be the case among cursorial land birds other than Galliformes (see LACK 1968: 206-7).

So far the evidence suggests that in nidifugous species the size of the clutch may have been evolved in relation to the average amount of food available for the hen. However, there seems to be one serious objection against this view. Some of the nidifugous species have been recorded as indeterminate layers (Table 2). This means that the hen can produce more than the usual number of eggs, when they are taken as laid. However, when the evidence concerning these species (the first six of Table 2) is considered critically, objections can be levelled against all of them. The data on the Mallard may have been gained from domesticated specimens. From the Shelduck once a maximum of 18 eggs has been collected, where the normal clutch ranges from 8-15 eggs, so that protracted laying is probably restricted. The data of the Scaled Quail are anecdotal and were not collected by WAGNER himself. Concerning the Pheasant, WESTERSKOV reports the removal of eggs and consequent laying of many more eggs, without actual data, and the same holds good for the Golden Pheasant. Finally, the eggs of the Moorhen apparently have been laid in cycles.

There is, however, one nidifugous species, the Lapwing, which does not feed its young, in which protracted laying has been established with certainty. This plover is not listed in Table 2, because it has never been studied how many eggs are produced in succession when any egg, including the first one, is taken as laid. The Lapwing always has four eggs in the clutch, and when the first two eggs are taken as laid, the hen produces four additional eggs in another nest nearby with the normal intervals (KLOMP 1951). This shows that the female is able to produce fifty per cent more than normal, and it is therefore highly improbable that the normal clutch has been evolved in relation to the average amount of food available for the hen. This is in accordance with the absence of an inverse relation between clutch-size and egg-size among some cursorial land birds, and even within the Charadriidae: the Dotterel, laying 3 eggs, does not have proportionately larger eggs than the Lapwing (LACK 1947-48).

The indeterminateness of some nidifugous species makes it worth considering one other possibility concerning the evolution of the size of the clutch. A mechanism may have been evolved for using the appropriate amount of energy for the production of eggs out of the total quantity of energy available for all reproductive activities. This implies that, if the bird should use a smaller or greater amount of energy for egg production, in both cases a smaller number of surviving young will be raised on the average. In the former case either the number or the size of the eggs may be smaller, and both will result in a smaller number of surviving offspring being produced. The young from smaller eggs will be born in a less advanced stage or with smaller reserves, decreasing their chances of survival.

In the latter case, when more than the appropriate amount of energy is used for the production of the eggs, the bird will raise less offspring on the average due to its exhaustion during the final phase of the reproductive cycle, too little energy being now available for incubation and guarding the young. On this hypothesis, the most productive brood-size will tend to equal the commonest one, but the scanty field evidence available does not point that way (p. 76).

As far as I know, the influence of the size of the clutch on the exhaustion of the parents has never been investigated in nidifugous birds, but KLUYVER (1963) has presented evidence for the Great Tit, which is worth considering in this connection. He showed that the number of fledglings from the first brood was not related to the proportion of female parents recovered after a year in the breeding area. Consequently, the amount of energy used for the production and raising of the brood had no effect on the subsequent survival of the parents. Moreover, the proportion of pairs producing a genuine second clutch increased parallel to the size of the first clutch. However, large first clutches tend to be laid early in the season, and as shown by KLUYVER (1951) the production of a second clutch depends among other factors on the earliness of the start of the first laying. These findings do not suggest that the activities of the parents are affected by the size of the first brood, not even in nidicolous birds which have to spend much energy in feeding a large brood. Therefore, as yet there is no evidence supporting the last hypothesis.

3.5. REGIONAL DIFFERENCES IN CLUTCH-SIZE AND THEIR SIGNIFICANCE

3.5.1. THE SOUTH-NORTH TREND IN THE OLD WORLD

It has been reported by RENSCH (1938) that an increase of clutch-size with latitude has been recognized since the eighteenthirties. The oldest statements refer to differences of clutch-size between tropical, temperate and arctic regions on the northern hemisphere of the Old World. Such differences have not only been found between the species of one genus or family, but also between related subspecies. Several examples of this South-North trend have been given in the classic contributions of HESSE (1923), STRESEMANN (1927-34), GROEBBELS (1937), RENSCH (1938) and GROTE (1939), summarized by MOREAU (1944a) and LACK (1947-48; 1954). Among Passerines which are widespread over the northern part of Africa and Europe, or over Eurasia, South-North trends of clutch-size have been established in such species as the Sky-lark, Barn Swallow, Sand Martin, House Martin, Magpie, Jay, Great Tit, Tree Creeper, Nuthatch, Dipper, Wren, Blackbird, Song Thrush, Wheatear, Great Reed-warbler, Hawfinch, Yellowhammer, House Sparrow, and Tree

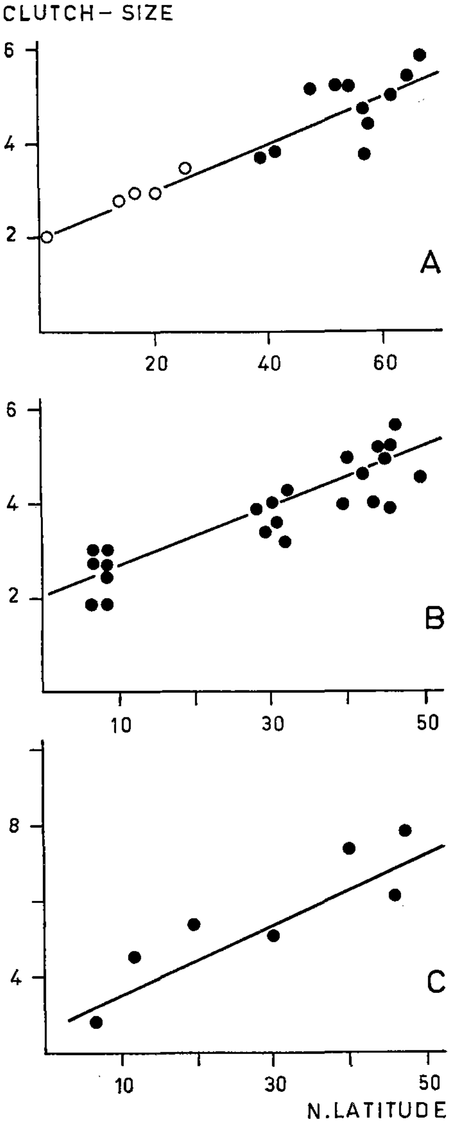

FIGURE 10. Trends of clutch-size on the northern hemisphere. **A** in the genus *Emberiza* (buntings) in Africa (open circles), and Eurasia (dots). **B** in the species of the family Icteridae in North America. **C** in the genus *Oxyura* (stiff-tailed ducks) in Europe and America. After CODY (1966).

Sparrow. The Wren, for instance, has 3 eggs on the island of Sicily, 5-6 eggs in England, 6 in Germany, and 6-8 in Russia. The Blackbird has 1-3 eggs in the Canary Islands, 3-4 in Spain, 5-6 in Germany, and 5-7 in Russia. The Wheatear is recorded to have 5 eggs in Morocco, 5-6 in Germany, and 8-9 in Greenland. Another example is given in Figure 10 A.

In later years similar trends have been established in other Passerines, such as the Robin (LACK 1945, 1954), recently slightly corrected by VON HAARTMAN (1967b), the Blue Tit (LACK 1950), the Meadow Pipit (COULSON 1956), and the Goldfinch (FRITH 1957). The Spotted Flycatcher and the Chaffinch are recorded to have larger clutches in Finland than England (VON HAARTMAN 1967b).

In some cases significant differences in clutch-size between populations of the same species have been found over much smaller distances. The Nuthatch, for instance, has an average clutch of 6.5 eggs in Switzerland, and of 7.1 eggs in south Germany (LÖHRL 1966). Again, the clutch of the Spotted Flycatcher is 4.2 in southeast England, and 4.4 in Scotland. On the other hand, the clutch of other species does not vary significantly over England and Scotland, like that of the Blackbird and Song Thrush (SNOW 1955), the Chaffinch (NEWTON 1964), the Tree Sparrow (SEEL 1964), and the Meadow Pipit (COULSON 1956). Titmice even show a reversed trend: the clutch of the Great, Blue and Coal Tit is smaller in Scotland than in south England (LACK 1950).

Comparisons between different species of the same subfamily or family have been made by LACK (1947-48; 1968), who studied 14 different groups of Passerines with representative species in tropical Africa and middle Europe. Roughly, the clutch appeared to be about twice as large in Europe as in Africa.

Among the passerine species which are widespread over north Africa and Europe or Eurasia, there seem to be very few exceptions to the general South-North trend of clutch-size. Most of those recorded as such in fact deviate from this trend only over part of their range. The clutch of the Song Thrush, for instance, clearly increases from south to north over Europe, but it is said to decrease again at latitudes over 65° (SIIVONEN 1939). Again, titmice have been found to lay a smaller clutch in Sweden than Holland, but the Great and Blue Tits do show the general South-North trend over other parts of their vast ranges (LACK 1950, 1955). As yet, only three species do not comply with the general rule: the Raven, the Crossbill, and the Pied Flycatcher. The first two species have larger clutches in southern than northern Europe, and are exceptional in having breeding seasons before the vernal equinox (LACK 1947-48). The Pied Flycatcher has a normal breeding time; the regional variation of its clutch-size will be considered later in this section.

So much for the trends in clutch-size of passerine species in north Africa and Eurasia. In this geographical region similar trends have also been established for non-passerine species, both nidicolous and nidifugous, such as grebes, herons, storks, raptors, gallinaceous birds, rails, some waders, terns, owls, kingfishers, woodpeckers and hoopoes (RENSCH 1938; LACK 1947-48, 1954). The nidifugous Quail, for instance, has 6-7 eggs in equatorial Africa, 7-9 in the Canary Islands, 7-12 in England, and 8-15 in Denmark (LACK 1947-48; WESTERSKOV 1956). Another nidifugous species, the Rock Ptarmigan, lays 6.6 eggs on the average in Scotland, 8.6 in Finland, 10.0 in Iceland, and 9-11 in Greenland (WESTERSKOV 1956). The Moorhen, also nidifugous, but feeding its fledged young, has 2-4 eggs in equatorial Africa, 6-9 in India, and 7-10 in temperate Europe (LACK 1947-48).

LACK (1968) compared the average clutch-size of non-passerine nidicolous land birds in tropical Africa with that of the central European species of the same subfamily. All of the 12 subfamilies studied showed the same trend. On the average, the European species of hawks, owls, bee-eaters and woodpeckers have a clutch about twice as large as the African representatives. In several of the other subfamilies, buzzards, kites, swifts, kingfishers, rollers and hoopoes, the difference is smaller, and it is negligible in the pigeons and nightjars, most species of which have two eggs throughout, except some of the equatorial ones which lay only one egg.

Among the nidifugous species which do not feed their young, some of the limicoline birds in central Europe as compared with tropical Africa have clutches about half as large again. For instance, the northern plovers have four eggs, whereas the African species lay only two or three. Also, the European species of the snipe genus *Gallinago* have clutches of four, but the only tropical species lays 2-3 eggs. In other families the trend is absent, as in the stone-curlews.

LACK (1968) also studied the variation of clutch-size with latitude in waterfowl. The general trend present in swans, geese and ducks, the diving ducks partly excepted, proved to be exceptional in that clutch-size tended to be larger in the species which breed at middle than at high or low latitudes. In some of the diving ducks the clutch tended to increase with latitude more regularly, in agreement with the data of CODY (1966) for the stiff-tailed ducks (Fig. 10C).

3.5.2. THE SOUTH-NORTH TREND IN THE NEW WORLD

The tendency of clutch-size to increase from the tropics to the poles is also present in the New World. This has been established by BREWER (1963) for the Black-capped and Carolina Chickadees, by JOHNSTON (1964) for the Song Sparrow and by WESTERSKOV (1956) for the Pheasant in western North America. Further, comparisons among members of one family revealed the trend to be present in the Troglodytidae, Tyrannidae, Icteridae, Traupidae, and Parulidae. The North American species of these families proved to have a larger average clutch than the Central American representatives (CODY 1966; Fig. 10B). Again, the tropical and subtropical Sooty and Bridled Terns and the Noddy have clutches of one, but the northern species, such as the Arctic and Common Terns, have three eggs (AVERILL 1933). Finally, the clutch of the Eider Duck seems to increase slightly towards the north along the east coast of North America (PAYNTER 1951).

3.5.3. THE NORTH-SOUTH TREND ON THE SOUTHERN HEMISPHERE

On the southern hemisphere an increase of clutch-size away from the equator has been found in Africa and South America. Of 141 species common to equatorial and southern Africa, 38 per cent has a larger clutch and only 3 per cent a smaller one in south than central Africa, though the average difference is only small, less than half an egg (MOREAU 1944a). Similarly, of 59 species occurring in the equatorial and southern states of South America, 63 per cent had a larger clutch, and only 14 per cent a smaller one in the southern states (SNETHLAGE 1928).

3.5.4. THE WEST-EAST TREND IN EUROPE AND NORTH AMERICA

Besides the South-North trend, in Europe a West-East trend has been established. Thus, at about the same latitude the clutch of the Robin has 5.1, 5.7 and 6.0 eggs in England, The Netherlands and Poland, respectively (LACK 1945). In early spring the mean clutch of the Starling in England is 4.9 eggs, but in The Netherlands it is 5.2 in early layings (LACK 1948b). Similar trends have been found in the Sky-lark (DELIUS 1965), the Wren (ARMSTRONG 1955), Great Tit (LACK 1950), Yellowhammer (PARKHURST & LACK 1946), and Goldfinch (FRITH 1957). Comparisons of species within the same subfamily have been made by LACK (1968). In 10 out of 13 subfamilies studied, the average clutch-size of the species breeding in England was smaller than that of the central

European species by an average of 0.3 egg. In the shrikes, finches and starlings the clutches were the same in both regions.

As to the European West-East trend in non-passerine species, this seems to be present in raptors, gallinaceous birds and owls (LACK 1947-48, 1954), and in the Swift, which has an average clutch of 2.4 eggs in central England, and 2.7 in Switzerland (LACK & LACK 1951). This trend is presumably absent in ducks, pigeons, stone-curlews and other limicoline birds.

Like in Europe, the West-East trend is also present in North America. It has been established in the Long-billed Marsh Wren (VERNER 1965), in the Song Sparrow (JOHNSTON 1954), the House Finch (WAGNER 1957), and the Pheasant (WESTERSKOV 1956).

3.5.5. THE SIZE OF THE CLUTCH ON ISOLATED ISLANDS

There is a tendency for the average clutch to be smaller in the species or subspecies breeding on isolated islands than in related forms on the mainland. Thus, LACK (1954) has indicated that the limicoline birds breeding in the Falkland Islands, namely two species of plovers, two of oystercatchers, and one species of snipe, have clutches of 1 or 2 eggs smaller than their relatives breeding elsewhere on a continent. In his recent book LACK (1968) has shown that several species of ducks breeding on remote islands have clutches of 1.5 to 6 eggs smaller than their relatives breeding on the mainland. CODY (1966) has given a number of examples of passerine birds having smaller clutches on remote oceanic islands off the coast of New-Zealand, and on isolated islands in the Caribbean Sea, than on the nearest mainland.

3.5.6. DIFFERENCES IN CLUTCH-SIZE BETWEEN FOREST AND SAVANNA

MOREAU (1944a) has shown that in tropical Africa the birds of evergreen forest have slightly smaller clutches than their relatives in savanna. This was later confirmed by LACK & MOREAU (1965), who compared the clutches of a number of Passerines breeding in forest with those of related species within the same family breeding in savanna. LACK (1968) has extended this comparison to nine subfamilies, in seven of which the average clutch was between 0.3 and 0.7 egg smaller in species of evergreen forest than in those breeding outside it. In the flycatchers the difference was 0.2 egg only, and in the sunbirds, the only exception, the species of arid areas had an average clutch 0.2 egg smaller than those of forest.

In non-passerine species the same trend can be found. In tropical Africa there is one nightjar and one owl with clutches of one egg, and both breed in evergreen forest.

A similar trend has been found in tropical American birds, such as the American flycatchers and finches (LACK 1968).

3.5.7. THE SIGNIFICANCE OF REGIONAL DIFFERENCES

Summing up the previous subsections, it can be stated that the tendency for clutch-size to increase from the tropics outwards to the poles is unmistakable, though there are several exceptions especially on the southern hemisphere. The significance of the phenomenon has been discussed by many authors, and nearly all agree that it needs an ultimate explanation. Only VON HAARTMAN (1954) considers the possibility that the regional differences within Europe, such as occur between England and Scandinavia, are modifications of the same genotype, because the ranges of local modificatory variations in different regions widely overlap. In my opinion, this cannot be a sound argument against the existence of hereditary regional differences.

Two main hypotheses have been put forward to explain the trend. The first one, originally formulated by STRESEMANN (1927-34), and afterwards adopted by RENSCH (1938), MOREAU (1944a), and KIPP (1948), states that the reproductive rate, and hence clutch-size, has been adapted to the higher mortality rates in temperate and arctic regions than the tropics. The higher death rate outside the tropics is attributed to unfavourable weather conditions in winter in non-migratory species, and to the high risks en route in migrants (STRESEMANN *l.c.*). It is remarkable that KIPP (1948), though supporting the same hypothesis, concludes that migrants run a considerably lower risk than non-migratory relatives, and therefore have a smaller clutch.

The main difficulty of this theory lies in the question of why genotypes, arising by mutation and having a still higher reproductive rate than that necessary to counterbalance the mortality rate, do not spread through the population. To exclude such a spread of more prolific genotypes, WYNNE-EDWARDS (1955, 1962) has introduced the concept of group-selection, but as demonstrated by SMITH (1964) this type of selection requires such an extremely exceptional pattern of distribution and isolation of groups of animals that it can hardly be accepted as a general and operational mechanism (see also p. 97).

The other hypothesis, originally put forward by HESSE (1923), states that in any one geographical region it is the clutch-size that maximizes the reproductive rate under the given food conditions which has been evolved. In nidicolous birds the limits are set by the maximum amount of food the parents are able to collect for the young, and in nidifugous species by the amount of food available to the laying hen. The balance with mortality should be due to the density dependence of the death rate (LACK 1954, 1966).

On this hypothesis, which was also adopted by AVERILL (1933) and GROEBBELS (1937), the increasing trend of clutch-size away from the equator should be due to the increasing daylength, enabling the birds to forage over a longer time each day. Then, nidicolous birds will be able to feed more young, and nidifugous species to form more reserves for egg production, at least when they do so after the spring equinox.

It is far from simple to test this hypothesis. The most straight-forward method seems to be the study of the change of clutch-size when birds, after importation, colonize a new geographic region at another latitude. The very few examples of this have been studied very incompletely, and have revealed the final result of the change only. FRITH (1957) has reported that English Goldfinches have been introduced to Australia in 1860, at a distance from the equator comparable with north Africa. In England the average clutch is 5 eggs, and in Australia it was only 3.7 eggs during the nineteenfifties, that is much the same as in north Africa where the clutch has 4 eggs. Again, WESTERSKOV (1956) has shown that the clutch of the Pheasant in New Zealand after importation from England has decreased from 11.5 to 9.0 eggs. Although these changes support the hypothesis, it should be stressed that nothing is known about the way in which these changes came into being, and therefore the evidence is only suggestive.

Other successful colonizations refer to introductions to regions at the same latitude; these will be discussed later.

The hypothesis can also be tested by comparing the increase of daylength with the increase of clutch-size. Daylength increases from 12 to 18 hours from the tropics to temperate regions, and from 18 to 24 hours from temperate to arctic regions. Nevertheless, the average clutch shows a much greater increase from the tropics to temperate regions than from temperate regions to the arctic. LACK (1954) has suggested that the parent birds must spend some time in rest and sleep, for which they use the night in the tropics, but necessarily part of the long day in the arctic. Therefore, an increase in daylength from 12 to 18 hours may be more effective than an increase from 18 to 24 hours.

In temperate Europe daylength during the breeding season is about one-and-a-half times as long as in the tropics, but in Passerines and related orders of nidicolous birds the clutch is 2-2½ times as large. Therefore, VON HAARTMAN (1954) is of the opinion that the trend cannot be explained by the increase of daylength only, and he suggests that there is an additional effect of an unknown factor. However, HESSE (1923) has suggested that from the twelve hours of daylight in the tropics only 8-9 can be used for foraging owing to extremely high temperatures in the middle of the day. If this view is correct, clutch-size can be expected to increase about twofold from the tropics to central Europe. Where even this is probably insufficient to explain the increase of clutch-size in some species, HESSE (1923) has suggested that, in addition, the amount of food present during the breeding time may be higher in temperate than tropical regions.

LACK & MOREAU (1965), being aware of the discrepancy between the increase of daylength and clutch-size, have considered another explanation, originally formulated by ASHMOLE in his D. phil. thesis.ASHMOLE's view has briefly been formulated by LACK (1968) as follows:

> "In explanation, he (ASHMOLE) suggested that bird numbers in both regions may be held down by food shortage, but in different ways. In north temperate regions, birds are subject to a severe seasonal food shortage, usually near the end of the winter, so that their numbers are greatly reduced before the breeding season: then, with a flush of insects in spring, breeding birds are sparse in relation to the available food, so that each pair can feed a large family and has therefore evolved a large clutch. In the tropics, on the other hand, the seasonal changes in the environment, and hence in the supply of food, are much less marked, so that there may be no period of dearth, and hence no marked periodic reduction in the numbers of birds, and also no marked flush in insects and other food. Under such conditions, numbers may remain throughout the year close to the limit set by food, it will be difficult at all seasons to find the extra food needed to raise young, and at most only a small family can be raised, hence such species have evolved small clutches".

In my opinion, this question has two sides. Firstly, if the spring flush of food in temperate regions greatly exceeds the more constant food level of the tropics, then the discrepancy between the increases of daylength and clutch-size can be explained by the difference in the food supply, like HESSE (*l.c.*) has suggested. In this case the reduction in the numbers of the birds in winter does not need to be considered.

Secondly, if the spring flush of food does not exceed the tropical level, the birds in temperate regions can only be supposed to lay large clutches because of their low spring numbers, i.e. the amount of food they are able to collect for their young must be density-dependent. As yet, this has only been found in the Great Tit, where the number of young flying per pair decreases with an increase of breeding pairs (LACK 1966). Moreover, several species of tits lay smaller clutches at high than low density, and this response to density might be an adaptation to a lower average availability of food at the higher densities (p. 104). More evidence on differences between the food supply is needed to test the interesting supposition of ASHMOLE.

Another approach to the problem of the ultimate effect of daylength on clutch-size is the study of the exceptions to the rule. The Raven and the Crossbill, for instance, have larger clutches in south than north Europe. These species have been mentioned by LACK (1947-48) as the exceptions that prove the rule, since they lay their eggs before the spring equinox, i.e. when daylength in the south of Europe is longer than in the north. VON HAARTMAN (1954) has seriously doubted the validity of this argument, because—though the Crossbill indeed lays its eggs before the equinox—it feeds its young after it.

There is one other songbird which does not comply with the rule, the Pied Flycatcher. This species has been studied in widely separated populations all over Europe. The data were considered by CURIO (1959-60) and LÖHRL (1965), who inferred that neither the South-North nor the West-East trend was present in this species. The only significant deviation they established was the markedly large clutch in the population studied in England by CAMPBELL (1950, 1955). More recently, BERNDT & WINKEL (1967) reached the conclusion that, when the abnormal large size of the clutch in England is ignored, both a South-North and a West-East trend can be recognized on the European continent. This view has been criticized by VON HAARTMAN (1967b), who reconsidered all available data from European populations summarized in Figure 11. This figure indeed shows the total absence of any trend.

It is recalled that this Flycatcher is an exception in another respect as well: it is one of the very few, if not the only passerine species not supporting LACK's hypothesis on the evolution of clutch-size in nidicolous birds. In this connection it is worth quoting the work of CURIO (1959), who compared the feeding rate of birds of a Berlin population with that of Finnish birds measured by VON HAARTMAN (1954), and he found it to be higher in the former. The effect of the higher feeding rate was, however, compensated for by a shorter daylength, so that the total amount of food brought to a nestling per day turned out to be the same in both areas. Moreover, also the clutch-size proved to be the same in both populations, and therefore, CURIO concluded that the Pied Flycatcher in Finland apparently has not yet adapted to the northern conditions. However, the question may be raised as to whether it did adapt to the more southern European conditions, and if not, it may be expected that this species does not support LACK's hypothesis.

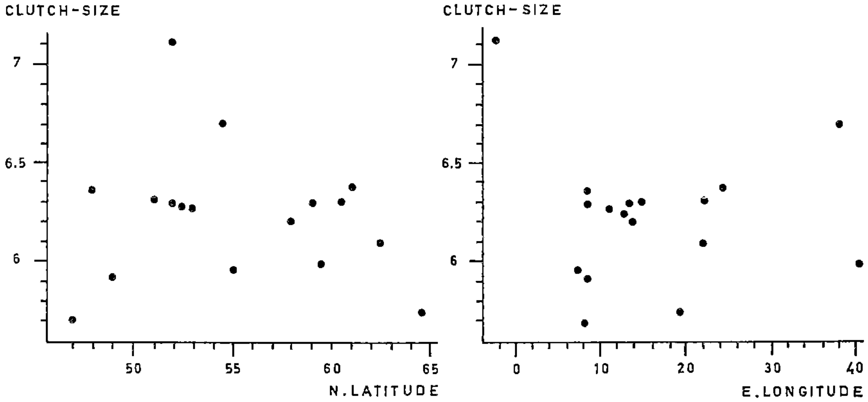

FIGURE 11. Mean clutch-size of the Pied Flycatcher in populations spread over Europe, showing the lack of a trend with latitude and longitude. After VON HAARTMAN (1967b).

Other exceptions to the rule are pigeons and nightjars. LACK (1947-48) has suggested that the constant clutch of two eggs in pigeons may be related to the feeding of the young with a product of the crop-gland. Nightjars are hunting during twilight, and therefore will not be influenced by daylength. The occurrence of a trend in owls, which are hunting during the night, has been related to the greater abundance of the staple food, voles, in temperate than tropical regions (LACK 1968).

So much for the exceptions in landbirds. Among seabirds the trend is absent in the order of the tube-nosed swimmers. All the species of this group lay a single egg, notwithstanding their diversity of structure and their wide distribution over the oceans (LACK 1967a, 1968). In the tropics daylength is shorter, and additionally tropical seas have a poorer food supply than temperate and arctic oceans. Therefore, tropical species could be expected to have smaller clutches, but this is not so. However, their chicks are characterized in having a slow growth rate as compared with non-tropical species. Therefore, it is most likely that in those species which live under less favourable conditions for feeding young, natural selection has favoured the evolution of a slower growth, enabling the parents to raise at least a single chick (LACK 1967a, 1968).

In another group of seabirds, the gannets and boobies, the trend of clutch-size with latitude is reversed, and this can also be related to the above principle. The species breeding at higher latitudes, both south and north, have clutches of 1 egg, whereas the tropical boobies have 2 to 3 eggs in the clutch. In the latter the growth rate of the chicks is comparatively very slow, enabling the parents to raise two young, even under the proportionately unfavourable tropical conditions. (The third chick normally dies of starvation.) Far away from the equator such a slow growth rate could not evolve because of the short duration of the period favourable for breeding (NELSON 1966; LACK 1967a, 1968).

The West-East trend in Europe is presumably related to regional differences in the food supply, which is probably higher in the warmer and dryer climate of central Europe than in the oceanic climate of western Europe. It is known that the fauna of central Europe is composed of more species, but very little is known about differences in the average abundance of animals in comparable habitats. Air-borne insects are probably more numerous in the fine and warm weather of central Europe than in the wet and cold weather of Scandinavia and England, and this is probably why the clutch of the Swift in Switzerland is larger than in north-west Europe (LACK & LACK 1951).

There are some examples of changes in clutch-size after successful colonization in another geographical region at the same latitude. The Little Owl, for instance, has been introduced to England from the European continent at the turn of the previous century. Shortly after settling, the clutch consisted of 4 to 6, rarely 7 eggs like on the continent, but round 1947 it had decreased to 3-5 eggs (LACK 1947-48; WESTERSKOV 1956). Again, the Capercaillie was reintroduced into Scotland from south Sweden in 1837-38, and this was also attended by a gradual decrease of the clutch during the following years (WESTERSKOV 1956). The Starling and the House Sparrow have been introduced to America from England, and both species seem now to have smaller clutches there than in the British Isles (MOREAU 1944b; SUMMERS-SMITH 1963). However, introductions to other continents at the same latitude, cannot contribute to the understanding of trends in clutch-size within the continents.

The view advanced by ASHMOLE to explain the variations of clutch-size with latitude has also been applied to the differences between forest and savanna in the tropics (LACK & MOREAU 1965; LACK 1968). Evergreen forests are stable throughout the year, but in the savanna long periods of drought alternate with restricted rainy seasons, in which there is a flush of food, and during which the birds breed. The rainy season should start with relatively low numbers of breeding birds, and it is supposed that they therefore would be able to raise a large family, and have evolved a large clutch.

Finally, CODY (1966) has applied the same principle to the differences in clutch-size between species of remote islands and their relatives on the mainland. The smaller clutches in the former should have been evolved in relation to the more stable food supply on the islands owing to a greater climatic stability.

In conclusion, it can be stated that one has tried to explain the regional variations of clutch-size by establishing general trends derived from comparisons of related species or subspecies living in different regions. There is, however, a great need to complete this circumstantial evidence with direct measurements of regional differences in food supply, the amount of food brought to the young, and the growth rate of the young. The significance of the last factor will be evident. DAVIES (1958) has shown that the Meadow Pipit has a larger clutch in Swedish Lapland than in England, whereas the clutch-size of the Bluethroat is apparently the same in Lapland and more southern parts of its range. However, in the former species the length of the nestling period is the same for both localities, but in the latter this period is shorter in Lapland. Clearly, in these species natural selection has directed evolution along two different ways.

3.6. PREDATION AS A FACTOR IN THE EVOLUTION OF CLUTCH-SIZE

Several species of birds do not incubate before the last egg has been laid, and consequently, the larger the clutch, the longer the unguarded eggs wil be exposed to predation. It has been discussed by LACK (1947, 1947-48) that this principle might contribute to an ultimate limitation of the size of the clutch. The Partridge, for instance, lays one egg daily, and if the chance of a nest being found by predators is greater than one in sixteen per day, genotypes laying fifteen eggs will, on the average, produce more offspring than those laying sixteen. If so, more than 6 per cent of the nests should be found and destroyed by predators daily, and LACK (1947) considers this to be too high a value. Moreover, the clutch of the Partridge is greater in Finland and Germany than in England, but the density of predators is presumably higher on the continent than in England.

To be effective as an ultimate factor, predation pressure has to be even higher in species with a clutch smaller than that of the Partridge. If, for instance, the clutch of the Common Eider would be limited to five eggs by predation pressure, one in six, or 17 per cent of the nests should be destroyed by predators daily during the laying period. This is a very unlikely high proportion, even among the Eiders on Kent Island, where 70 per cent of the nests were found by predators prior to hatching (PAYNTER 1951). Therefore, it can be concluded that clutch-size is unlikely to have evolved in this way, because the rate of predation on birds' nests prior to incubation should be improbably high, even for the larger clutches

Another way in which predation may have played a part in the evolution of clutch-size in nidicolous birds has been outlined by SKUTCH (1949). He has pointed out that tropical birds generally have a considerably smaller clutch than their relatives breeding in temperate regions, the commonest clutch being two eggs. SKUTCH further argued that in the tropics the parents do not forage at their maximum capacity. His argument is based on the observation that the feeding rate is readily adapted to the needs of the brood, when the number of nestlings is experimentally increased from 2 to 3 young. Moreover, tropical polygynous species have the same clutch-size as monogamous ones, in which the young are fed by both parents. Finally, SKUTCH calculated that in Costa Rica, where he made his observations, the needs of two nestlings of a song bird can easily be covered within twelve and a half hours of daylight, the average length of a day. However, this assertion is based on the assumption that large growing nestlings need the same daily quantity of food as active parents, but LACK (1949b) has pointed out that this is most probably an underestimation of the needs of the young.

On the above grounds, SKUTCH is of the opinion that clutch-size in tropical birds has not been evolved in relation to the amount of food the parents are able to provide for the young, but in relation to the intensity of nest-predation. If there were three young in the nest, the parents would have to visit the nest more frequently, and this would attract more often the attention of the predators, with an attending higher risk of nest-predation. If this would offset the advantage of one additional nestling, natural selection would favour a clutch of two instead of three eggs.

More than ten years later, SNOW (1962a) has put forward the same theory concerning the evolution of clutch-size in the Black-and-White Manakin on Trinidad. He argues that, since the male of this promiscuous species can find all its food in less than one tenth of a day, the female will be quite capable to find more food than needed for herself and the normal number of two young, which are fed with the same food. Therefore, the number of nestlings is unlikely to be limited by the feeding rate of the female parent. On the other hand, nest-predation in this species is extremely high (81 per cent of the nests were destroyed before fledging, mainly by snakes), and hence, a higher feeding rate might reveal so many nests to predators that the advantage of one additional nestling is offset.

If clutch-size in the tropics has been evolved under the influence of predation pressure, the rate of predation on nests should be considerably higher in the tropics than in temperate and arctic regions, which in general seems to be true (LACK, 1966). It is, however, questionable whether the predators find the nests by watching the parent birds. It has been pointed out by WAGNER (1957) that most of the nest-predation in the tropics is due to snakes, which are guided by olfactory rather than visual stimuli. This question has been discussed by LACK (1966) with reference to the Manakin referred to above. From SNOW's data it appears that, though the female leaves the nest once an hour during incubation, and visits the nest two to four times an hour during the nestling period, the chances of the nest being destroyed by predators are about equal during both periods.

The same was found in the Long-tailed Tit, where at least as many nests were destroyed by predators during laying and incubation as in the period when the young were fed and nest visits were much more frequent (LACK & LACK 1958).

Also PAYNTER (1954) is in doubt as to whether "more frequent visits by the parents would create a threshold so distinct that one or two extra nestlings would make the nest very much more conspicuous".

Hence, the available data do not suggest that predators find the nests by watching the parent birds, but it is possible that larger broods run a higher risk to be found because they are noisier. Thus, it has been shown by PERRINS (1965) that in the Great Tit large broods are taken more frequently by predators because they are calling more, and NEWTON (1964) has suggested the same for the Chaffinch. However, both authors report that the larger broods are noisier especially because they are hungrier, and this suggests that the more intense predation on the larger broods may be an ultimate factor additional to the amount of food the parents are able to provide for the young. In temperate and arctic regions the latter factor may be of primary importance, but in the tropics possibly the former. This should be studied experimentally in some suitable species by making up a large number of broods of above natural size, in which both the growth rate of the young and their mortality (and its causes) should be measured and compared with a large number of control broods of natural size, which are raised simultaneously with those manipulated.

All this refers to nidicolous birds. However, nidifugous birds in the tropics too have smaller clutches than their relatives in temperate and arctic regions, and an effect of the frequency of nest visits can be excluded in these birds. However, the risk of predation might be related to the size of the brood, because large broods may be more conspicuous than small ones, or because the effectiveness of the parental defence may be dependent on brood-size (PAYNTER 1951). This is probably of little significance in some species, because it has been observed in Pheasants (WAGNER *et al.* 1965), and ducks (PAYNTER 1951) that broods mingle after fledging, though this mingling may have survival value because the combined defending efforts of the parents may be more effective than those of the single female.

If later work would reveal that all these suppositions hold good, even then it is unlikely that clutch-size in nidifugous birds has been evolved in relation to predation pressure. For this it would be necessary that broods having an initial large size produce less mature offspring than those of medium size as a result of predation. This condition can be fulfilled in nidicolous birds, because once the nest has been found by predators it is normally totally destroyed. In nidifugous species, on the other hand, predation will generally reduce a large brood to one of medium size, but this will not occur in all of the larger broods, so that on the average they will produce more, not the same, number of mature offspring, but this should be investigated.

3.7. THE SIGNIFICANCE OF HYPERTHERMIA IN LARGE BROODS

It has been suggested by CAVÉ (1968) that clutch-size in nidicolous birds may have been evolved in relation to the regulation of body temperature of the nestlings. He refers to work of ROYAMA (1966) carried out on the Great Tit in Japan, showing that food consumption per nestling is about inversely proportional to the size of the brood, up to broods of 8 young. ROYAMA attributed this to a smaller heat loss per nestling in the larger broods, caused by the decreasing surface-volume ratio with increasing brood-size (cf. p. 46).

CAVÉ also refers to unpublished work of MERTENS (published 1969), who studied the heat production and the weight loss of nestling Great

Tits during the night at 12 °C and 18 °C, in relation to the size of the brood. MERTENS found that at 12 °C the heat production per nestling per hour decreased with an increasing brood-size over the range of 2 to 12 nestlings, and he could confirm ROYAMA's assumption that this energy saving was due to the decreasing surface-volume ratio. At 18 °C the heat production per nestling was about constant over the range of 3 to 7 nestlings, but slightly increased in larger broods.

The water loss per hour increased linearly with the weight of the brood at both temperatures, but at 18 °C water loss increased more sharply above a total nestling weight of 100 g, i.e. a brood-size of about six or seven nestlings.

MERTENS concluded from these findings that at 12 °C broods of 2 to 12 nestlings are able to maintain homoiothermia. At 18 °C this only holds for broods of up to 7 young, but when more nestlings are present they probably suffer from a slight hyperthermia, which they try to reduce by increasing their water evaporation, which slightly increases their metabolism and heat production.

Based on these observations, CAVÉ has pointed out "that only a slight increase of the air temperature, or a somewhat larger brood-size is needed to throw the situation into the fatal vicious circle of an increased metabolism and a consequently higher body temperature". On these grounds, he has suggested that brood-size in some species might be limited by hyperthermia, thus being the ultimate factor in the determination of clutch-size. So far, this hypothesis has not been tested in the field, but it seems worth while doing.

3.8. THE EVOLUTION OF LOW REPRODUCTIVE RATES BY GROUP-SELECTION

The theories on the ultimate determination of clutch-size discussed so far postulate that natural selection has favoured the genotype producing most surviving offspring, i.e. that genotype which has the highest reproductive rate and the lowest mortality rate. As a result, this genotype has spread through the population, while the others consequently have been eliminated. This implies that natural selection is continually favouring individuals with the highest possible recruitment. However, since bird populations in general do not steadily increase, the reproductive and mortality rates have, in the average, to be in equilibrium, and this can logically only be effectuated through the density-dependency of either or both of these rates, apparently in most species the mortality rate (LACK 1954, 1966).

In his book on animal dispersion, WYNNE-EDWARDS (1962) has discussed the existence of such density-governed reaction and the resulting balanced system. He argues that the regulation is due to interactions between the members of the population, which arise from their social organization. The relation with density is achieved by communal displays, such as for instance the synchronized vocal displays of territorial males, and the intensity of the resulting interactions determines the size of the reproduction, migration and mortality rates. At high intensity the reproductive rate can be reduced by holding down the number of ova fertilized per female, or restricting the number of females breeding and the frequency of successive broods. On the other side of the balance, the death rate can be influenced by density-induced variation of, what is named, social mortality, such as stress disease, cannibalism or infanticide.

These suggested density-governed processes differ markedly from those which generally are considered of paramount importance by other ecologists, such as competition for food, or predator-prey interactions. This is directly related to WYNNE-EDWARDS's view that the density of populations should be regulated according to the optimum density principle. On this view, which is based on the catastrophic effects of overexploitation of fish populations, density should be limited while food is still plentiful, so that "at all times the members are able to obtain a sufficient diet and still preserve an essential safety margin for the future" (WYNNE-EDWARDS 1966). Regulation of numbers at this optimum level would be of an advantage for the population, because overexploitation at very high densities would result in a chronic food shortage, and this could only result in lasting detriment and the risk that the food might be completely exhausted.

Population homeostasis thus outlined involves complex social adaptations, in which the interests of the individual are subordinated to those of the community (WYNNE-EDWARDS 1962). Such a system cannot evolve through natural selection of the most prolific genotype, because by this means those individuals would be favoured, which leave more offspring than others, and this would inevitably lead to surpassing the optimum level of density. Therefore, WYNNE-EDWARDS has stated that the density-governed social adaptations have been evolved by group-selection, a type of selection concerned with the viability and survival of the population as a whole. He has not, however, provided a model or mechanism by means of which the operation of group-selection can be understood. This problem has been considered by SMITH (1964), who has stated that a character, which is individually disadvantageous but increases the fitness of the group, can only spread to all members by genetic drift. For this to occur, the population should be divided into a large number of small, local groups, between which there is a neglectable amount of gene flow. This situation seems very rarely to be realized, and even then several problems arise which make the operation of intergroup-selection appear extremely unlikely.

Notwithstanding the improbability of group-selection, we will continue WYNNE-EDWARDS's argument further to appreciate its implications for the evolution of clutch-size in birds. At the optimum density level, the balance between reproduction and immigration on the one side, and mortality and emigration on the other can in principle be realized at any one value of the components. If, for instance, a great surplus is produced by reproduction, this can be levelled off by a high rate of social mortality. This would put the population recurrently under high social stress, which may be disadvantageous for the group. It is probably for this reason that WYNNE-EDWARDS has advocated the view that in several species low reproductive rates have been evolved to balance the uncontrollable mortality, i.e. the losses inflicted by agents independent of the intensity of the social interactions between the animals. Such independent losses should especially be low in long-lived species like sea-birds and large raptors, and these birds consequently have a low reproductive rate, including a low clutch-size (WYNNE-EDWARDS 1955).

Similar ideas have been presented by SKUTCH (1967) in his theory of adjusted reproduction, according to which the reproductive rate is determined by the average annual mortality: a species reproduces slowly, i.e. it has among other adjustments a small clutch-size, if it has low annual losses. This adjusted rate is named the optimum rate.

SKUTCH is of the opinion that in a population that is reproducing at a rate above the optimum, a mutation that reduces the number of eggs is likely to persist, and even to spread, because it increases the birds' adaptation to their environment. Thus the small clutch of some species of pigeons in the tropics, laying one instead of two eggs, would have been evolved, because the reduced fecundity has decreased the relatively high mortality necessarily occurring in species laying two eggs.

I agree with SKUTCH that it seems reasonable to assume that the species with only one egg in the clutch have been evolved from those with two eggs, which is the normal and most wide-spread clutch-size. However, in my opinion the genotypes laying one egg could only spread through the population, because in the tropical habitat they produced more, not less, mature offspring than the genotypes laying two eggs, unless the populations of these tropical pigeons are split up in small groups, and the character "one egg' happened to spread in all these groups by genetic drift, which seems to be unlikely.

The same view has been put forward by RENSCH (1938) and KIPP (1948) to explain regional differences in clutch-size: the northern breeding birds would have evolved a larger clutch to balance the higher mortality rates in the harsh regions as compared with the subtropics and tropics.

On the above grounds, WYNNE-EDWARDS has argued that it is unlikely that birds reproduce at their maximum capacity. In a postscript to PERRINS' 1964 paper, he has pointed out that it is therefore that both in the Red Grouse in Scotland and in the Swift in England the mean size of the clutch is smaller than the most productive one. This view has been criticized by LACK (1964a). With reference to the Red Grouse LACK has remarked that in this nidifugous species clutch-size has probably been evolved in relation to the amount of food available to the laying female, and if so, the most productive clutch-size may well be larger than the most frequent one.

As to the Swift in England, where the most productive clutch-size is 3, the hereditary tendency to lay 2 eggs may persist in the population, since in wet and cold years more young fledge from clutches of 2 than 3 eggs. WYNNE-EDWARDS, however, claims that such bad summers are in the minority and, where Swifts live 4 to 5 years on the average, on LACK's hypothesis those that consistently lay 3 eggs will, on balance, leave more offspring than those that lay 2. Moreover, he consideres the experiments of PERRINS (1964), in which artificial broods of 4 young proved to produce less than 2 fledglings, as inconclusive, since the parents have become physiologically conditioned to making a reproductive effort of a certain magnitude (WYNNE-EDWARDS 1964).

The evolution of low clutch-sizes in birds by group-selection has been dismissed by AMADON (1964), because of lack of a sound genetic basis. Nearly all of the species with a low clutch-size are characterized by having slowly growing young, and AMADON gives several arguments supporting the view that the parents are not able to raise more, or more rapidly growing young than they normally do, as a result of food shortage.

Many arguments against the view of WYNNE-EDWARDS have been given by LACK (1966), which were reviewed in the foregoing sections, and which need not be repeated here. His opinion can best be expressed in his own words:

> "I cannot conceive of any effective way in which group-selection could under normal conditions restrict the reproductive rate of an animal below that which natural selection would permit. Moreover, natural selection provides a satisfactory explanation of the known facts relating to clutch-size".

4. THE ADAPTIVE SIGNIFICANCE OF PHENOTYPIC VARIATIONS

It has been shown in Section 2 that the size of the clutch of an individual bird can be modified by internal and external factors. Such factors may have a direct effect on the physical condition of the female, which in its turn has an influence on the number of eggs laid. If so, the nature of the modification is non-adaptive. On the other hand, the response of the bird may have been fixed in its genetic make-up, having been favoured by natural selection, because it contributes to a larger number of surviving offspring being produced.

This interesting question will be considered for each of the modifying factors, which proved to have an effect on clutch-size.

4.1. THE SIGNIFICANCE OF AGE-SPECIFIC DIFFERENCES IN CLUTCH-SIZE

The most likely hypothesis on the evolution of clutch-size in nidicolous birds postulates that the number of eggs laid is related to the amount of food the parents are able to provide for the young (Section 3.3). On this hypothesis, the production of a smaller clutch by females breeding for the first time (Section 2.2; Table 3) may have adaptive significance, if these birds are less efficient in searching for food than older ones.

Some evidence for such an age-specific difference has been collected by SCHÜZ (1957) for the White Stork in Germany. Of 142 pairs breeding for the first time, 17 did so when aging 3 years, 57 when 4, and 68 when 5 years old. In these three categories the proportions of pairs raising at least one young were 53, 60 and 78 per cent, respectively. Moreover, the average numbers of young raised in the successful nests (at least one young fledged) were 1.8, 1.9 and 2.3, respectively. However, the numbers of eggs laid by females of the various age categories are not known, and therefore, the trend in the numbers of young raised may be merely a reflection of the original trend in clutch-size. This consideration may also throw some doubt on the relation between age and the proportion of successful nests given earlier, because young Storks may occupy nests without laying eggs. This argument against the existence of an age-specific difference in food-collecting ability seems only to be countered by the observation that it is especially the young males which throw chicks out of the nest (p. 42).

In the Kittiwake, where first breeders lay on the average about half an egg less than experienced breeders, the former are most probably less efficient in collecting food for the young than the latter. In simultaneously raised broods of 2 young, the weight of a chick increased with 16.7 g per day when fed by experienced parents, but only 14.8 g when raised by inexperienced parents (COULSON, quoted by LACK 1966).

SNOW (1958) has shown that in the Blackbird more efficient parents, usually old birds, can raise a larger brood than less efficient ones, because the former tend to look after the young better, and so lose fewer. This holds especially for yearling males after the young have fledged and the females are concerned with the preparations for the next brood. Thus, old males raised 70 per cent of the fledged young to an age of 15-20 days, whereas only 56 per cent of the young of yearling males reached that age.

In the Sky-lark in England 51 per cent of the eggs laid by old females produced young leaving the nest, and of the eggs laid by yearlings only 15 per cent produced fledglings. Nevertheless, DELIUS (1965) found no difference between the mean clutch-size of yearlings and older females.

Finally, a difference in the capacity for raising young between yearlings and older birds has been observed in the Great Tit by PERRINS (1965). Though the former lay about half an egg less than the latter, both the survival of nestlings and of fledglings is lower in the offspring of yearling parents than that of more experienced ones. Of the young of the former 13.4 per cent survived to an age of three months after fledging, whereas 16.8 per cent of the young of older parents reached that age.

Age-specific clutch-size differences have also been observed in nidifugous species (p. 11). If clutch-size in these birds had been evolved in relation to the amount of food available for the laying hen (Section 3.4), then the efficiency in searching for food might also be responsible for the smaller first layings in this group. But in this case a direct effect of the quantity of food consumed on the ripening of follicles is likely to be the causing agent, and if so, the phenomenon will have no adaptive significance.

4.2. THE ADAPTIVE SIGNIFICANCE OF THE RELATION BETWEEN CLUTCH-SIZE AND FOOD QUANTITY

Food may affect clutch-size proximately in either of two ways. Firstly, the food quantity available for the reproducing birds can have a direct influence on the physical condition of the female, so that the number of eggs produced is determined by the amount of material available for yolk and albumin deposition. This is called here the *direct effect* of food.

Secondly, food quantity does not influence the physical condition of the female, but affects the physiological mechanism controlling ovarian activity. In this case the response of the bird to food quantity will have adaptive significance and may, for instance, have been evolved in relation to the amount of food available for the young some time later. This is called here the *indirect effect* of food.

In both cases there will be a positive relation between food quantity and clutch-size, several examples of which have been given in Section 2.3.1. The discrimination between the two principles will be impossible in most of the field data available. The crucial point is that in the case of a direct influence of food indeterminate layers will not protract laying when eggs are removed from the nest, but in the case of an indirect influence they will. In determinate layers this test is futile, but in some cases other criteria may be helpful to discriminate.

As long ago as the twenties it was claimed that several phenomena concerning clutch-size could be explained by a direct effect of food quantity on the physical condition of the female. Thus, TOLLENAAR (1922) postulated that the clutch-size of tits was directly related to the amount of food the female was able to collect. HESSE (1923) stated that the small clutch in the tropics was related to the female's inability to build up large enough reserves under the short tropical day. Moreover, he ascribed the relation between vole plagues and clutch-size in owls to a direct effect of food on the female. Some years later HAUN (1931) attributed the small first laying of the Sky-lark to the fact that they cannot find enough food that early in spring.

More recently, WAGNER (1957, 1960) made a plea for such a direct effect of food. He is of the opinion that the size of the clutch is hereditary, and that the maximum number of eggs laid is proximately determined by the contact of the bird with the eggs in the nest. This maximum, however, should very rarely be reached in nature as a result of food shortage. However, not any of the arguments used to support his view is valid, and in fact they can also be used in favour of an indirect effect of food, such as the relation between vole plagues and clutch-size in owls and birds of prey (HESSE 1923; LACK 1947-48), the effect of drought on the delay of breeding and on clutch-size in African birds (HOESCH 1936) and the seasonal decline of clutch-size.

As indicated earlier (p. 34), a high density of voles at the start of laying may be followed by a high abundance of prey later in the season when the young are fed, and also drought in arid regions at the beginning of the breeding season may be indicative for a low prey abundance later on. Therefore, the response of the birds may well serve to adapt the size of the brood to the future food supply. Finally, the seasonal decline of clutch-size may have adaptive significance (p. 104).

The effect of cold weather on clutch-size in the Swift (p. 13) was initially interpreted by LACK (1956a, b) to be due to a direct effect of food shortage on the bird's physical condition: low temperature giving a heavy decrease of air-borne insects, with the result that the hen cannot find enough food to produce an egg. Later (1966: 6) he explained the smaller clutch as an indirect effect of food on the bird:

> "...when food is sparse in the laying period, there is some risk to the adult female in using its food reserves to form eggs. Under these conditions it may, on balance, be more advantageous for a bird to produce two eggs instead of three, even though this means that, on average, it will raise a slightly smaller brood than if it laid a clutch of three".

4.3. THE SIGNIFICANCE OF HABITAT- AND DENSITY-LINKED VARIATIONS

Habitat-linked differences of clutch-size have been found in the Great and Blue Tits, the Pied Flycatcher and the Blackbird (Section 2.3.2). These differences might have adaptive significance, if broods raised in the habitats with the larger mean clutch survive better than those of the same or smaller size raised in the other habitats.

The clutch-size of the Great Tit is largest in oak forest, and smallest in gardens. The proportion of young fledged of those hatched in first broods is over 95 per cent in the former, and 88 per cent in the latter habitat. In Scots pine in England the clutch-size is the same as in broad-leaved forests, but only 62 per cent of the hatched young fledge (LACK 1958). In Holland the mean clutch in Scots pine is 0.7 egg smaller than that of Great Tits breeding in oak, and like in England, the young raised in the former habitat survive less well than in the latter (KLUYVER 1963). In England Great Tits lay slightly smaller clutches in Corsican than in Scots pine, and in parallel, the young survive slightly worse in the former (LACK 1958; GIBB & BETTS 1963).

In the Blue Tit the mean size of the clutch is 11.5 in oak, 10.4 in Scots pine, 9.6 in gardens, and 9.0 in Corsican pine, and the proportions of young fledged amount to over 95, 71, 86 and 62 per cent, respectively (LACK 1958).

There is no evidence concerning the survival of the Pied Flycatcher in relation to habitat.

Blackbirds have larger clutches in broad-leaved forests than in gardens, yet the young survive better and leave the nest at higher weights in the former than in the latter (SNOW 1958).

These facts seem to indicate that tits and Blackbirds are able to vary the size of the clutch in accordance with those qualities of the habitat determining its favourableness for raising young, which in its turn is mainly dependent on the food supply (LACK 1955). The relation is, however, complicated by the fact that different habitats may differ considerably in population density. As shown in Section 2.3.3, the clutch-size of the Great Tit increases at the lower densities. On this ground, the relative large size of the clutch of the Great Tit in pine forest has been attributed to low population density. Also, the density of Blackbirds in broad-leaved forest studied by SNOW proved to be lower than in gardens (p. 16), which is surprising because these forests appeared to be more favourable than gardens for raising young.

As shown in Section 2.3.3, population density may affect clutch-size directly in some species, but as yet it is not known whether this phenomenon has adaptive significance. For this to be established, nestling survival in relation to clutch-size should be studied in one and the same habitat at very different densities, but to my knowledge this has never been accomplished.

4.4. THE EVOLUTION OF SEASONAL VARIATIONS OF CLUTCH-SIZE

It has been shown in Section 2.3.4 that the size of the clutch of many species varies with laying date. In most nidicolous birds clutch-size decreases right from the start of the breeding season, and this may have adaptive significance when conditions for rearing young deteriorate later in the season. There is some evidence from literature supporting this view.

In deciduous forest in England most *Great Tits* feed their young when caterpillars are most numerous (LACK 1955; PERRINS 1965). After the peak in the second half of May, the density of the caterpillars falls steeply, and in parallel, the young of late broods are mainly fed with adult insects and spiders (Gibb 1950). This food is probably more difficult to collect, or has a lower nutritive value, since late broods often starve (Gibb 1955), and their young have lower weights at fledging, though late broods are smaller than early ones (Gibb 1950; Lack, Gibb & Owen 1957; Perrins 1965). Again, in England the proportion of young flying from first broods was 94 per cent, and from second broods 37 per cent, notwithstanding their smaller size (Lack 1955).

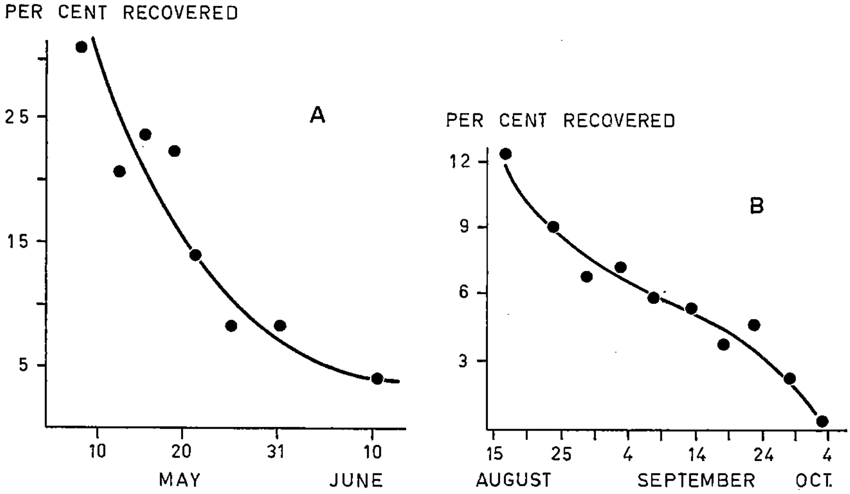

Figure 12. **A.** Post-fledging survival of young Great Tits in relation to date of hatching, expressed as the proportion of ringed young recovered when at least three months old. Data from Wytham, Oxford, 1963. After Perrins (1965). **B.** Survival of young Manx Shearwaters in relation to date of ringing, expressed as the proportion of young recovered after 31 December of first year. Data from Skokholm Island off South Wales; several years combined. After Perrins (1966).

After fledging the early hatched, heavy young survive better than late hatched, light young. As shown in Figure 12A, the proportions of ringed young, recaptured when at least three months old, fall markedly with a later date of hatching, and this is most probably due to a differential mortality during the first month after leaving the nest (Perrins 1965; Lack 1966).

In mixed and deciduous forests in Holland, the main nestling period of Great Tits also coincides with the peak abundance of food. However, in contrast to English tits, the proportions of young flying from the smaller second broods are equal to those from first broods, but Dutch birds agree with English tits in having a differential recovery rate after leaving the nest. Of young ringed before 16 June 7.4 per cent is subsequently recovered in the breeding area, whereas of those ringed after 15 June only 4.5 per cent return to their birth-place, but this difference has been attributed by KLUYVER (1951) to a higher emigration rate of late fledglings. This supposition was later confirmed for Belgian Great Tits by DHONDT and HUBLÉ (1968).

In the *Blue Tit* of mixed broad-leaved forest in England, 95 per cent of the young fledged from first broods, and only 75 per cent from second broods, though the latter were smaller than the former. In addition, a greater proportion of early fledged young reached an age of at least three months, as compared with late ones. In conifers second broods have a higher fledging rate than first ones, and in this habitat the seasonal decline of clutch-size is less pronounced than in deciduous forest (LACK 1955).

Similar observations have been made in the *Pied Flycatcher*. Thus in a German population, 62.9 per cent of the nestlings fledged from 540 early, large broods, and 54.5 per cent from 66 late, small broods (CREUTZ 1955). Similar trends were found by CAMPBELL (1955) in England, and by CURIO (1959-60) in central Germany. In addition, there is a differential mortality after fledging. Of Finnish Pied Flycatchers, fledged from nests started in the periods 14-25 May, 26 May-4 June, and 5-29 June, 2.8, 2.0 and 1.1 per cent, respectively, were recovered in the study area one year later. Hence, the post-fledging mortality rate of late-born young is apparently greater, though the size of the broods is smaller (VON HAARTMAN 1967a).

There are some observations on tits and flycatchers which seem to militate against an adaptive significance of the seasonal trend of clutch-size. In English pine forests, unlike broad-leaved, the supply of caterpillars does not culminate at the end of May, and in parallel the average clutch of the *Coal Tit* does not vary between 1 April and 10 May. After mid-May the average clutch is one egg smaller than in April, though there is a further increase in the supply of caterpillars up to mid-July (LACK 1966). The parent Coal Tits apparently are well able to exploit this stock of food, since the mean weight of nestlings of late broods is higher than that of early ones (GIBB and BETTS 1963). In the *Spotted Flycatcher* in the British Isles the proportions of young fledged from nests which raised at least one chick were 93, 93 and 96.5 per cent in the months May, June and July, respectively, whereas the clutch-size decreased over this period. These figures are based on data of nest-record cards from all over the country, and therefore this species should be studied in more detail within one population (SUMMERS-SMITH 1952).

The proportions of ringed young of Swiss *Starlings* recovered more than three months old are depending both on brood-size and fledging date. Of those ringed in May, 2.1, 2.1, and 1.7 per cent were recovered from broods of 4, 5 and 6 young, respectively. Of those ringed in June and July, the corresponding proportions were 2.2, 1.8 and 1.4 per cent, showing that the post-fledging chances of survival of the larger broods decrease (LACK 1948b).

The mean clutch-size of early layings of Scottish Starlings is 5.1, and the proportion of young fledged of those hatched amounts to 93 per cent, when total losses are excluded. Late layings have 4.6 eggs on the average, but nevertheless only 84 per cent of the chicks fledge, in spite of a longer day and a higher density of the main prey, leatherjackets (DUNNET 1955).

In the *Barn Swallow* in Poland, the young of the first broods fledge at a higher weight (18.9 g) than those of the second broods (14.2 g). Also, the proportion of young fledged is greater in the former than in the latter, notwithstanding the smaller size of late broods (KUZNIAK 1967).

Before finishing the discussion on Passerines, we have to deal with three species, the clutch-size of which shows an initial increase followed by a decrease still later in the season. In the *Blackbird* nesting in the Botanic Garden in Oxford, England, the mean size of the brood in March, April, May and June is 2.6, 3.0, 3.6 and 2.5 young, and their corresponding mean weights on the eighth day are 53, 59, 59 and 53 g. Moreover, for each clutch-size nestling mortality in June is higher than in earlier months (SNOW 1958).

In the *House* and the *Tree Sparrow* the size of the clutch culminates about three weeks before the summer solstice, with the result that the middle of the main nestling period coincides with the longest day, and family-size varies roughly in parallel with daylength (SEEL 1968).

As to the other orders of nidicolous birds, the data collected on *Swifts* suggest that it is harder to raise young successfully late than early in the season. In Switzerland 91 per cent of the young of this species fledged in broods of 2, when the clutch was started before 8 June, and 71 per cent when the clutch was started later. In England the corresponding figures were 80 and 75 per cent. The more critical comparison for broods of 3 could not be made, because late broods never have 3 young (WEITNAUER & LACK 1955).

Similarly, in the *Alpine Swift* in Switzerland, 1, 1.8 and 2.4 young fledged from broods of 1, 2 and 3, respectively, when the clutch was started in May. When the clutch was started later the mean numbers of young fledged per brood were 1, 1.6 and 1.9, respectively (LACK & ARN 1947).

In the *Oilbird* of Trinidad the breeding season starts in December and goes on well into August and even September. The size of the clutch gradually decreases over this period (Table 5). Most of the food of this fruit-eating bird is available in the months March to June, when most of the young are in the nest. After June the food supply gradually decreases parallel to the size of the clutch. Earlier nests are probably more successful than later ones, but this was not due to starvation (SNOW 1962b).

There is some evidence suggesting the existence of differential survival rates for early and late hatched gulls. Of the *Herring Gull* of eastern Canada 67 per cent of the early born chicks survived to their thirtieth day, but only 48.5 per cent of the late born ones reached that age. This difference was attributed by PAYNTER (1949) to a more intensive predation on chicks by other gulls. Of the *Glaucous-winged Gull* of western Canada 1.84 chicks, on the average, survived to fledging from clutches of 3, when these are laid before 3 June, and 1.73 young reached fledging age from clutches of 3 laid after 2 June. A corresponding difference was found for clutches of 2. The cause of the differential survival is unknown (VERMEER 1963). In contrast, in the Herring Gull on Skomer off Wales both hatching and fledging success increase later in the season (HARRIS 1969).

In the *Kestrel* in Holland the survival rate of nestlings in nests started before 1 May is slightly higher than that of chicks in nests started after 30 April. The proportions of young fledged of those hatched from broods of 4, 5 and 6 young are 89, 90 and 83 per cent, respectively, for broods of the first category, and 85, 85 and 75 per cent, respectively, for broods of the second group, the difference being only statistically significant for broods of 6 young. In addition, there is a differential mortality among young Kestrels after leaving the nest. Of 303 recoveries of young ringed before 1 July, 53 per cent were recovered in the first year after fledging, and 47 per cent in the second and third year. Of 118 recoveries of young ringed after 30 June, 65 per cent were recovered in the first year, and 35 per cent in the second and third year. The change of the ratio is statistically significant, showing that late hatched young have a higher death rate in their first year, and the dates of the recoveries strongly suggest that this is especially so between fledging and 1 September (CAVÉ 1968).

Detailed evidence for an effect of fledging date on subsequent survival has been collected for young *Manx Shearwaters* by PERRINS (1966) in a British colony. During the period 1947-1961 more than 17,000 young were ringed shortly before fledging between 17 August and 5 October. This period was subdivided in intervals of 5 days, and the number ringed and the proportion recovered after 31 December of the first year were determined for each interval. As shown in Figure 12B, the porportion recovered declines steadily with a proceeding date of fledging, showing that early fledged young survive better during late summer than late ones during autumn. Shearwaters always lay one egg, and do not produce repeat layings when the egg is lost. One would expect all females to lay as early as possible, but though the earliest fledged young, leaving the breeding grounds in August, have the highest chances of subsequent survival, only 20-30 per cent of the adults have full-grown chicks in August. In explanation, PERRINS has suggested that most females cannot find enough food in early summer so as to lay their eggs in the most favourable period.

So far reference has been made to birds feeding their young in the nest. There is one nidifugous species, the *Oystercatcher*, feeding its young until they are about ready to fly, in which breeding is progressively less successful later in the season. HARRIS (1967) has shown that on Skokholm off South Wales the proportion of chicks surviving to their thirtieth day of life is 60-70 per cent for early hatched young, but only 5-20 per cent for those hatching at the end of the breeding season, in spite of the smaller size of late broods (Fig. 13). Post-fledging survival was found to be the same for early and late breeders, which may be related to the feeding on the beds of mussels and cockles after leaving the island (HARRIS 1969).

The evidence from literature referred to so far shows that it is more difficult to raise young late than early in the season, and the seasonal decrease of the average clutch-size is presumably an adaptation to this situation. There is, however, very little evidence showing that the decrease is related to a deterioration of the food supply. The preferred food of Great and Blue Tits in broad-leaved forest declines sharply after the month of May, but in other species, like the Coal Tit, the Starling and the Kestrel, the food supply seems to increase from early spring up to the end of the breeding season, though the availability of the food might decrease.

CAVÉ (1968) has put forward the hypothesis that large broods may

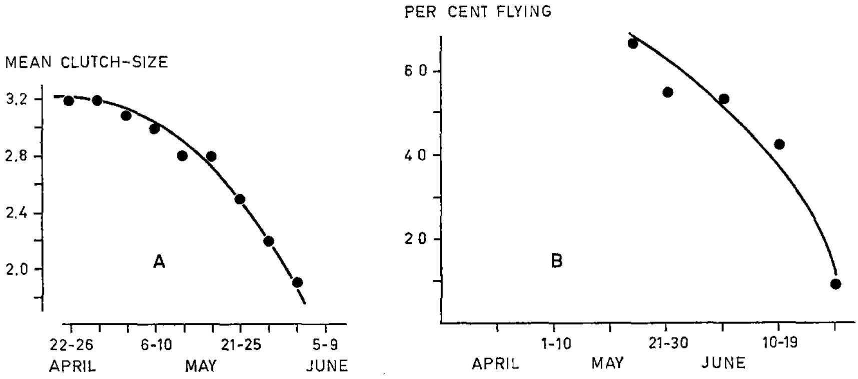

FIGURE 13. **A.** Decline of mean clutch-size in the Oystercatcher in relation to laying date of first egg. **B.** Survival of young Oystercatchers in relation to date of hatching, expressed as the proportion of young surviving to the thirtieth day after leaving nest, when they are about ready to fly. Data from Skokholm Island off South Wales; several years combined. After HARRIS (1967).

suffer more readily from hyperthermia late than early in the season due to rising spring temperatures, and if so this might also explain the lower weights and higher mortality rates of the young in the late and large broods (cf. p. 108). Though this hypothesis seems worth testing for hole-nesters and species with well isolating cup-shaped nests, it cannot hold for gulls, oystercatchers, and other nidifugous birds.

As to the last category of birds, in which seasonal declines of clutch-size have frequently been observed (Table 5), the mean size of the clutch cannot have been evolved in relation to a seasonal deterioration of the food conditions for the young, unless the chicks of one brood compete for food among each other, which is unknown. It has been suggested (p. 75) that the mean size of the clutch in nidifugous birds has been evolved in relation to the amount of food available to the laying hen, but this view is not supported by the occurrence of a seasonal decline of clutch-size, because the food supply for the parent birds is likely to increase rather than decrease over the first part of the breeding season.

To sum up, the adaptive significance of the seasonal decline of clutch-size is still very vague in many of the nidicolous and all of the nidifugous birds, and the question may be raised as to whether the downward trend of the clutch cannot be due to a proximate effect without having any ultimate adaptive significance. Later layings are often by birds which have already raised or attempted to raise a brood, and thus will have used a part of the energy required for producing eggs and rearing young. As a result, they should not only lay fewer eggs in the clutch later in the season, but in addition, these eggs may have a reduced quality giving rise to less vigorous chicks.

This hypothesis has been put forward by WAGNER *et al.* (1965) to explain the seasonal trend of clutch-size and the higher mortality rate of late hatched chicks in the Pheasant in Wisconsin. The decreasing survival of the chicks, also observed in Pheasant's chicks in Ontario by STOKES (1954), is unlikely to result from less favourable food conditions, since the relevant data suggest that there is more food later than early in the season, although nothing is known about its availability.

LACK (1966) has suggested the same hypothesis to explain the apparent discrepancy between the declining clutch-size of the Coal Tit after mid-May and the protracted increase of the caterpillar supply. The late breeding birds may have been in a weakened state by having already raised or attempted to raise a brood earlier in the season.

Finally, CAVÉ (1968) has suggested that some of the observations made on the breeding success of the Kestrel can be explained on this hypothesis. In this species the seasonal trend of clutch-size finds expression in a relatively large dispersion of starting dates of first layings. As already discussed (p. 14) late breeders have most probably been under less favourable conditions or have inferior abilities to find food, and CAVÉ suggests that it is therefore not unlikely that they have less energy available for egg production.

4.5. THE ADAPTIVE SIGNIFICANCE OF ANNUAL VARIATIONS

As discussed in Section 2.3.5, part of the annual variations of mean clutch-size is due to changes in the age composition of the population, to fluctuations of density and food supply, and to shifts of the mean laying date. Consequently, some aspects of the adaptive significance of such variations have already been discussed. There are, however, some topics which deserve special attention.

Firstly, it should be stated that some of the annual variations in relation to the food supply are evidently caused by a direct effect of food on the physical condition of the laying hen, such as those found in gallinaceous birds (p. 33). Consequently, these variations are unlikely to have adaptive significance.

Secondly, in some nidicolous species such as raptors feeding on voles, the amount of food in early spring may be indicative for its quantity later in the season when the young are fed. Then the response of the bird may well serve to adapt the size of the brood to the later food supply. Thus, the annual differences of clutch-size in the Nutcracker discussed earlier (p. 32) may result from a direct effect of food quantity on the female, but an indirect effect cannot be excluded. These birds store hazelnuts in autumn, and feed their young primarily with this stored food next spring. Consequently, varying the clutch-size according to the size and the number of the stores might have adaptive significance.

Similarly, MOREL *et al.* (1957) have shown that the Black-faced Weaverbirds in W. Africa lay smaller clutches when rains start late and are less abundant. This might be due to a direct effect on the laying female. However, it also appeared in such years that many of the parents cannot bring enough food to raise a third nestling, and therefore, the response of the bird might well be adaptive.

Finally, we have to consider some aspects of the annual variations of clutch-size in nidicolous birds, where the supply of food shortly before and during the laying period seems not to be related to its abundance later in the season. In some of these, like the Great Tit and the Pied Flycatcher, the annual variations of the mean clutch tend to fit in with the seasonal trend characteristic for the species, i.e. in late seasons the mean clutch tends to be smaller (p. 29, Fig. 5). Now in late seasons the peak abundance of food for young Great Tits is also late, but there is no evidence suggesting that the peak is on a lower level under such conditions (LACK 1966). CAVÉ (1968) has suggested that the response of the hen might be adaptive, when clutch-size has been evolved in relation to the increasing risk of hyperthermia due to rising spring temperatures.

As discussed on p. 30, the fit with the seasonal trend can only account for part of the annual variations of clutch-size; apart from this there is a rest-variation. It has been shown by LACK (1955) for the Great Tit, and by LACK, GIBB & OWEN (1957) for the Great and Blue Tits, in Marley wood, Oxford, that this variation is related to the density of caterpillars during the period of peak frass-fall. However, PERRINS (1965) has shown that, when the data on clutch-size are adjusted for date of laying and population density, the correlation with the amount of caterpillars is very low and insignificant.

In the Alpine Swift in Switzerland, in which the annual variations of clutch-size do not fit in with the seasonal trend, the proportion of pairs with 3 to 4 eggs is highly variable year by year (LACK & ARN 1947). This proportion proved to be positively correlated with the survival rate in broods of 3 young. These observations suggest that Swifts are able to vary the size of the clutch according to the food supply later available for the young, so that these annual variations are likely to be adaptive.

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SAMENVATTING

1. De legselgrootte is voor elke vogelsoort karakteristiek. Op de vraag hoe het aantal eieren dat een vogel legt tot stand komt, kunnen twee verschillende antwoorden worden gegeven. Het eerste antwoord heeft betrekking op de werking van het mechanisme dat de activiteit van de eierstok regelt. Het tweede antwoord betreft de wijze waarop in de loop van de evolutionistische wording van de soort onder invloed van milieufactoren het meest productieve legsel is uitgeselecteerd. Onder het meest productieve legsel wordt verstaan het legsel dat het grootste aantal geslachtsrijpe nakomelingen oplevert.

2.1. Wat het regel-mechanisme van de eierstok betreft, blijkt dat bij een grote groep van vogelsoorten het legsel niet door de aanwezigheid van eieren in het nest wordt beïnvloed (Tabel 1, Fig. 1). Bij de overige soorten gebeurt dat wel en wordt het aantal te leggen eieren door contact van de vogel met de eieren in het nest bepaald. Over de wijze waarop dit contact tot stand komt en het moment waarop dit gebeurt zijn een aantal proeven gedaan die kort worden beschreven (Tabel 2, Fig. 2).

2.2. Bij beide groepen van vogels staat het mechanisme dat de activiteit van de eierstok regelt onder invloed van in- en uitwendige factoren. Zo blijkt dat vogels die voor het eerst een legsel produceren gemiddeld minder eieren leggen dan ervaren dieren (Tabel 3).

2.3. Voorts blijkt dat de legselgrootte afhankelijk kan zijn van de voedselvoorraad, het weertype, de geografische hoogte, de aard van het woonterrein

en de bevolkingsdichtheid (Tabel 4). Bij veel vogelsoorten neemt de legselgrootte af wanneer de eieren later in het seizoen worden gelegd, of de grootte van het legsel neemt eerst enige tijd toe en neemt pas in het laatste deel van het seizoen af. Van beide categorieën zijn voorbeelden gegeven in de Tabellen 5 en 6 en de Figuren 3, 4 en 5. Door al deze invloeden kunnen van jaar op jaar verschillen in de gemiddelde legselgrootte optreden binnen een zelfde populatie van broedvogels (Tabel 7, Fig. 5).

3.1. Hoofdstuk 3 is geheel gewijd aan de evolutie van de legselgrootte. In de eerste plaats is nagegaan of de legselgrootte erfelijk is vastgelegd. Het blijkt dat bij in het wild levende vogels hiervoor slechts weinig indirecte evidentie is aan te voeren: in een bepaalde populatie is de variatie in legselgrootte bij één vrouwtje als regel geringer dan die tussen verschillende vrouwtjes.

3.2. In de tweede plaats worden de factoren besproken die bij het selectieproces een rol kunnen hebben gespeeld. Hierbij blijkt dat bij alle onderzochte soorten, misschien met uitzondering van enkele Limicolae, het gemiddelde aantal eieren per legsel kleiner is dan het maximale aantal dat door de vogel met succes kan worden uitgebroed.

3.3. Vervolgens wordt uitvoerig aandacht geschonken aan de theorie van LACK, welke inhoudt dat bij nestblijvers de legselgrootte is aangepast aan het grootste aantal jongen dat door de ouders met succes kan worden grootgebracht. Deze theorie wordt door een aantal waarnemingen gesteund. Zo ontvangen de jongen in grote broedsels in het algemeen minder voedsel per jong dan in kleine. Dit leidt er toe dat bij een aantal soorten de jongen van grote broedsels in het nest een hogere sterfte hebben en bij een aantal andere soorten, dat zij het nest verlaten met een lager gewicht dan de jongen van kleine broedsels. In het laatste geval is de sterfte na het uitvliegen bij de lichte jongen groter dan bij de zware jongen, wat hieruit blijkt dat van de eerste categorie een lager percentage drie maanden na het uitvliegen wordt teruggemeld dan van de tweede categorie. Voorbeelden hiervan zijn gegeven in de Tabellen 8 t/m 14 en in de Figuren 6 t/m 8. Deze gegevens zijn echter nog onvoldoende om de juistheid van LACK's theorie aan te tonen. Volgens deze theorie moet de sterfte van de jongen van de grote broedsels zo hoog zijn, dat deze broedsels minder nakomelingen voortbrengen dan broedsels van middelmatige grootte, die in de populatie het meest voorkomen; m.a.w. volgens deze theorie moet het meest frequente legsel tevens het meest productieve zijn. Dit bleek het geval te zijn bij 10 van de 22 onderzochte soorten. Bij 11 soorten was het meest productieve legsel iets groter dan het meest voorkomende. De mogelijke oorzaken hiervan worden besproken.

3.4. Bij vele nestvliedende soorten, waarvan de jongen zelf hun voedsel zoeken, kan de voedercapaciteit van de ouders geen rol hebben gespeeld in de evolutie van de legselgrootte. Voor deze groep van vogels zijn t.a.v. het ontstaan van het karakteristieke legsel verschillende theorieën opgesteld, die achtereenvolgens worden besproken. De theorie, welke het beste door de beschikbare feiten wordt gesteund, stelt dat de legselgrootte geëvolueerd is in relatie tot de gemiddelde hoeveelheid voedsel die voor de leggende vogel beschikbaar is gedurende de periode kort voor en tijdens het leggen van de eieren. Deze theorie wordt o.a. gesteund door de negatieve relatie tussen de grootte van het ei en het aantal eieren per legsel. Zo blijkt in Figuur 9 dat bij de hoenderachtigen, bij vergelijking van vogels van, bijvoorbeeld, ongeveer 1000 g lichaamsgewicht uit verschillende families, de Cracidae aanzienlijk grotere eieren leggen dan de Tetraonidae. De eerste hebben 2-3 eieren per legsel, de laatste gemiddeld ongeveer 10. De theorie wordt niet gesteund door de waarneming dat een aantal nestvliedende soorten meer eieren legt dan normaal, wanneer er tijdens de legperiode eieren worden verwijderd.

3.5. In Eurazië, Afrika en Amerika is waargenomen dat de legselgrootte bij een soort met een ruime verspreiding, of bij verwante soorten die samen een groot areaal bezetten, toeneemt naarmate de vogels verder van de aequator broeden (Fig. 10). Verder werd zowel in Europa als in Noord Amerika waargenomen dat de legselgrootte de neiging heeft om van West naar Oost toe te nemen. In beide categorieën komen ook uitzonderingen voor (Fig. 11). De betekenis van deze verschijnselen wordt uitvoerig besproken. Zij houden waarschijnlijk ten dele verband met regionale verschillen in daglengte en voedselkwantiteit.

3.6. In dit hoofdstuk wordt de theorie van SKUTCH besproken. Veel zangvogels in de tropen hebben slechts 2 eieren. Wanneer er meer dan twee jongen in het nest zouden zijn, zou het risico dat het nest door roofvijanden gevonden wordt door de hogere frekwentie waarmee de ouden het nest bezoeken zodanig worden verhoogd, dat broedsels van 3 gemiddeld genomen minder nakomelingen zouden produceren dan broedsels van 2. Er zijn enkele waarnemingen die aantonen dat van zangvogelnesten in de tropen inderdaad een hoger percentage door roofvijanden wordt gevonden dan in gematigde gebieden, maar het is onwaarschijnlijk dat de roofdieren de nesten vinden door het waarnemen van de ouders die het nest bezoeken.

3.7. CAVÉ heeft gesuggereerd dat bij nestblijvers met goed geïsoleerde nesten de grote broedsels in het nadeel zouden kunnen zijn, omdat ze in de gematigde gebieden op warme dagen niet in staat zijn om hun lichaamstemperatuur te handhaven, terwijl kleine broedsels door hun relatief groter oppervlak dat wel kunnen. Om dezelfde reden zou de legselgrootte in de tropen kleiner kunnen zijn dan in de gematigde gebieden.

3.8. WYNNE-EDWARDS heeft de hypothese opgesteld dat de grootte van het legsel door zogenaamde groep-selectie is aangepast aan de sterftesnelheid van de adulte vogels. Deze theorie steunt o.a. op de waarneming dat grote roofvogels en zeevogels, die een lage sterftesnelheid hebben, slechts 1 of 2 eieren leggen. De genetische basis van deze theorie is zwak.

4. In het laatste hoofdstuk wordt de adaptieve betekenis van de in hoofdstuk 2 behandelde variaties in legselgrootte besproken. Jonge vogels blijken minder efficiënt te zijn in het verzamelen van voedsel dan ervaren ouders. Het kleinere legsel van de eerste kan een aanpassing zijn aan dit verschijnsel. De Koolmees heeft in eikenbos, waar de jongen het beste overleven, het grootste legsel.

Voor veel nestblijvers is het moeilijker om laat in het seizoen jongen groot te brengen dan vroeg in het seizoen (Fig. 12). De afname van de legselgrootte in de loop van het seizoen zou hieraan kunnen zijn aangepast. Bij nestvlieders, die hun jongen niet voeden, kan de seizoenstrend in de legselgrootte niet geëvolueerd zijn in relatie tot een afnemende trend in de voedselvoorraad voor de jongen. Er worden argumenten aangevoerd ten gunste van de opvatting dat de seizoenstrend geen adaptieve betekenis heeft, maar een direct gevolg is van het feit dat laat leggende vogels minder energie tot hun beschikking hebben voor de productie van eieren.