had fledged. Six female ducklings fledged at 54 ± 4 days, and had an average of five primary feathers clear (rachis translucent); and six males fledged at 56 ± 3 days, and had six primary feathers clear ($P > 0.05$).

PRENUPTIAL MOLT

The first prenuptial molt of Greenland Mallard males began shortly after fledging and was nearly complete at the time head plumage was replaced. Several males showed indications of green head-feathering at 75 days of age. All eight males in 1968 acquired completely green heads in an average of 118 ± 16 days (range 98–134).

SUMMARY

Captive Greenland Mallards, one generation removed from the wild, nested during mid-April in North Dakota. Forty-one eggs averaged 42.49 mm wide, 58.54 mm long, and 58.00 g. Artificial incubation to hatching occurred in an average of 25 days and 15 hr. Ducklings grew most rapidly during the 3rd through 5th weeks after hatching. Tarsus growth was nearly complete by week 5; however, culmen growth continued through week 8. Females fledged at an average of 54 days and males, at 56 days. Males acquired green head plumage when an average of 118 days old.

SEASONAL PREDATION ON MOLES BY THE RED-TAILED HAWK

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On 10 March 1972, a known pair of Red-tailed Hawks (*Buteo jamaicensis*) were sighted at 133 m elevation 2 km N of Clayton, Contra Costa County, California. At 08:45 the male dove and landed on the ground. After 5 min on the ground, the hawk flew toward the female, clutching a western mole (*Scapanus latimanus*). Perching beside his mate, the male regurgitated a pellet, then began to feed on the mole held in its talons. Both the mole (a juvenile) and the regurgitated pellet were collected. The pellet contained remains of an adult mole.

Significantly, it appears that moles occur as prey of Red-tailed Hawks exclusively during winter and spring (Austing, The world of the Red-tailed Hawk, J. B. Lippincott Co., Phila., 1964; Fisher, Bull. U.S. Dept. Agri., Div. Ornithol. and Mammal. 3:48, 1893; Roest, J. Mammal. 33:110, 1952; pers. observ.). This seasonal vulnerability is apparently related to their reproductive period. During breeding and dispersal of the young, moles temporarily abandon their burrows (Arlton, J. Mammal. 17:349, 1936), and only then are readily available as prey. The ability of "general feeders" such as adult Red-tailed Hawks to utilize other species when rodents tend to be scarce could explain the occurrence of moles as prey (Craighead and Craighead, Hawks, owls and wildlife, Dover Pub., New York, 1969).

THE INHERITANCE OF CLUTCH SIZE IN THE GREAT TIT (*PARUS MAJOR* L.)

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It is fundamental to theories concerning reproductive rates and population regulation (Lack 1954; Wynne-Edwards 1962) that the clutch sizes of birds have evolved through natural selection, and are therefore, at least in part, genetically determined. While this is now generally accepted, the role of inheritance in the determination of clutch size has not yet been demonstrated.

Several factors associated with egg production in poultry are known to be genetically determined because it has been possible to improve production by artificial selection (Nordskog et al. 1967), but since the eggs are not normally laid in clutches, it has not been possible to investigate factors affecting clutch size. Among wild birds, the clutch sizes of many species are constant, and it may be argued that this is an inherited characteristic. However, since in such cases there is no observable intraspecific variation, the extent to which the clutch size of the offspring is determined by inheritance from the parents cannot be estimated. Other species, for instance, tits of the genus *Parus*, which lay relatively large clutches, show considerable variation in clutch size between individuals of the same species. A wide range of geographical variation occurs in the Great Tit (*Parus major*), clutch size increasing with increasing latitude (cf. Hoogerwerf 1949; Heim de Balsac 1952; Balat 1970; von Haartman 1969). Since this variation is associated with subspecific differences in size and plumage characteristics, which are presumably inherited, it seems reasonable to suppose that the clutch-size difference might also be inherited. However, it becomes possible to test this assumption only where a high degree of intraspecific variability in clutch size occurs within the same population.

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In deciduous woodland in Britain Great Tits in any one area normally lay between 7 and 11 eggs, but clutch sizes outside this range are frequently recorded (Gibb 1950). In the Great Tit (Kluijver 1951; present study; von Haartman 1969), as well as in some other species that lay a variable number of eggs, e.g., Starling (*Sturnus vulgaris*) (Lack 1948) Collared and Pied Flycatchers (*Ficedula albicollis* and *F. hypoleuca*) (Lohrl 1957; Curio 1959), Skylark (*Alauda arvensis*) (Delius 1963), Reed Bunting (*Emberiza schoeniclus*) (Haukioja 1970), and Velvet Scoter (*Melanitta fusca*) (Koskimies 1957), it has been shown that the variation in the size of clutches laid by the same female in successive years is significantly less than the variation of clutch size in the population as a whole. However, as pointed out by Kluijver (1951) for the Great Tit, individual constancy in clutch size need not imply that genetic factors are involved. Many females breed in the same place in successive years, and since it is known that the nature of the habitat may affect the clutch size phenotypically, it is likely that individual Great Tits will show a certain degree of constancy in clutch size that is independent of any genetic determination. Thus Krebs (1970) showed that over several years different individual Great Tits tended to lay large clutches in some parts of an area of woodland, whereas in other parts of the same wood they tended to lay small clutches.

While habitat type may exert a constant influence on the clutch size of an individual female Great Tit throughout her life, other environmental factors known to affect clutch size vary in their effect from year to year; these include the age of the female, the date when the clutch was started, and the density of breeding pairs (Kluijver 1951; Lack 1966). Variation in clutch size due to these factors appears to be adaptive, and in one area that was intensively studied, some 70% of the observed variability could be accounted for in these ways (Perrins 1965). The influence of each of these factors must be taken into account before any assessment of the genetic contribution to clutch size can be made. From a long-term study of a marked population of Great Tits, sufficient data have now been accumulated to estimate the effects of these environmental factors. This paper attempts to show that once environmental effects of clutch size have been eliminated, much of the remaining variability in clutch size is genetic in origin, showing a high degree of heritability between parents and offspring.

MATERIALS AND METHODS

The data presented here were collected as part of a long-term population study of the Great Tit carried out on the Wytham estate near Oxford. Since 1960, females have been trapped at the nest and marked individually with numbered bands, and since 1964 a similar procedure was adopted for the breeding males. One-year-old birds were distinguished from older birds by plumage characteristics. Since many of the breeding birds had been banded as nestlings in previous years, comparable breeding data were available for large numbers of both parents and offspring. Clutches laid during the period 1960–69 by females of known age were first analyzed with respect to those factors known to affect clutch size, in order to quantify the effects of each (see appendix). It was then possible

to use these quantities as correction factors to eliminate much of the variation in clutch size due to the part of the wood in which it was laid, the age of the female, and a "year-effect" which included the density of breeding pairs and any undetected annual factors. Such variation was presumably largely environmental, but may have included inherited components; correction for such factors may therefore have removed some of the genetic contribution to clutch size. However, since this would tend to reduce the contribution of inheritance to clutch size, not increase it, correcting the clutch size in this way cannot exaggerate the correlations shown below. Further analysis for other factors indicated that the age of the male, and either the nest box itself or the habitat immediately surrounding it might slightly affect the laying date, but did not affect the clutch size by a statistically significant amount. A significant, though small, inverse correlation between clutch size and egg weight [the latter showing a high degree of heritability (Jones 1973)] did not affect the data presented here.

Also 107 clutches were excluded from the analysis. These were second clutches of females known to have laid previously that year, and clutches with a corrected size of less than 6.5 eggs. An additional advantage of this correction was that the normality of the distribution of clutch sizes was improved. Inclusion of such doubtful clutches produced a positively skewed distribution. This lower limit was fixed arbitrarily, but an analysis of the rejected group revealed that many were probably replacement clutches of birds that had not been identified earlier in the season, and some may have been incomplete since gaps had occurred in the laying sequence. There remained 1276 clutches for use in the analysis. The mean corrected clutch size was 8.91 (SD = 1.21).

ANALYSIS

Two hundred sixty-seven different females laid clutches in more than one year. It was therefore possible to compare the corrected clutch size of a female in one year with her clutches in subsequent years (referred to as repeat clutches). All possible combinations of pairs of clutches from each female were used, so that a female which laid clutches in 3 years gave three pairs, a female with four clutches, six pairs, etc. By doing this, extra weight was given to females with a large number of clutches, but since there were few such birds, this is not a serious objection. The method is in any case unbiased, the only objection being to its efficiency. The variance of the corrected clutch sizes of all birds was 1.48 (d.f. = 1274); the variance of the repeat clutches of the same female (the "within-bird" variance) was 0.72 (d.f. = 428). The co-variance between repeat clutches (the "between-bird" variance) can be estimated as $1.48 - 0.72 = 0.76 \pm 0.05$, and the "repeatability" as $0.76/1.48 = 0.51 \pm 0.04$ (Falconer 1960). The co-variance calculated would be affected if the distribution of clutch sizes of those birds which laid in more than one year was different from that of birds for which only one clutch was recorded. For instance, this could occur if the mortality of females raising large broods was higher than that of females raising few young. However, the variances of clutch sizes in the two groups showed no significant difference. This indicates that after the influence of all known en-

vironmental factors has been eliminated, approximately half of the remaining variability is due to a source of variability which is constant within each individual female. This may be wholly genetic, or it may also include environmental factors which could raise the repeatability; for instance, how well a female was raised as a nestling might permanently affect her body size and condition, and hence her clutch size.

During the course of the Wytham study, a large number of breeding records have become available for females which had been raised in the study boxes in previous years, and for whom data were also available on their mothers' breeding histories. Some daughters had laid in 2 or more years. Where this was the case, the mean number of eggs calculated from all their corrected clutches was compared with the number of eggs in the clutch from which they had been raised. This provided 256 pairs of observations for comparison; the correlation coefficient obtained between mothers' and daughters' corrected clutches was

$$r = 0.24 \pm 0.05.$$

Where all the "between-individual" variance is additive genetic and none is due to environmental factors, the heritability for clutch size equals the repeatability, which in this case is 0.51, since

$$\text{heritability} = \frac{\text{additive genetic variance}}{\text{total (or phenotypic) variance}}$$

(Falconer 1960).

However, where comparison is made between offspring and only one parent (in this case the mother), the expected resemblance would be only one-half the total heritability, or 0.51/2. The observed correlation of 0.24 is very close to this figure.

Since, in birds, the female is the heterogametic sex, it remains possible, though unlikely, that this correlation could be accounted for by inheritance from the Y-chromosome. The remaining half of the observed repeatability could then be due not to inheritance from the male parents, but to environmental factors (as yet undetected) that are constant for an individual female. It is possible to show, however, that environmental factors are not likely to be important, and that the remaining half of the repeatability is likely to derive from the male. We have information on breeding of 48 pairs of full sibling (raised in the same nest) sisters and three sets of triplets. The latter were treated as three pairs each, giving 57 pairs of corrected clutches. The correlation obtained,

$$r = 0.20 \pm 0.13,$$

is not significant, perhaps because of the small sample size, but comes close to the 0.24 correlation expected between full siblings with normal autosomal inheritance. If factors deriving from common environment were permanently influencing the clutch size of a bird, it seems most unlikely that these could be effective at any time other than during the growing period of the young birds. Full siblings, sharing a common nest environment, should therefore show a correlation much higher than 0.20, since they should have a sister-sister correlation of about 0.24 plus a common environment correlation also of about 0.24. Since this is

not so, common nest environment can have very little effect, and the inheritance is assumed to be autosomal. The respective contributions of mother and father must therefore be approximately equal (at about 0.24 ± 0.05 each), so that together they account for the total variability (0.51). The possibility of other than normal autosomal inheritance seems unlikely and will not be considered further.

It is not, of course, possible to measure the clutch size of the male directly, but it is possible to examine the correlation between clutch sizes of daughter Great Tits and their paternal grandmothers. However, the predicted correlation would be only one-eighth ($\frac{1}{4} \times 0.51$) of the variation observed and the data are too few to obtain a significant result.

DISCUSSION

After removal of some of the major environmental variations in clutch size, the remaining variation in the clutch size of the Great Tit shows a high heritability. It must be stressed, however, that because of the considerable variation in mean clutch from year to year, Great Tits clearly do not inherit the tendency to lay a clutch of a particular size, but rather to lay a clutch of a certain size *in relation to the mean clutch-size in the population at that time*. Thus descendents of a female that laid 11 eggs in a year when the mean clutch was 10 might be expected to lay, on average, 9 eggs in a year when the mean clutch was 8, or 13 when it was 12. The mechanisms whereby the adjustment of clutch size is brought about are completely unknown. Such adjustments are often appropriate to the subsequent availability of food for the young in the nest (Perrins 1965), but usually they do not seem to be controlled by the food supply for the female during laying, though the timing (date) of laying appears to be regulated in this way (Perrins 1970; Jones 1973).

The productivity of broods of different sizes varied markedly between habitats and under different conditions in the same habitat (Perrins 1965; Lack 1966). The ability to vary the clutch size appropriately in relation to environmental conditions is therefore clearly advantageous. However, since part of the variation is heritable, there must presumably be an associated small shift each year in the relative frequencies of different genotypes dependent on whichever brood size was the most productive the year before, but it has not yet been possible to demonstrate this. Similarly, since some brood sizes are likely to be more productive of offspring than others in different types of habitat, and since Great Tits tend to settle within a few hundred meters of their birthplace (Kluijver 1951; Bulmer, in press), one might expect to find slightly different frequencies of genotypes relating to clutch size in different areas. However, for this to occur to any great extent, large, discrete tracts of similar habitat would be required in order that the level of interchange of individuals between two populations was very low. These conditions do not apply in southern Britain today, where the land is so greatly dissected by man's activities that areas of good and poor habitats are everywhere closely interdigitated, and it is unlikely that there remain any areas large enough for discrete populations with different frequencies of genotypes to have arisen.

We owe a great debt of gratitude to M. G.

Bulmer of the Department of Biomathematics, Oxford, for his guidance and help with the analyses presented here. Many people have helped with the field work over the long period of years, many others have read and criticized earlier drafts of the paper; these include J. M. Cullen, J. W. F. Davies, D. G. Dawson, J. R. Krebs, D. Lack, J. H. Lawton, D. H. Morse, D. N. Nettleship, and D. B. Roberts.

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APPENDIX

THE CALCULATION OF THE CORRECTION FACTORS APPLIED TO THE CLUTCH-SIZE DATA

Age. In order to eliminate the effects of area and year (see below) from the analysis of clutch size with repsect to the age of the female, the mean differences betwen yearling and 2-year-old females, and between yearlings and birds older that 2 years, were calculated for each area/year category separately. Weighted average differences were obtained as in table A1.

In table A1 the age of the male is not considered, but a separate analysis was carried out on a smaller sample of clutches where the age of the male was known. Although the results suggested that both young and old females lay slightly larger clutches when mated to an old male, the difference is small and not significant (0.25 ± 0.02). Since the ages of the males were not available for the majority of clutches, and the effect, if real, was in any case small, this factor was ignored in the analyses.

Area and year. Five principal areas of the Wytham estate have shown consistent differences in mean clutch size, date of laying, and breeding density, and were accordingly treated separately in the analyses. Components of the "area" effect include habitat type and consistent differences in mean date of laying between years. Components of the "year" effect include annual differences within each area in mean date of laying and density of breeding birds. The mean clutch size, corrected for age, was calculated separately for each area and year. There was no evidence of any appreciable interaction between area and year in the period 1961–69, but the mean clutch size for Great Wood in 1960 was considerably lower than that in Marley Wood, though in all other years they were similar. Corrections for year and area 1961–69 were calculated on the assumption that they were additive, but a separate correction was made for Great Wood in 1960. The weighted average of the difference between Great and Marley Woods for 1961–69 was 0.3 eggs. The differences in the

TABLE A1. Difference in clutch size due to age of female.

Comparison	Mean weighted difference (eggs ± SE)
2-year-old vs. 1-year-old	0.56 ± 0.10
3-year-old vs. 1-year-old	0.62 ± 0.10

TABLE A2. Clutch size differences in five areas of Wytham estate.

Area	Mean weighted deviation from standard (see text)
Marley Wood	−0.2 (+0.2 in 1960)
Great Wood	+0.1 (−1.2 in 1960)
Bean Wood	+0.1
Marley Plantation	−0.5
Singing Way	−0.7

TABLE A3. Annual difference in clutch size in Wytham 1960–69.

	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Mean difference	+0.3	−0.7	nil	+0.8	+0.7	+0.6	−0.2	−0.2	−0.3	−0.4

three other areas were calculated by comparing them with ⅓ mean clutch Marley + ⅔ mean clutch Great Wood, and then averaging over years, as in table A2.

The effect of year, which includes effects of date and density, was based on the value for Marley Wood + 0.2 in 1960, and on ⅓ Marley + ⅔ Great Wood for 1961–69. The effects are given in table A3.

Habitat. Differences in habitat type, classified as "good" and "bad," within each area produced a small, but only just significant, difference (mean weighted difference 0.17 ± 0.08 eggs), which was not considered worthwhile applying as a correction factor in the present analysis. The classification into "good"

and "bad" was made subjectively by the authors, and is not comparable to that of Krebs (1970), who used consistently occurring extreme values for clutch size as criteria for habitat quality and ignored middle values.

Corrections applied. To allow for the effects of "area" and "year" the effects calculated above in tables A2 and A3 were substracted from each observed clutch size. To allow for the effect of the age of the female, 0.3 eggs was added to the clutch of a yearling and subtracted from that of an older bird.

Accepted for publication 7 August 1973.

AN UNUSUAL HOUSE SPARROW ROOST

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On numerous occasions through the winter of 1970–71, I observed a dozen or more House Sparrows (*Passer domesticus*) entering a subterranean transformer vault shortly before nightfall. The vault, next to a building on the campus of Tarkio College, Tarkio,

Missouri, was ca. 3 m deep, with an opening in the top ca. 2 × 15 m which was covered by an iron grate flush with the surface of the ground. The birds entered through the grate and roosted under protection of the overhanging concrete roof about 1 m below the ground's surface.

Although the House Sparrow is very adaptable in its roosting and nesting sites, this situation seems unusual even for this species.

Accepted for publication 16 February 1973.

PREDATION OF XANTUS' MURRELET BY WESTERN GULL

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At about noon on 4 May 1972, while passing between the main north and south Coronado Island aboard a sports fishing boat, I observed a Xantus' Murrelet (*Endomychura hypoleuca*). The boat returned to this position about half an hour later, where what was presumed to be the same bird was observed. The boat slowly turned and stopped. The bird was swimming away from the boat calling continuously in a typical manner, reminiscent of a passerine. Suddenly one of several Western Gulls (*Larus occidentalis*) in the area swooped down and with open bill scooped the murrelet out of the water. The murrelet struggled

briefly waving a leg and wing, but was almost immediately swallowed whole by the gull. The murrelet appeared to be in full adult plumage and healthy condition.

A. C. Bent (Life histories of North American gulls and terns, Dover Publ., Inc., New York, 1963) and F. M. Bailey (Handbook of birds of the western U.S.A., Houghton, Mifflin and Co., Boston, 1902) suggest that the food of the Western Gull consists of eggs of murres (*Uria*), cormorants (*Phalacrocorax*), pelicans (*Pelecanus*), sea urchins, crabs, fish (often stolen from nests), and sometimes rabbits and young murres. Bent also remarks (quoting Bryant 1888) that they will scavenge the bodies of dead murres. Although adult Xantus' Murrelet may be as small as some young murres (8 inches), the observation of a Western Gull taking an adult which would be capable of flight or diving is of interest.

Accepted for publication 16 February 1973.