

GENETIC AND ENVIRONMENTAL FACTORS INFLUENCING CLUTCH SIZE IN EQUATORIAL AND TEMPERATE ZONE STONECHATS (*SAXICOLA TORQUATA AXILLARIS* AND *S. T. RUBICOLA*): AN EXPERIMENTAL STUDY

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ABSTRACT.—European Stonechats (*Saxicola torquata rubicola*) from Austria usually lay 5.0 to 5.6 eggs per clutch, whereas their African conspecifics (*S. t. axillaris*) from Kenya lay 3.0 to 3.1. To determine if this difference has a genetic basis we examined clutch size in both subspecies, as well as in F₁-hybrids from pairs that were held in aviaries (either under a changing European photoperiod, indoors or outdoors, or under a constant 12.25-h photoperiod, indoors). Data (114 clutches from 26 European females, 254 clutches from 34 African females, and 41 clutches from 6 F₁-females) were subjected to residual maximum-likelihood analysis. The genotype of the female had a highly significant effect on clutch size: after adjustment for other significant effects, the estimated means were 5.09 eggs per clutch for the European and 3.44 for the African birds. The clutch size of the F₁-females was intermediate (4.07 eggs per clutch) in that it was significantly different from the clutch size of both the European and African subspecies. In contrast, the genotype of the male mate had no significant effect (i.e. clutch sizes of females paired with males from the other subspecies were not different from those of females paired with males from the same subspecies). The age of the female and holding conditions had no or only marginal effects, but there were significant effects of both season and year in which the clutch was laid. Our results suggest that clutch size can be influenced to a limited extent by some of the environmental variables studied, but that the difference in clutch size between the two subspecies is largely genetically determined. Received 4 October 1994, accepted 8 August 1995.

CLUTCH SIZE OF BIRDS varies between and within species or populations. One of the most conspicuous variations between populations is that clutch size generally increases with latitude (e.g. Lack 1947-1948, 1968, Cody 1966, Klomp 1970, von Haartman 1971, Ricklefs 1980, Winkler and Walters 1983). Within populations, clutch size often varies with season, the largest clutches being laid during the early or middle part of the breeding season (e.g. Klomp 1970, Toft et al. 1984, Nur 1986, Meijer et al. 1990). The age of the laying female also can influence clutch size in a systematic manner (e.g. Cody 1971, Nur 1986). Superimposed upon these general trends are individual variations. For example, in certain populations different females of one and the same age class may differ consistently with regard to the number of eggs laid per clutch at a given time of the year (e.g. Klomp 1970, van Haartman 1971, Högstedt 1980, Winkler and Walters 1983, Nur 1986, MacInnes and Dunn 1988, Meijer et al. 1990).

Variability of clutch size usually is assumed to result from an interplay of environmental and genetic factors. Environmental factors known to influence clutch size are territory quality, food availability, weather, nutritional reserves (e.g. Jones and Ward 1976, Drent and Daan 1980, Högstedt 1980, Findlay and Cooke 1983, MacInnes and Dunn 1988) and—in hole-nesting birds—the size of the nest cavity (Löhr 1973, Karlsson and Nilsson 1977, Trillmich and Hudde 1984, van Balen 1984, Slagsvold 1989). Genetic factors are assumed to account for some of the variability in clutch size within populations (e.g. Perrins and Jones 1974, van Noordwijk et al. 1981, Gustafsson 1986, Boag and van Noordwijk 1987, Findlay and Cooke 1987), heritability quotients usually ranging from 0.05 to 0.48. However, heritabilities may reflect maternal rather than genetic effects (Schluter and Gustafsson 1993); hence, the actual genetic contribution to clutch size expressed in heritability quotients is often not clear. Similarly, it remains

unknown to what extent differences in clutch size found between populations are determined by genetic factors.

Most of the conclusions and concepts discussed today are based largely on correlational field studies, and there is an obvious need for experimental work. Our investigation is based on the premise that some of the particularly interesting questions can be approached by studying aviary birds for which environmental factors can be rigorously defined and manipulated, and which can be used for cross-breeding experiments. The investigation was carried out on captive Stonechats originating from populations in middle Europe (*Saxicola torquata rubicola*) and equatorial Africa (*S. t. axillaris*). In the field, clutch size of birds from these two populations differ conspicuously, averaging from 5.0 to 5.6 eggs in continental European birds and from 3.0 to 3.1 eggs in East African birds (Dittami and Gwinner 1985, Flinks and Pfeifer 1987, Keith et al. 1992). We focussed on four major sets of questions: (1) To what extent are the latitudinal variations in clutch size between populations genetically determined? To answer this question the clutch size of pairs of birds from both populations as well as aviary-bred F_1 -hybrids were determined under rigorously defined environmental conditions. (2) Does photoperiod, which is so conspicuously different in the breeding areas of the two subspecies, affect clutch size? To investigate this question, clutch size data from birds of both populations kept either in a constant equatorial or in a changing Temperate Zone photoperiod were analyzed. (3) Is clutch size a characteristic feature of an individual female (i.e. is it repeatable)? (4) To what extent can clutch size of an individual female be modified by the male partner of either subspecies? In addition, we also analyzed our data with regard to possible confounding effects of age, year and season.

METHODS

Origin of birds and holding conditions.—We used 66 female Stonechats (26 European, 34 African, and 6 F_1 -hybrids) in this study. Between 1983 and 1992 these females produced 409 complete clutches (114 European, 254 African, and 41 F_1 ; see Table 1) that are the basis of our analysis. Most of the birds used were taken from the field as nestlings and hand-raised (Gwinner et al. 1987). Five European, nine African, and six F_1 -females were bred in our aviaries and either raised by their parents (Europeans and Africans) or

TABLE 1. Number of clutches laid by European (*rubicola*), African (*axillaris*), and F_1 -hybrid female Stonechats under different holding conditions. Some of experimental females contributed data to more than one holding condition: (E_o) outdoors, southern Germany; (E_i) indoors, changing photoperiod of southern Germany; (A_i) indoors, constant 12.25-h equatorial photoperiod.

Holding conditions	No. females	No. clutches
European (<i>rubicola</i>)		
E_o	9	23
E_i	19	81
A_i	3	10
African (<i>axillaris</i>)		
E_o	7	15
E_i	22	123
A_i	22	116
F_1-hybrids		
E_o	3	10
E_i	6	31
A_i	—	—

by us. All F_1 -hybrids had European mothers. Of the 409 clutches, 398 were from paired females and 11 from (7 European) unpaired females. Unpaired females lived in the same type of aviary as the paired birds, but without a mate. The floor of each each aviary was covered with a thick layer of hay, moss, and grass tufts, as well as stumps and stones, providing several sites for the birds to nest. Coconut fibers and lint were offered as nesting material.

Adult birds were fed a standard diet consisting of 25% commercial insect food (Eckrich), 30% hard-boiled eggs, 15% bread crumbs, 21% curds, 3% beef heart, and 6% ground egg shells, plus 10 mealworms per day. After the young had hatched, live insects also were provided, mainly crickets, waxmoths as larvae and imagoes, and ant pupae. Once a week, the drinking water was enriched with vitamins (Vitin, Chevit GmbH).

Birds were kept in one of three groups under the following conditions: (group 1) the European photoperiod outdoors (E_o), which involved the natural changes of photoperiod and temperature in Andechs (48°N, 11°11'E); (group 2) the European photoperiod indoors (E_i), which involved a changing photoperiod simulating that of Andechs; and (group 3) the African photoperiod indoors (A_i), which involved a constant photoperiod of 12.25 h, simulating that of the equator (0°).

The captive Stonechats usually bred readily, but in most cases they abandoned or killed their chicks shortly after hatching; subsequently, they frequently built a new nest and laid another clutch. In that way, individual females produced up to nine clutches within a breeding season (Gwinner et al. 1987).

TABLE 2. Summary of results for fixed effects and their interactions.

Fixed effect	Wald statistic	df
Female genotype	106.1***	2
Holding conditions	8.7*	2
Male partner	0.0	2
Year of clutch	25.5**	9
Age	0.1	1
Season	10.6**	1
Season \times female genotype \times holding condition interaction	16.6*	7

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Statistical analysis.—The data were analyzed with residual maximum likelihood (REML; Patterson and Thompson 1972) using the REML option within the statistical software package Genstat (Genstat 5 Committee 1993). REML allows mixed-model analyses to be performed, with the random effect of the individual birds together with the fixed effects of genotypes of birds, holding conditions, etc., included in the same model. REML is particularly valuable for fitting mixed models to unbalanced data (with incomplete cross-classification, missing observations, etc.), such as those from this study, which cannot be adequately analyzed using standard ANOVA methods. REML, thus, allows the structure of the data to be correctly modelled and provides better estimates of effects of environmental or other variables and their standard errors than other methods.

The 66 females considered in our study originated from a total of 46 nests. Thirty-one of these sibling groups were represented by one, and the remaining 15 groups by two or three females. Accordingly each sibling group was represented by 1.4 females on average. Hence, family effects were highly confounded by individual effects. For this reason we were able to consider only the individual female effect (repeatability, see below) in our analysis.

The following effects were examined: (1) repeatability; (2–5) fixed effect of female genotype, holding conditions, male partner, and experimental year, respectively; (6) age of the bird; and (7) season.

For repeatability (random effect of bird), repeat clutches were recorded for many birds. Thus, by incorporating a random effect for the bird, variation in clutch size could be partitioned into that among birds (σ_a^2) and that within (σ_w^2). This allows the calculation of the intraclass correlation coefficient (or repeatability) of clutch size as:

$$r = \sigma_a^2 / (\sigma_w^2 + \sigma_a^2). \quad (1)$$

The fixed effect of female genotype took into account whether the bird was a European subspecies, or an African subspecies, or an F_1 -hybrid. The fixed effect of holding conditions was categorized as E_c , E_i

or A_i (see earlier part of Methods). The fixed effect of male partner took into account whether the female was mated or not and, if mated, whether the mate was from the European or African subspecies, or was an F_1 -hybrid. The fixed effect of experimental year took into account whether the clutch was laid between 1983 and 1992. The age of the bird was fitted as a linear covariate.

In order to test for seasonal trends, each month of the calendar year was subdivided into three 8- to 11-day intervals. The day on which the first egg of a clutch was laid was allocated to one of the resulting 36 intervals. Subsequently, data were examined for linear or quadratic trends.

The fixed and random effects were included together in a complete model. The significance of each fixed effect was tested using Wald statistics (Genstat 5 Committee 1993). These have an asymptotic chi-squared distribution with degrees of freedom equal to those of the model term. In additional analyses we examined all possible two-way interactions between the fixed effects; none of these interactions was significant.

The clutch-size data (adjusted for effects of season and year of clutch) of *rubicola*, *axillaris*, and F_1 -females also were analyzed with a one-way ANOVA using contrasts to test for differences among the means for different genotypes and holding conditions.

RESULTS

Repeatability.—The overall intraclass correlation between the size of clutches laid by the same bird was significant ($P < 0.05$) and estimated at an r of 0.22. Thus, clutch size is to a limited extent, a characteristic feature of individual females.

Genotype of female.—The genotype of the female had a highly significant effect on clutch size ($P < 0.001$; Table 2, Fig. 1). After adjusting for the significant effects of holding condition, experimental year, and season, the estimated genotypic means were: $5.09 \pm \text{SE of } 0.13$ for the Europeans; 3.44 ± 0.13 for the Africans; and 4.07 ± 0.23 for the F_1 -hybrids. The clutch size of F_1 -females was intermediate in that it was significantly ($P < 0.05$) different from that of both the European and African subspecies. There was no evidence for dominance of the genes controlling clutch size.

Holding conditions.—After adjusting for other significant effects, differences between holding conditions were significant ($P < 0.05$); Table 2). The corresponding mean clutch sizes were: (E_c) 4.23 ± 0.16 ; (E_i) 4.40 ± 0.10 ; and (A_i) 3.97 ± 0.15 (Fig. 1). Within the three genotypes none

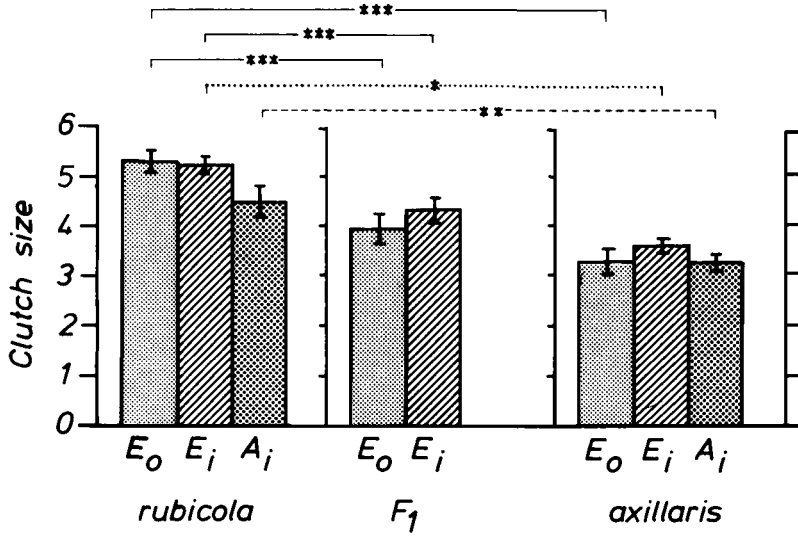


Fig. 1. Mean clutch sizes (\pm SE, adjusted for effects of season and year of clutch) of European (*rubicola*), African (*axillaris*), and hybrid (F_1) female Stonechats held under three different conditions: (E_0) outdoors in southern Germany; (E_i) indoors under changing photoperiod of southern Germany and; (A_i) indoors under constant 12.25-h equatorial photoperiod. Significant clutch-size differences from ANOVA indicated with asterisks (***, $P < 0.001$; **, $P < 0.005$; *, $P < 0.05$). None of clutch-size differences within a genotype were significant. For further details, see Table 1 and Methods.

of the differences between holding conditions were significant.

Male partner.—Genotype of the mate and mating status (mated or unmated) had no significant effect on clutch size (Table 2). Means for each class, after adjustment for other effects, are shown in Figure 2. Note that there is only a low level of cross-classification between these effects so that the power of the aforementioned tests of effect of mate is low.

Experimental year and age.—There was a significant effect of the year in which the clutch was laid on clutch size ($P < 0.01$; Table 2), with clutch size increasing towards the end of the experiment. The overall age of a bird when a clutch was laid was $3.1 \pm$ SD of 1.6 years (range 1 to 8). The age of the bird, treated as a linear covariate, had no significant effect on clutch size (Table 2). In addition, there was no significant difference between clutch sizes of first-year and older females.

Season.—While the analysis revealed no evidence for a nonlinear trend, there was an overall significant ($P < 0.01$; Table 2) linear decline of clutch size with season. The estimated regression coefficient (r) of clutch size on time of year was $-0.026 \pm$ SE of 0.008 (equivalent to a decline of approximately 0.078 ± 0.024 eggs per

month over the year). In an additional model, the interaction of the effect of season, genotype, and holding condition was included. This effect was of borderline significance ($P = 0.05$). The individual estimates of the regression of clutch size on time-of-year for each genotype, holding condition, and year of clutch are given in Table

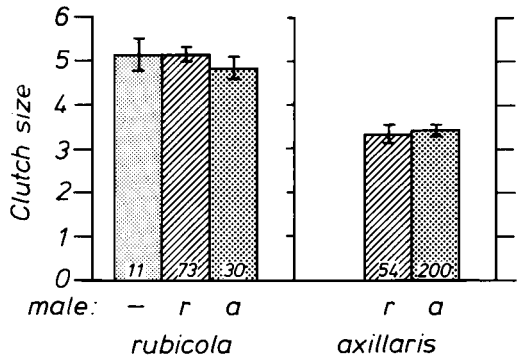


Fig. 2. Mean clutch sizes (\pm SE, adjusted for effects of season, year of clutch, and holding condition) of European (*rubicola*) and African (*axillaris*) female Stonechats that were unmated (-) or mated with males of either subspecies (r = *rubicola*, a = *axillaris*). Numbers at bottoms of columns denote sample sizes of clutches in respective groups.

TABLE 3. Individual regression slopes (\pm SE, n ; adjusted for year of clutch) of clutch size on time of year for each genotype and holding condition.

Genotype	Holding conditions		
	European photoperiod outdoors	European photoperiod indoors	African photoperiod indoors
<i>rubicola</i>	-0.091 ± 0.060 (23)	-0.012 ± 0.030 (78)	-0.037 ± 0.036 (10)
<i>axillaris</i>	-0.264 ± 0.076 (15)**	-0.054 ± 0.017 (121)***	-0.011 ± 0.010 (111)
F ₁	0.007 ± 0.087 (10)	-0.042 ± 0.033 (27)	—

** $P < 0.01$; *** $P < 0.001$.

3. All but one of the estimates were negative. However, the estimates were variable and only those for birds of the African subspecies held under European conditions (outdoors and indoors) were individually significantly different from zero ($P < 0.001$ and 0.01 , respectively).

DISCUSSION

The major and most clearcut result of our study is that the aviary-kept African and European Stonechats had clutch sizes similar to those recorded from free-living birds of the respective populations. F₁-hybrids laid clutches intermediate in size.

When analyzing for effects of female genotype, we made adjustments for all other significant effects. One could argue that the two non-significant factors—male partner and age—might have biased clutch size. However, given that the P -values for these two effects were extremely low ($P = 1.0$ and >0.7), respectively, this is very unlikely. Moreover, the medium age of the females at the time a clutch was laid was very similar in the three female genotypes (two years in the European and F₁-females; three years in the African females).

Nongenetic maternal effects also are an unlikely, exclusive explanation of the observed differences between the three genotypes. Since the mothers of the hybrids were all European birds, strong maternal effects should have biased hybrid clutch size towards that of the Europeans. This, however, was not the case (Fig. 1). It could still be argued that, in contrast to the majority of the European and African Stonechats that were taken from the field, the F₁-hybrids were all bred and raised in captivity, which might have influenced their subsequent clutch size. While this is principally possible, it would be difficult to understand why F₁ clutch

size should be intermediate. Moreover, the few clutch-size data that we obtained from European and African Stonechats bred in captivity suggest that early developmental influences of this kind are small or absent. Taken together, then, the present results lend strong support to the hypothesis that the differences in clutch size normally found between these two subspecies are genetically determined.

Although the clutch-size differences observed between the captive and, by inference, free-living African and European Stonechats must be due primarily to genetic effects, our data suggest that there also may be environmental factors that limit clutch size of the free-living African Stonechats. While clutch size of free-living Stonechats from southern Germany is very close to that of our caged birds, free-living African Stonechats appear to have smaller clutches (3.0–3.1) than their conspecifics in aviaries (3.3–3.6), irrespective of holding conditions. However, field data on clutch size of African Stonechats are not very extensive and, therefore, we cannot make rigorous comparisons.

While the genotype of the female drastically affects clutch size, the genotype of the male has no impact. Studies on other passerine species also indicate that the quality of the male (Slagsvold and Lifjeld 1990), or a change of the male (MacInnes and Dunn 1988), does not affect clutch size.

As in other multiple breeders (Klomp 1970), clutch size of free-living European Stonechats initially increases and then decreases as the season progresses; however, the changes are relatively small (Glutz von Blotzheim and Bauer 1988, Flinks and Pfeifer 1987). Whether such a change in clutch size with season also occurs in free-living African birds is unknown. When analyzing the data from all genotypes and holding conditions together, we found a significant de-

cline of clutch size with season. Moreover, although significant only in tow cases, all but one of the eight individual regressions of clutch size on calendar date calculated for individual genotype/holding condition associations were negative. Quite unexpectedly, the two significant negative regression coefficients were found for the two groups of African Stonechats held under European conditions.

In other studies (Gwinner et al. 1983, Gwinner and Dittami 1985), we have found that several seasonal parameters of African Stonechats respond to photoperiod despite the equatorial origin of these birds. Therefore, the significant seasonal decline of clutch size found in African Stonechats under the varying European conditions, but not under the constant equatorial conditions, may be another expression of these birds' capacity to respond to photoperiod. However, there is as yet no evidence from any species that the decline of clutch size with season is a direct result of changing photoperiod (Meijer 1989).

Indeed, although not significant, a seasonal decline of clutch size also was suggested for both the African and European birds held in the constant photoperiod (Table 3). The effect may reflect some kind of exhaustion of the females (Klomp 1970) of which many produced a large number of repeat clutches within a relatively short period of time. In view of the difficulties in interpreting these results, we presently are inclined to treat this effect mainly as a confounding variable for which the data had to be adjusted, rather than providing a clearcut explanation for it.

Although our study was conducted in the laboratory and basic food quality and quantity were unchanged throughout the experiment, the analysis revealed a significant influence of experimental year on clutch size. It is possible that laying date and/or female age might be responsible for this effect. Owing to the design of the experiment it is not possible to separate possible effects of these two factors from those of the experimental year. However, the effect had to be considered in the data analysis.

Repeatability describes the likelihood of an individual female to consistently produce clutches of a specific size in relation to the mean clutch size of the population at a given time (Perrins and Jones 1974). Repeatability is considered to be based on both internal genetic and maternal effects, as well as environmental fac-

tors such as site-specific effects (e.g. van Noordwijk et al. 1981, van Noordwijk 1987, Schluter and Gustafsson 1993). Thus, having high repeatability represents the upper limit of heritability (Falconer 1981).

Several field studies (e.g. Perrins and Jones 1974, van Noordwijk et al. 1981) have revealed relatively high repeatabilities ($r = 0.3$ to 0.5) for passerines. The values of this individual trait are likely to be affected by temporal environmental factors (e.g. seasonal variation of clutch size; Myrberget 1989) or changes in female condition (e.g. age; Kennedy and White 1991). Correspondingly, higher repeatabilities would be expected under the controlled conditions of captivity. However, in contrast to this expectation, repeatability in captive Stonechats was low ($r = 0.22$), although determined after adjustment for other significant effects. In this context one must consider that our estimate of repeatability is based on a relatively small set of individual females (17 Europeans, 28 Africans, 6 F₁-hybrids). Therefore, the calculation is likely to be sensitive to confounding factors. For example, age of a female could have affected the value of our parameter estimate. Kennedy and White (1991) have found that in House Wrens (*Troglodytes aedon*), intraseasonal repeatability of clutch size is considerably lower in first-year females than in older females. Female condition, which may change both within and between breeding seasons, could affect clutch size and, hence, reduce repeatability. In view of the large number of repeat clutches produced by the females of the present study, changes in female condition are quite conceivable. Evidence for adjustments of clutch size to actual female condition has been obtained in studies of experimentally handicapped female Pied Flycatchers, Blue Tits (*Parus caeruleus*), and Coal Tits (*Parus ater*) (Slagsvold and Lifjeld 1988, 1990).

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