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On the genetical basis of the laying-date in an island population of blue tits

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Abstract

There are striking differences in life-history traits associated with reproduction, between an insular population of the blue-tit and one on the nearby mainland. In order to test the extent to which these differences are genetic, two samples of birds, one from Corsica and one from mainland southern France, were hand-raised. These birds bred subsequently in aviaries at Montpellier during three consecutive years, at the same date and in the same way as did the natural populations from which they came. It is concluded that the difference in laying-date between the two samples has a genetic basis. The adaptation to each particular set of environmental conditions is discussed.

Introduction

Comparative studies on the life-histories of two populations of the blue-tit *Parus caeruleus*, one in a continental habitat (Mont-Ventoux, Southern France) and the other on the island of Corsica, have shown striking differences in ecologically important traits (Blondel 1985, Blondel et al. 1987). The Corsican tits start to breed on average 15 days later than their mainland counterparts, their clutch size is reduced by 27% (6.3 eggs ($N = 435$) *vs* 8.6 on the mainland ($N = 147$)) and they never have second broods. At first sight these differences are surprising since the Corsican climate is much milder and much more predictable than the mainland climate (Blondel 1985).

Life-history traits associated with reproduction are assumed to be determined by natural selection in such a way as to maximize the production of offspring (Baker 1938, Lack 1954). Such a process involves genetical variability, the existence of which has been fully demonstrated for life-history traits associated with reproduction (van Noordwijk 1987), especially the laying-date (van Noordwijk et al. 1981). An important question is whether the differences between the Corsican and mainland populations fall within the scope of the phenotypic plasticity ("reaction norm") of the two populations considered together, or express genetical differences between them. Indeed, it might be that such differences between life-history traits are the phenotypic expressions of the same genotype under different climates, food supplies or other environmental factors. The problem is to determine the genetical and environmental components of the difference between the two populations. The most direct way to work out this problem is to breed birds from the two habitats in standardized conditions in order to leave the genetical component to be fully expressed. This can be achieved by moving samples from one habitat to the other or, better, by moving samples from the two habitats into a third different one, to see if the differences between life-history traits remain or not. This should be done by raising newly-born nestlings in order to eliminate environmental imprinting of the birds. Since the two samples are in a same and new environment, any difference between life-history traits will be genetical (van Noordwijk et al. 1980). The aim of this paper is to test to what extent the differences in laying-date between the two populations is genetically determined.

Material and methods

Two samples of twelve nestlings each were collected during the spring of 1985 in both the mainland study site (Mont-Ventoux) and on Corsica (see Blondel 1985 for a description of the sites). The birds were collected two days after hatching, from unrelated parents in three different nests. They were then hand-raised till fledging and were put in six large aviaries, 3m*3m*3m*, erected at the CNRS site in Montpellier. Environmental conditions and provision of food were the same for all birds. The food supply consisted of mealworms, sunflower seeds and a mixture of protein-rich food especially devised for insectivorous passerines. Pairing of these monomorphic birds was performed using the ratios of oestrogenous/androgenous hormones in the faeces, assuming that this ratio expresses the metabolism of the totality of the sexual hormones produced by the birds (Colomb 1984). The technique proved to be successful since all the birds were correctly sexed. As far as possible we tried to change the partners of the pairs in the different years (see identification numbers in Table 1).

Results

Six cases of breeding, at least up to hatching, were recorded in the aviaries for each sample between 1986 and 1988 (see Table 1). Data on clutch size will not be discussed because artificial food conditions in the aviaries made it difficult to interpret them. Notice, however, that the average clutch size of captive Corsican tits is nearly the same as that of the wild population, while the average clutch size of captive mainland tits is much lower than that of the wild population.

Table 1. Identification of pairs, dates of nest-building and of laying-date and clutch size of the mainland and of the insular samples of blue-tits in the aviaries. Mean values in the wild are given for comparison. Standard deviation of the means in brackets.

Mainland Year	Identification		Building	Laying	Clutch size
	Male	Female			
1986	348	522	27 March	26 April	9
1987	350	522	31 March	22 April	5
1987	570	524	17 March	27 April	5
1988	570	524	15 March	23 April	5
1988	505	522	28 March	22 April	5
1988	809	808	4 April	29 April	9
	Mean (aviaries)		26 March (7.9)	25 April (2.9)	6.3 (2.1)
	Mean (wild)		2 April (9.4)	27 April (8.5)	8.6 (1.8)
Corsica Year	**Male**	**Female**	**Building**	**Laying**	**Clutch size**
1986	474	401	24 April	10 May	7
1987	474	401	29 April	8 May	8
1987	792	488	5 May	11 May	6
1988	474	401	25 April	14 May	7
1988	796	488	5 May	10 May	7
1988	788	478	8 May	20 May	5
	Mean (aviaries)		1 May (5.8)	12 May (4.3)	6.7 (1.0)
	Mean (wild)		26 April (7.8)	9 May (13.9)	6.3 (1.1)

Nest building

The continental blue-tits started to build their nest on average on March 26 (s.d. = 7.9) whereas their insular counterparts began to build their nest on May 1 (s.d. = 5.8). These figures are very similar to those recorded in the wild populations to which the captive birds belong (Table 1).

Laying-date

The time-span between the laying-date of the mainland and insular captive samples is also of the same order of magnitude in all cases (Table 1). Captive mainland birds laid their first egg on average on April 25 (s.d. = 2.9) and island

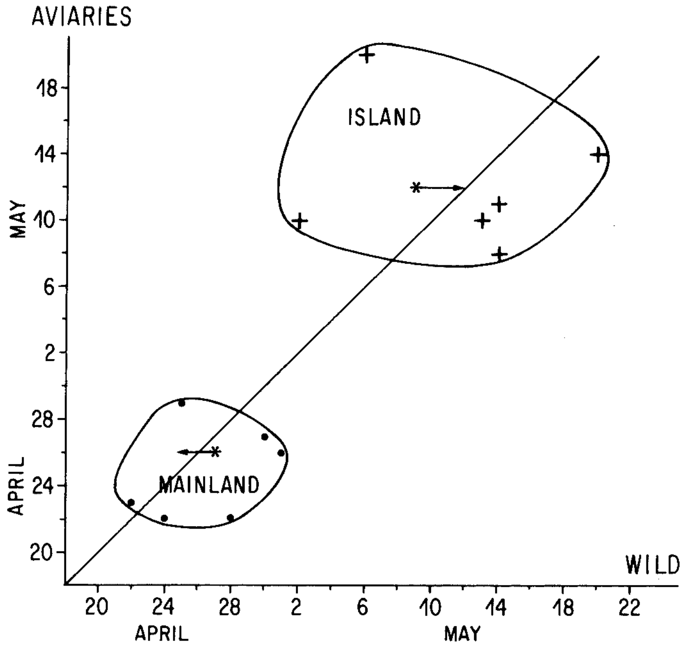

Fig. 1. Relation between the laying-date of captive birds (lower envelope for mainland, upper envelope for island) and the laying-date of 12 (six for each region) randomly selected pairs of the wild populations. * Asterisks indicate laying-date of the wild populations for the years 1986–88 combined. Arrows indicate the numbers of days of earliness (mainland) and lateness (island) of the experimental samples in comparison with the wild populations.

birds on average on May 12 (s.d. = 4.3). The difference between the two samples is highly significant (Wilcoxon's test, $P < 0.001$). These dates are very similar to those recorded for the years 1986–88 combined in the wild populations: April 27 (s.d. = 8.5) in Mont-Ventoux and May 9 (s.d. = 13.9) in Corsica. Mainland captive birds started to lay on average 2 days ahead of their wild counterparts and island captive birds 3 days later. Thus, differences between the two populations have even been accentuated in the aviaries. To illustrate the results, we have plotted the six data of each experimental sample against the laying-date of six randomly selected pairs of the wild populations (Fig. 1). This figure illustrates (1) a clear correlation between the laying-date values of the experimental and of the wild samples, (2) a larger variation for this trait in the island population compared to that on the mainland, and (3) that the mainland birds were slightly earlier and the island birds slightly later than their wild counterparts (see arrows on Fig. 1).

The large differences between the two wild populations in the time-span between nest-building and egg-laying, i.e. 25 days on the mainland and 13 days on Corsica, were maintained by the captive samples and were even slightly accentuated. In the aviaries, the differences were 30 days for the mainland sample and 10 days for the insular one. Thus, there is a conspicuous contraction of the breeding cycle on

Corsica, the biological meaning of which will be discussed later. It is noteworthy that such important differences between the two populations remained unchanged over the three years of the experiment. The Corsican captive birds did not adjust these life-history traits to their new environment and bred as if they were still on Corsica.

Discussion and conclusion

The fact that such large differences in life history traits persisted while the two experimental samples were submitted to a new environment supports the hypothesis that the differences in these traits are largely genetically determined. Indeed, possibilities of genotype-environment interactions, as well as of maternal effects, were eliminated from the experiment by removing the young from their nest soon after hatching. On the other hand, this experiment does not say anything about the genetic mechanisms, which are probably complex because traits with high adaptive value such as laying-date or clutch size are polygenic (Boag et al. 1987). In terms of selection and evolutionary potential, knowledge of the genetic variance of demographic traits requires measures of quantitative genetics. For example, van Noordwijk et al. (1980) and Jones (1973) found for the great-tit *Parus major* repeatability values for the laying-date of 0.27 and 0.34 respectively. Moreover, heritability values of an order of magnitude of 0.35 to 0.40 for traits associated with reproduction have been found in this species (van Noordwijk et al. 1981, van Noordwijk 1987). Such values express strong genetic components for these traits. If heritability values of the laying-date are of a similar order of magnitude in the Mediterranean populations of the blue-tit as in those of the great-tit cited above, then the high inter-individual variation of this trait (s.d. = 8.5 days on the mainland and 13.9 days in Corsica) means that directional selection might act very rapidly.

Any demonstration of a genetic component of ecologically important traits emphasizes the need to identify selective pressures that have shaped the mean values. The adaptive significance of the differences in life-history traits between the mainland and the insular populations should be examined through detailed studies of ecological constraints. These will be very briefly summarized here (see Blondel 1985, Blondel et al, 1987 for more details). In contrast to what is commonly thought about insular biotas, the Corsican environment of the tits is characterized by two sets of severe constraints: (1) climatical constraints at the end of the breeding season with very high temperatures (up to 34° C) as early as mid-June, and (2) constraints due to a very low food supply, especially at the beginning of the breeding season (Blondel et al. 1987). Moreover, we have shown (Blondel et al. in prep.) that the proportion of caterpillars, a water-rich prey that is actively searched for by the tits (van Balen 1973), is much lower on Corsica (17.4% of the diet) than on the mainland (57.7%). A large part of the diet of the Corsican nestlings is composed of spiders, the water content of which is much lower (Eguchi 1980). Therefore, problems of hyperthermia in late broods are problably made worse by a deficit in the water balance of the nestlings. For this reason, the probability of successful fledging is extremely low for broods still in the nest after the 20th of June (average fledging date = 17 June). These constraints at both extremities of the breeding event force the birds to complete their breeding cycle between two close and impassable limits. This explains why the breeding cycle starts so late on the island, why it is so much contracted, and why there are never any second broods and very few repeat clutches. The low clutch size on Corsica probably also results from this set of constraints. While the food supply is very low and occurs late in the season (Zandt et al, in press), the best compromise between clutch quality and probability of survival of both the young and the female is to lay a small clutch adapted to the few young that adults are able to raise (see Martin 1987, Nur 1988). Thus, date of nest-building, laying date and clutch size are assumed to have evolved in relation to one another, as a response to the local constraints of the Corsican environment. In this context, it is noteworthy that the clutch size of the Corsican captive birds was almost the same as that of the natural population (Table 1).

Since the captive birds were removed from their nest soon after hatching, our experiment does not support the hypothesis of non-genetical maternal effects or of genotype-environment correlations. The differences in laying-date and associated traits between the two experimental samples, and the fact that these differences have persisted over the three years of the experiment, is a demonstration that these traits are adapted to the specific set of environmental factors of each region. Results so far accumulated on the genetics of ecologically important traits (van Noordwijk 1987), justify the interpretation according to which the phenotypic variation of traits such as the laying-date has an additive genetic component allowing them to respond to selection. However, microevolutionary processes that determine genetic changes over time could be demonstrated only through long-term experimental studies using quantitative genetics.

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