

Genetic and photoperiodic control of an avian reproductive cycle

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Abstract. European blackcaps, *Sylvia atricapilla*, with one breeding season per year, have a single-peaked annual testes cycle. However, African conspecifics from the Cape Verde Islands with two breeding seasons per annum demonstrate a two-peaked cycle. Both population-specific cycles reflect differences in the respective endogenous circannual rhythms. Experimental hybridization of birds of the two populations resulted in an intermediate pattern of testes cycle, thus demonstrating that there are genetic components for some temporal aspects in an avian reproductive cycle. Another characteristic of the African birds, their extremely rapid juvenile development and early sexual maturity (at an age of 5–6 months) proved largely to be a photoperiodic (short-day) effect in birds hatched in autumn. The same effect could also be induced in European conspecifics exposed to correspondingly short day-lengths.

Key words. Reproductive cycle; *Sylvia atricapilla*; genetic and photoperiodic control; annual rhythms; breeding seasons.

Although reproductive cycles of free-living birds have been studied since the beginning of the century¹, little is known about their control mechanisms. In seven species it has been shown that the annual gonadal cycles are based on endogenous so-called circannual rhythms^{2,3}, and in many species photoperiod has been shown to play an important role in synchronizing these rhythms with the environment². Other potential environmental controlling factors have been examined less intensively⁴. Studies on tropical species or populations are scarce³, and data on possible genetic control mechanisms have generally not been presented^{2,5}.

The blackcap, *Sylvia atricapilla*, provided the opportunity to investigate the respective roles of genetic and environmental factors in controlling reproductive cycles. There were two reasons for the choice of species. First, the tropical African population on the Cape Verde Islands has two distinct annual breeding seasons⁶, whereas the Eurasian and northern African populations have only one⁷. And second, blackcaps can be readily bred and hybridized in captivity⁷.

Materials and methods

We used changes in the testes length of male blackcaps as an index of reproductive condition. In addition, actual breeding and female ovarian cycles were checked. For Eurasian birds, the testes cycle of a migratory South German population was established. During its stay on the breeding grounds from March to October, monthly data samples of 7 individuals were collected during 1968–1970. From November to February 1984/1985 testes size was determined by monthly laparotomy

in 6 males kept under the natural S. German photoperiod (fig., top row). By keeping 16 hand-raised S. German blackcaps in various constant experimental conditions for up to 3 years it was shown that their testes cycle displayed endogenous circannual rhythmicity⁸.

Thirty African blackcaps from the Cape Verdes (Santiago) were collected at the end of October 1982 as nestlings at an age of about a week during the autumn breeding period⁶. These birds were transferred to Radolfzell, S. Germany, where they were held under photoperiodic conditions simulating those of the Cape Verde Islands until March 1983. They were then divided into 3 groups: 6 males and 3 females in simulated Cape Verdes light conditions (fig., second row); 7 males and 3 females under a constant light-dark cycle of 13:11 h (400 lux, 25 °C; fig., third row); and 5 males and 6 females in aviaries in S. Germany for cross-breeding experiments with S. German birds. From the last group a total of 35 hybrids were obtained in 1983 and 1984, of which 11 males (and 10 females) were kept under light conditions simulating those of the Cape Verdes (fig., fourth row). Finally, 14 S. German blackcaps (10 males, 4 females) were hand-raised and kept under a photoperiod simulating that of the Cape Verdes. The conditions simulated an October hatch date. Testes size was established by laparotomy at approximately monthly intervals. In addition, body weight, moult and locomotor activity were regularly recorded⁹.

Results and discussion

In accordance with the single breeding season per year, European blackcaps have a single testes cycle per an-

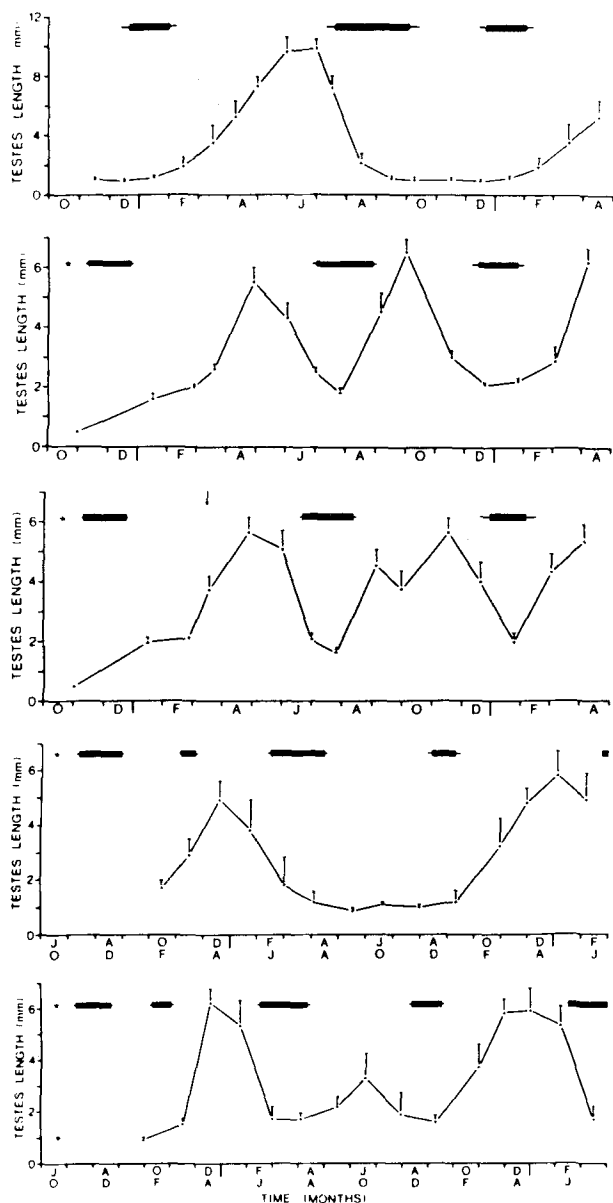


Figure. Testes cycles of 5 groups of blackcaps. 1st row, S. German birds, from October in the first year to April in the third year; March to October from birds in the wild, for the other months from experimental birds; 2nd row, birds from the Cape Verdes, kept under photoperiodic conditions of these islands; 3rd row, birds from the Cape Verdes, from March (arrow) kept under constant experimental conditions; 4th row, S. German birds, kept under photoperiodic conditions of the Cape Verdes. The upper scale of months indicates the real time the birds have lived in, the lower gives the time scale of photoperiodic simulation. 5th row, hybrids of S. German and Cape Verdean birds kept under the photoperiodic conditions of the Cape Verdes, scales as 4th row. Asterisks, mean dates of hatching; vertical bars, standard errors; thick horizontal bars, moult periods with standard errors. For more details see 'Materials and methods'.

num (fig., top row). The biannual breeding season of the Cape Verdean population corresponded to the two-peaked annual testes cycle which was found in these birds (fig., second row). Since testes developed to full breeding maturity twice a year (seminiferous tubules at

their maximum diameter) it is likely that individual birds are ready to breed twice a year. Hence spring and autumnal breeding appears not to be the result of the presence of different groups of birds. In both populations, moult periods are interposed between testes cycles. In European birds the summer moult is a complete one; in African birds, that after the first testes cycle.

The two-peaked testes cycle of the Cape Verdean birds as well as the specific moult periods also persisted under constant experimental conditions (fig., third row). This, and the slight deviation of the cycles from the calendar year in the second year, indicated that their biannual nature was integrated into an endogenous circannual rhythmicity, as the cycles are in European conspecifics⁸. Thus the two-peaked testes cycle in Cape Verdean blackcaps seems to be a heritable, population-specific characteristic like the one-peaked one in Eurasian birds. This is supported by the fact that S. German blackcaps still show their normal one-peaked testes cycle when they are raised and kept under photoperiodic conditions simulating those of the Cape Verdes (fig., fourth row). A genetic basis for the second autumnal testes development of the Cape Verdean birds is finally shown in the hybridization experiment. Population hybrids showed an intermediate second peak of testes development in June (fig., bottom row). The hybrids had significantly larger testes than both S. German bird groups (under both Cape Verdean and European photoperiodic conditions) in all months from May to August and September to November, respectively ($p < 0.05$ to < 0.001 , U-test). The secondary gonadal peak around June was recognizable in all 11 experimental male hybrids.

Cape Verdean blackcaps with an October hatch date were found to reach breeding maturity the following spring at an age of only 5–6 months, after an extremely rapid juvenile development (fig., second row). We tested whether this was another heritable characteristic of this population or a result of the short and decreasing day-lengths experienced by these birds. Such cues are known to accelerate annual processes in birds strongly². S. German blackcaps were used to test this. Birds hatched in June were exposed to the photoperiodic conditions they would have experienced when hatched at the end of October on the Cape Verdes (fig., fourth row). After a similar rapid juvenile development, full testes size was reached in these birds after 5–6 months. This contrasts with normal conditions where European blackcaps attain breeding maturity for the first time only after about 9–13 months⁷. Thus this early breeding maturity is largely a photoperiodic effect induced by short, decreasing day-lengths.

Females, where samples were checked monthly, showed reproductive cycles basically like those of males.

In conclusion, the various reproductive cycles of different African and European blackcap populations are the result of different endogenous circannual rhythms obvi-

ously based on genetic control mechanisms and photoperiodic effects which set a relatively early phase of breeding conditions in African birds.

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