Endogenous Reproductive Rhythms in a Tropical Bird

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Like other tropical birds, African stonechats breeding at the equator reproduce once a year during the main rainy season and subsequently carry out a complete molt. These two activities are controlled by endogenous circannual mechanisms: in stonechats held in constant conditions of photoperiod and temperature, a rhythm of gonadal size and molt persisted for up to 7.5 years, which would be a lifetime for free-living conspecifics. The fact that the period of these rhythms deviated from 12 months demonstrates their true endogenous nature. The results represent the longest circannual reproductive rhythm yet documented and suggest that circannual mechanisms may be of particular importance for reproductive timing in tropical organisms.

IN MANY TROPICAL ANIMALS, REPRODUCTION and other seasonal events are organized on the basis of an annual rhythm. This is true even in areas close to the equator, where environmental conditions often show only minor and irregular seasonal fluctuations. In tropical birds, reproduction is generally timed to the rainy or dry seasons, and thus the annual precipitation cycle itself has been assumed to provide major stimuli for the control of breeding activities (*1–4*).

However, because gonadal recrudescence and the physiologic and behavioral changes associated with it are time-consuming processes, a long period of preparation is necessary. Moreover, reproduction must be suitably timed with other seasonal activities such as molt or migration. Because of their complexity, it is unlikely that these external and internal temporal adjustments are exclusively controlled in a simple way by environmental cues. It has been suggested that endogenous factors play a crucial role in these adjustments by preprogramming the approximate timing and proper sequence of activities. The possible involvement of circannual rhythms, generated in the organism itself and capable of persisting for years in the absence of annual environmental changes, has been considered (*5–16*).

Evidence in support of such a mechanism is still unconvincing, primarily because the possible involvement of environmental timing cues has not been excluded with certainty (*16*). We investigated whether the annual cycles of gonadal function and molt of an equatorial bird, the stonechat (*Saxicola torquata axillaris*), can result from a circannual mechanism.

The experimental birds originated from a breeding population in Kenya, less than 30 km south of the equator. In the field, these birds start gonadal development in October and November, following termination of the complete postnuptial molt, and egg-laying normally begins in April or May, at the onset of the main rainy season (*17*). In the laboratory, we tested birds under constant conditions with two different light-dark cycles. Experiment 1 was carried out with seven males and ten females held for 28 or 29 months in a constant photoperiod of 12.25 hours per 24-hour day. In experiment 2, another five males and ten females were kept for either 29 months (three males, six females) or 90 months (two males, four females) in a slightly longer photoperiod of 12.8 hours. A 12.25-hour photoperiod corresponds approximately to the length of day measured at the equator between a 10-lux threshold in the morning and evening and thus presumably represents a realistic simulation of the length of day experienced by an equatorial bird (*18*). A 12.8-hour photoperiod, on the other hand, corresponds to the length of day measured between 0.1-lux

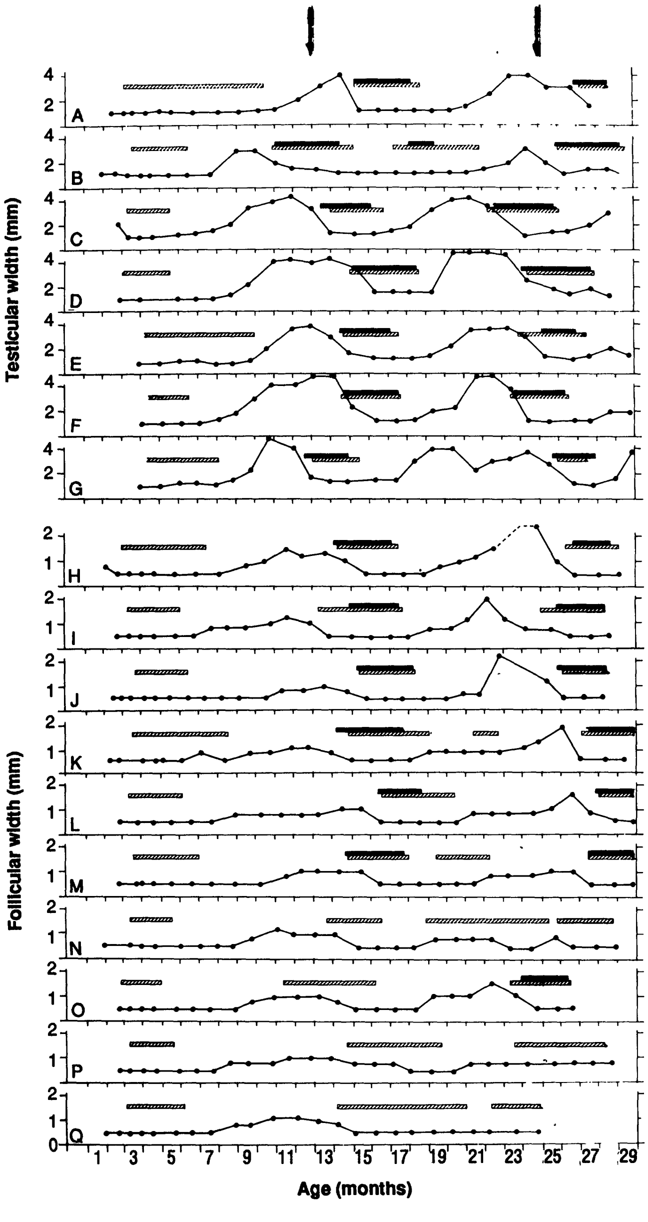

Fig. 1. (**A–G**) Changes in testicular width of seven male stonechats. (**H–Q**) Width of the largest ovarian follicle of ten females that were held for 24 to 29 months in a constant photoperiod of 12.25 hours. Bars indicate the occurrence of molt (black bars = molt of flight feathers, hatched bars = molt of body plumage). The two arrows indicate the birds' first and second birthdays. Female H laid an egg at an age of 23 months, and a measurement of follicular width could therefore not be taken. This is indicated by the dashed line. Female Q died when 24 months old. Although the birds were held in constant conditions of photoperiod and temperature, the gonadal and molt cycles observed in most birds during the first year were similar to those of free-living conspecifics, which begin gonadal growth at an age of about 7 months and begin molting at about 14 months (*17*). During the second year, however, the gonadal and molt cycles tended to occur earlier or later in the experimental birds than in free-living birds, because the overall periods of the circannual rhythms of the experimental birds were not 12 months.

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thresholds and thus presumably represents a longer day than that normally experienced by an equatorial bird (*18*). As an index of reproductive capacity, we measured testicular width in the males and the diameter of the largest ovarian follicle in the females at 3- to 8-week intervals. In addition, birds were checked for molt once a week (*19*).

After postjuvenile body molt, essentially all the birds of experiment 1 went through two successive gonadal cycles that were separated by 9 to 15 months (Fig. 1). A full molt was carried out by most birds after each gonadal cycle. Among the 15 birds of experiment 2 that were exposed to the slightly longer photoperiod of 12.8 hours, only six birds (three males and three females) went through two gonadal cycles within the first 29 months ($P < 0.01$, Fisher exact test). Thereafter, four of the six birds that were left in the 12.8-hour photoperiod for a total of 90 months continued to cycle until the end of the experiment.

Figure 2 shows records of the two stonechats that exhibited the clearest circannual rhythms. In the male, the periods of both the testicular and molt rhythms were consistently shorter than 12 months. The mean (±SD) period measured between successive onsets of body molt was 9.1 ± 1.9 months. As a result, nine cycles occurred within the 7.5 years of the experiment. In the female, the period was also much shorter than 12 months (between 9 and 10 months) over the first 3 years but lengthened thereafter to values close to 12 months (*20*).

Although endogenous circannual rhythms have been observed in other organisms, previous results from tropical birds have been ambiguous. This has been particularly true of experiments where rhythms with periods very close to 12 months were observed because of the possibility that the origins of these rhythms were exogenous, that is, the rhythms were caused by some uncontrolled environmental variable (*16*). The results from our experiments with stonechats exclude such a possibility. In the two birds shown in Fig. 2, the consistent deviation of the period from 12 months resulted in a net gain of one subjective year (female) or one and one-half subjective years (male) over the 7.5-year study. These results cannot be reconciled with any model for the exogenous production of these rhythms. Because it is likely that stonechats only rarely reach an age of 7.5 years, the results also indicate that circannual mechanisms may play a role throughout life.

In several animal species, circannual rhythms persist only under a very limited set of photoperiodic or temperature conditions, which are sometimes even different from those normally experienced in nature (*21, 22*). In such species, the most conspicuous feature of circannual rhythms—their persistent, self-sustaining behavior—may be of no functional significance in normal life because the circannual rhythms are not expressed under naturally occurring conditions. This is clearly not the case in the tropical stonechats, which would benefit directly from an endogenous timing device that would continue to cycle in a constant environment similar to that normally experienced in nature. Moreover, as shown in Fig. 1, essentially all birds held in the 12.25-hour photoperiod went through circannual gonadal and molt cycles. This suggests that the vast majority of individuals in this population could normally rely on a circannual mechanism. In contrast, under the 12.8-hour photoperiod, which is presumably an abnormally long simulation of an equatorial day (*18*), only about 40% of the birds exhibited circannual rhythms. These results therefore suggest that the circannual system

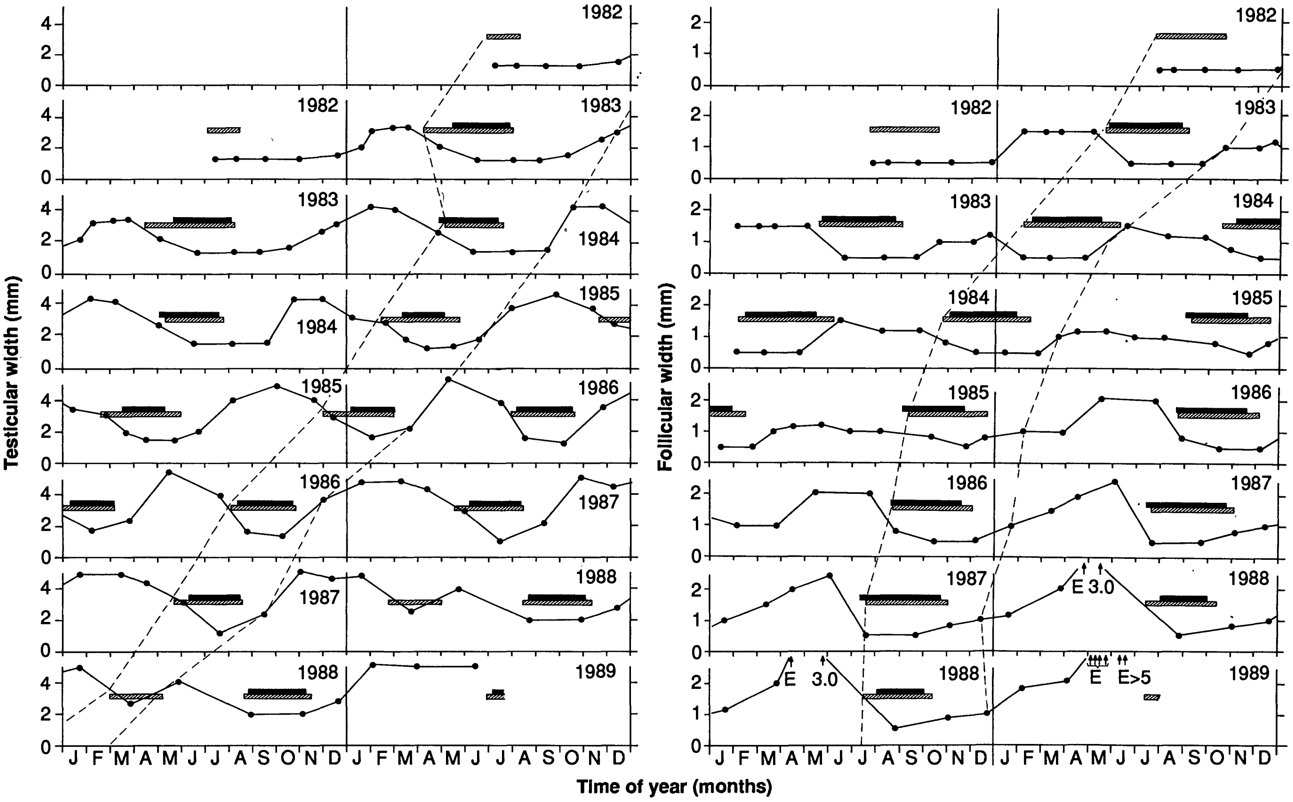

Fig. 2. Changes in testicular width of a male stonechat (**left**) and in the width of the largest ovarian follicle of a female (**right**). Both birds hatched in Kenya and subsequently were held for 7.5 years in a constant photoperiod of 12.8 hours. Bars indicate the occurrence of molt (black bars = molt of flight feathers, hatched bars = molt of body plumage). In both diagrams, data from successive years are mounted underneath each other, and the original record is double-plotted on the right. For each bird, the dashed line on the left connects successive onsets of body molt, and the dashed line on the right connects successive onsets of gonadal growth. Onsets of gonadal growth were defined as the dates at which testicular widths of more than 3 mm and follicular diameters of more than 1 mm were measured for the first time during successive gonadal cycles. E below an arrow indicates that the female laid an egg; 3.0 and >5 below arrows indicate offscale diameters of 3.0 mm and >5 mm of the largest follicle.

of these birds, like that of other species (*21, 22*), is adjusted specifically to the naturally occurring photoperiodic conditions.

In all experimental birds that had a complete molt, the molt started as the gonads began to regress, which is consistent with the situation in free-living conspecifics (*17*). This contrasts with findings in some other avian species, where the rhythms of gonadal size and molt tend to dissociate in the absence of environmental synchronizing agents (*16, 23, 24*). The rigidity of the temporal relation between the gonadal and molt cycles in the African stonechats suggests that circannual mechanisms in this species play an important role not only in the adjustment of seasonal activities to the environment but also in the maintenance of internal temporal order in an environment that lacks pronounced external seasonal information.

Although our results strongly suggest that the basic mechanism underlying annual periodicity in these tropical birds has a strong endogenous component, they do not exclude the participation of environmental timing cues. On the contrary, the fact that the period of rhythmicity tends to deviate from 1 year in constant conditions indicates that external stimuli are usually involved in synchronizing circannual rhythms with the calendar year. Factors related to the rainy or dry seasons are likely candidates (*1–4, 17*).

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18. Data obtained from other avian species suggest that full photoperiodic responses occur only at light intensities of 10 lux or more [G. A. Bartholomew, *Bull. Mus. Comp. Zool. Harv. Univ.* **101**, 433 (1949); M. Menaker and A. Eskin, *Science* **157**, 1182 (1967)]. Results from other species have indicated that the expression of circannual rhythms may depend on the appropriate duration of constant photoperiod (*21, 22*). It was therefore of interest to find out whether the circannual cycles of our equatorial stonechats would also require an appropriate simulation of constant photoperiod.
19. Five males and four females of experiment 1 (**A**, **B**, **E–K** in Fig. 1) and all birds of experiment 2 were collected in April and May near Nakuru, Kenya (0°15′S, 36°0′E), and transported to Andechs, West Germany, within 2 weeks. These birds were collected when they were 4 to 8 days old. Two males and six females (**C**, **D**, **L–Q** in Fig. 1) were bred from African birds caged in Andechs. The birds were handraised and subsequently fed as described [E. Gwinner, V. Neusser, D. Engl, D. Schmidl, L. Bals, *Gefiederte Welt* **5**, 118 (1987); *ibid.*, p. 145. They were kept in individual cages, housed in groups of six to nine in temperature-controlled environmental chambers (20° ± 3°C). Testicular width or follicular diameter were determined by laparotomy [E. Gwinner, *Tierpsychol.* **38**, 34 (1975).] We assessed molt by checking birds for the occurrence of growing body feathers (body molt) or flight feathers (flight-feather molt). We established the length of the circannual period of the gonadal cycles by determining the interval between times at which testicular width exceeded 1.2 mm and follicular width exceeded 0.5 mm during successive phases of gonadal growth.
20. Of the remaining two birds that exhibited circannual rhythms, one had a long period (about 18 months) during the first three cycles and a shorter one (about 14 months) during the last three cycles. The period of the other rhythmic bird was close to 12 months. In the two arrhythmic birds, gonadal size went through irregular cycles of growth and regression and molt occurred at variable intervals.
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Increased Life-Span of *age-1* Mutants in *Caenorhabditis elegans* and Lower Gompertz Rate of Aging

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A mutation in the *age-1* gene of the nematode *Caenorhabditis elegans* has been shown to result in a 65 percent increase in mean life-span and a 110 percent increase in maximum life-span at 25°C. One of the hallmarks of organismic aging and senescent processes is an exponential acceleration of age-specific mortality rate with chronological age. This exponential acceleration is under genetic control: *age-1* mutant hermaphrodites show a 50 percent slower rate of acceleration of mortality with chronological age than wild-type strains. Mutant males also show a lengthening of life and a slowing of the rate of acceleration of mortality, although *age-1* mutant males still have significantly shorter life-spans than do hermaphrodites of the same genotype. The slower rates of acceleration of mortality are recessive characteristics of the *age-1* mutant alleles examined.

A NOW CLASSIC OBSERVATION IN gerontology (*1*) is that human aging is associated with exponential accelerations of age-specific mortality rate, $m(t)$. Moreover, similar exponential relations between $m(t)$ and chronological age (t) are observed to result from mortality due to any one of many distinct causes, including both diseases and accidents (*2*). In a variety of other species, both vertebrate and invertebrate (*3, 4*), exponential accelerations of mortality rate with increasing chronological age also are observed; Sacher has termed this age-related acceleration the actuarial aging rate (*4*). These observations are consistent with the definition of senescence in evolutionary theory as "the tendency for the age-specific survival probabilities . . . to decline with increasing age . . ." (*5*, p. 214); however, theory makes no prediction about the form or nature of this decline. The nematode *Caenorhabditis elegans* shows exponential increases in age-specific mortality rate (*6*) with increasing chronological age that are specified in part by a polygenic system (*7*). Age-specific mortality rate can be accurately modeled as a function of chronological age with the use of only two parameters: A, initial mortality rate, which here is used as a measure of mortality rate at maturity; and α, the exponential Gompertz component, which describes the rate of acceleration of age-specific mortality with chronological age. These two parameters are related to $m(t)$ at age t by the Gompertz equation:

$$m(t) = Ae^{\alpha t}$$

Despite consistent findings of an expo-

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