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Circannual rhythms in tropical and temperate-zone stonechats: a comparison of properties under constant conditions*

Ein Vergleich circannualer Rhythmen bei Schwarzkehlchen aus den Tropen und den gemäßigten Breiten

Von Eberhard Gwinner

Dedicated to Dr. Hans Löhrl on the occasion of his 80th birthday.

Key words: Stonechat, *Saxicola torquata*, circannual rhythms, reproductive cycles.

Abstract

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Male and female stonechats (*Saxicola torquata*) of the equatorial subspecies *axillaris* from Kenya and of the temperate zone subspecies *rubicula* from central Europe were handraised and subsequently held for 24 to 30 months in a constant 12.25 h equatorial photoperiod.

Gonadal size and molt were assessed at regular intervals. Most birds of both subspecies went through two successive circannual cycles in gonadal size and molt. This suggests that circannual rhythms play a role not only in birds inhabiting tropical environments characterized by small and often irregular seasonal variations but also in birds of higher latitudes. Some of the differences observed in the pattern of the gonadal and molt cycles can be interpreted as adaptations to the different environmental conditions to which the two subspecies are normally exposed.

Zusammenfassung

GWINNER, E. (1991): Ein Vergleich circannualer Rhythmen bei Schwarzkehlchen aus den Tropen und den gemäßigten Zonen. Ökol. Vögel 13: 5-14.

Männliche und weibliche Schwarzkehlchen (*Saxicola torquata*) der am Äquator vorkommenden Unterart *axillaris* aus Kenia und der in den gemäßigten Breiten brütenden Unterart *rubicula* aus Mitteleuropa wurden von Hand aufgezogen und anschließend 24 bis 30 Monate lang in einer konstanten 12.25-stündigen äquatorialen Photoperiode gehalten. Ihre Gonadengröße und Mauser wurden in regelmäßigen Abständen bestimmt. Die meisten Vögel beider Unterarten gingen durch 2 aufeinanderfolgende circannuale Zyklen der Gonadengröße und der Mauser. Die Ergebnisse sprechen somit dafür, daß circannuale Rhythmen nicht nur bei solchen Vögeln eine Rolle spielen, die in einer äquatornahen Umwelt leben, sondern auch bei Vögeln höherer geographischer Breiten. Einige kleinere Unterschiede im Muster der Gonaden- und Mauserzyklen lassen sich als Anpassungen an die unterschiedlichen Umweltbedingungen interpretieren, denen die beiden Unterarten normalerweise ausgesetzt sind.

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1. Introduction

Endogenous circannual rhythms persisting for several cycles in annually constant conditions have been demonstrated in more than 40 species of plants and animals. These include: rhythms of growth and longevity of hydrants in coelenterates (BROCK 1975 a-c), diapause in insects (BLAKE 1959 a, b), behavioral thermoregulation in fish (KAVALIERS 1982), locomotor activity in reptiles (STEBBINS 1963), moult, migratory disposition and reproductive capacity in birds, and hibernation, breeding activity and food and water intake in mammals (GWINNER 1986 for review). Although these investigations have attested to a previously unexpected wide distribution of circannual rhythms, particularly among long-lived organisms, both their physiological bases and functional significance have remained obscure. The aim of the present investigation was to elucidate the biological role played by circannual rhythms in the organisation of avian annual reproductive and moult cycles. This was done by comparing the performance of a tropical and a temperate-zone avian subspecies of a passerine bird, held under the same seasonally constant conditions.

For our investigation we have selected the stonechat (*Saxicola torquata*), a species with an unusually wide breeding range in Eurasia and Africa (Figs. 1 and 2). The subspecies *S.t. axillaris*, and *S.t. rubicula* (in the following called *axillaris* and *rubicula*, respectively) were examined. *Axillaris* breeds in Eastern Africa. Birds in a

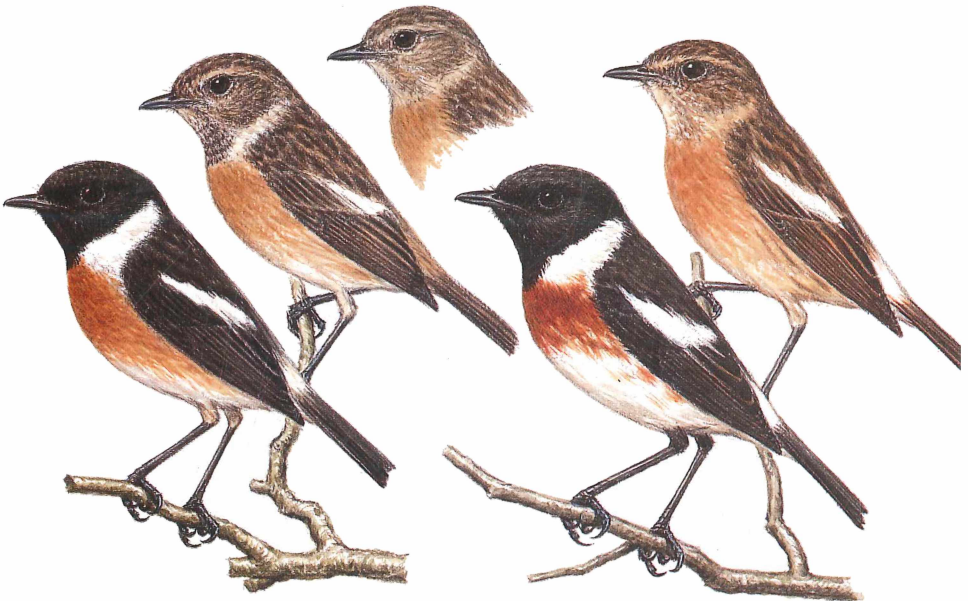


Fig. 1. European (*Saxicola torquata rubicula*) and East African (*S.t. axillaris*) stonechats. From left to right: *rubicula* ♂; *rubicula* ♀ (autumn and winter); *rubicula* ♀ (spring); *axillaris* ♂, *axillaris* ♀. Illustration by H. KACHER.

population living close to the equator in Kenya have a well-defined breeding season that begins with the onset of the main rains in March, April or May (BROWN and BRITTON 1980, DITTAMI and GWINNER 1985). *Rubicula* has a breeding distribution all over Europe and Northern Africa, where it reproduces in spring and early summer. In both subspecies the breeding season is followed by a complete molt (GLUTZ VON BLÖTZHEIM and BAUER 1988). The annual changes from reproductive to non-reproductive conditions are accompanied by pronounced seasonal changes in gonadal

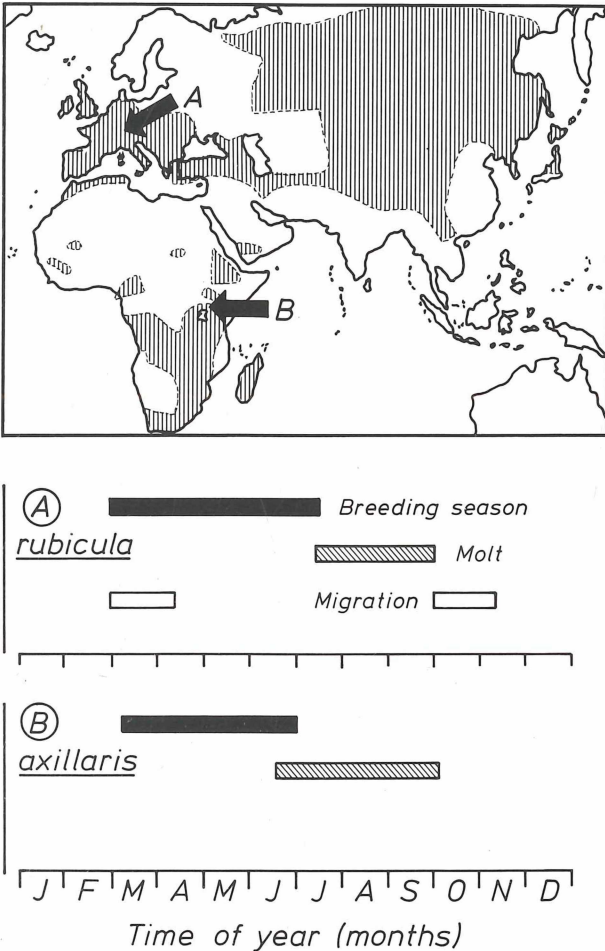


Fig. 2. Upper diagram: Breeding distribution of the stonechat (modified from Voous 1960). The arrows mark the sources for experimental *rubicula* (A) and *axillaris* (B). Lower diagrams: Approximate seasonal occurrence of the breeding and molting seasons in the two subspecies as well as timing of migration in *rubicula*. (Based on data in GLUTZ VON BLÖTZHEIM and BAUER 1988, DITTAMI and GWINNER 1985, ZINK 1973, and on unpublished data).

size and plasma concentrations of LH, testosterone and estradiol (DITTAMI and GWINNER 1985; SCHWABL, FLINKS and GWINNER, unpublished data). A body molt is carried out by both subspecies after fledging. It starts later and lasts longer in *axillaris* than in *rubicula* (GWINNER et al. 1983).

We have shown previously that in *axillaris* the annual rhythms of gonadal size and molt are controlled by endogenous circannual rhythms (GWINNER and DITTAMI 1990). Evidence for such a mechanism came from the finding that birds held for up to 7½ years in constant conditions of photoperiod and temperature continued to go through repeated cycles of gonadal size and molt. The period of these rhythms tended to deviate from one year, thus attesting to their true endogenous nature. These results are consistent with an old hypothesis suggesting that endogenous circannual rhythms may play a particularly important role in the control of the annual cycles of tropical organisms inhabiting environments with only small and often irregular seasonal variations (e.g. MOREAU 1931, CHAPIN 1932, BAKER & BAKER 1936, BAKER & RANSON 1938, MOREAU et al. 1947, ASCHOFF 1955, MARSHALL 1959, 1960a, b, MARSHALL & SERVENTY 1959, IMMELMANN 1971, GWINNER 1986). In such species endogenous timing mechanisms may make up for the lack of reliable exogenous time-giving cues. If a tropical environment does, indeed, exert particularly strong selective pressures on the evolution of circannual rhythms, one might expect that circannual mechanisms are less well developed in taxa occurring at higher latitudes than in related lower latitude birds. We have tested this prediction by keeping *rubicula* and *axillaris* from birth for more than two years in constant photoperiodic and temperature conditions similar to those normally experienced by free-living equatorial birds.

2. Methods

Five male and four female *axillaris* were collected as nestlings in April and May near Nakuru, Kenya (0°14'S, 36°0'E) and transported to Andechs, West Germany within two weeks. Two additional males and six females (C, D, L-Q in Fig. 2) were bred from African birds caged in Andechs. 13 male and 7 female *rubicula* were collected as nestlings in Mai, June and July near Vienna, Austria (47°40'N, 36°30'E) and transported immediately to Andechs. All birds were hand-raised as described in GWINNER et al. (1987). They were kept in individual cages, housed in groups of 6 to 9, in temperature controlled chambers at 20±3°C. Photoperiod was held constant at 12.25 hours. At intervals of one week or less birds were checked for the occurrence of body and flight feather molt. The onset of molt was defined as the date between the last check without molt and the first check with molt. Every 3 to 8 weeks birds were laparotomized to determine the testicular width in the males and the diameter of the largest ovarian follicle in the females. In the males, the onset and end of testicular growth was defined as the time at which testicular width first reached 1.5 mm during successive phases of gonadal recrudescence and regression. Correspondingly 0.8 mm for the diameter of the largest follicle was taken as a threshold value for assessing the onset and the end of the female ovarian cycle. — The time interval between onsets and ends of testicular and follicular cycles is subsequently referred to as «duration of the sexually active phase». The time intervals between successive onsets of testicular or follicular growth and between successive onsets of post-nuptial flight feather molt are referred to as circannual period of the gonadal and molt rhythms, respectively. Results on the duration of molt and the sexually active phase and on circannual period length were analyzed by ANOVA. Results on onsets and ends of molt and the sexually active phase were analyzed with the non-parametric Kruskal-Wallis test because homogeneity of variances could not be achieved by transformations of these data. — T-tests and Mann-Whitney U-tests were used for post-hoc analyses as well as for the comparison of circannual period lengths.

3. Results

3.1 Persistence and clearness of the gonadal and molt rhythms

Following fledging free-living *axillaris* and *rubicula* carry out a post-juvenile body molt. Later on, they go through a gonadal cycle which is followed by a complete molt and this pattern is then repeated every year. — As shown on Fig. 3. for *axillaris* 6 of the 7 males behaved like free-living conspecifics in that they completed two gonadal cycles within the 28 to 29 month experimental period and carried out (or initiated) two complete molts. Only one male (b) showed a slightly atypical pattern in that it went through an extra (flight feather and body) molt in the middle of its second year of life. — Among the 10 females, 6 (h-m) showed relatively normal patterns with 2 cycles of follicular growth and regression and 2 complete molts, although in 2 of these birds (k,m) some body feathers were also replaced between the main molting periods. Three of the 4 remaining females (n-p) went through 2 follicular cycles, but their pattern of molt was irregular in that one or both postnuptial molts were restricted to the body plumage and often lasted much longer than normal. The last female (q), finally, went through only 1 gonadal cycle and never molted any flight feathers, but since this female died at an age of 24 months, its data must be treated with reservation.

In the male *rubicula* circannual rhythms tended to be less clearly expressed than in the *axillaris* (Fig. 3). Only 6 of the 13 individuals (a-e,h) went through 2 successive testicular cycles and 2 complete molts ($p=0.08$, χ^2 -contingency tables, for the comparison with *axillaris* where 6 of 7 males showed a normal pattern; see above). Five of the others (f,g,i-k) also completed 2 testicular cycles, but one or both of their postnuptial molts were comprised of only body feathers. The sixth bird (l) showed one initial testicular cycle, but subsequently its testes remained small and body molt went on almost continuously. In the final male (m) the testes never developed and body molt was also almost continuous.

The females of *rubicula* were about as variable with regard to the persistence of circannual cycles as the *axillaris* females. Four of the 7 birds (n-q) developed close to normal patterns with 2 follicular cycles and 2 complete molts ($P>0.1$ for the comparison with *axillaris* where 6 out of 10 females showed close to normal patterns), while 2 others (r,s) went through 2 follicular cycles but their molt was partly reduced to a body molt which was timed irregularly. The final female (t) began initial follicular development at about the same time as the others but with 16 months it started egg-laying which continued irregularly for about 10 months. During this period which was interrupted at an age of 18 and 19 months by a complete molt, this female laid a total of 75 eggs.

3.2 Timing of activities

To compare the rhythms of the two subspecies and to evaluate the period of the rhythms, mean values were calculated for the onsets, ends, and durations of the sexually active phases as well as for the onsets, ends and durations of all molts (Figs. 4 and 5). With regard to *molt duration*, the statistical analysis revealed a significant

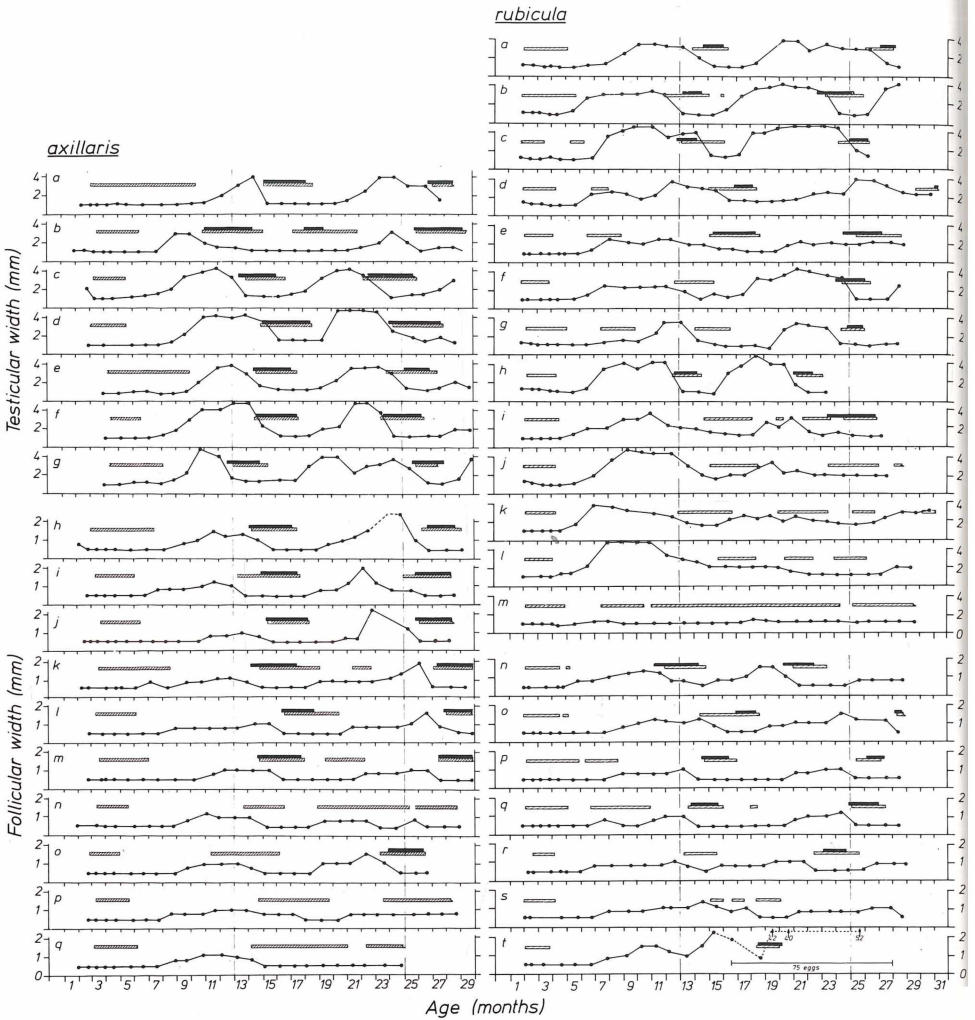


Fig. 3. Left: Changes in testicular width (a-g) or in the width of the largest ovarian follicles (h-q) of 7 ♂ and 10 ♀ African stonechats (*axillaris*) held for 24 to 29 months in a constant 12.25 h photoperiod. (From GWINNER and DITTAMI 1990). Right: the same for 13 ♂ (a-m) and 7 ♀ (n-t) European stonechats (*rubicula*) held for 25 to 30 months in the same conditions. Bars show the occurrence of molt (black bars: molt of flight feathers; hatched bars: molt of body feathers). Data are plotted against the birds' age and dashed vertical lines indicate the end of the birds' first and second year of life. *Axillaris* ♀ h laid an egg at an age of 24 months and a measurement of follicular width could not be taken at that time. *Rubicula* ♀ t started egg-laying at an age of 15 months and subsequently follicular measurements could be taken only occasionally. Off-scale follicular widths are indicated by the numbers underneath the arrows.

difference between the 2 subspecies ($p < 0.001$; ANOVA). Post-hoc t -tests indicated that all 3 body molts and both flight-feather molts lasted longer in *axillaris* than in *rubicula* ($p < 0.01$). The duration of the sexually active phase was indistinguishable between the females of the two subspecies but a significant difference was found

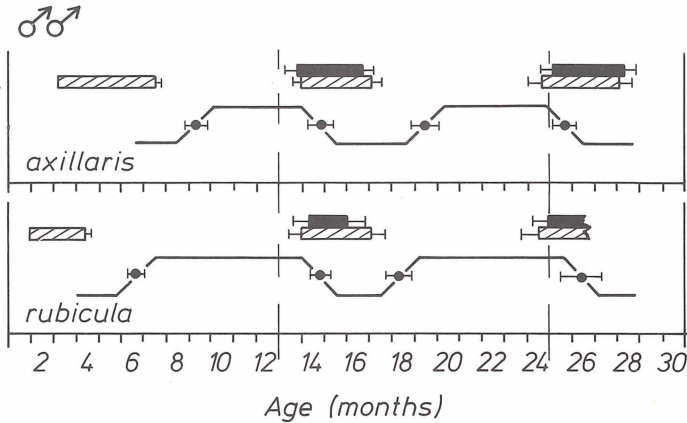


Fig. 4. Average time course of the testicular and molt cycles of the σ African (*axillaris*, upper diagram) and European (*rubicula*, lower diagram) stonechats shown on Fig. 2. The left and the right margins of the bars indicate the mean onsets and ends of flight feather molt (black bars) and body molt (hatched bars); horizontal lines: SE. The solid circles represent the mean onsets and ends of gonadal cycles (with SE) as defined in the methods section. For the calculation of the molt onsets and ends the following (presumably atypical) molts were ignored: *axillaris*: third molt of bird b; *rubicula*: second molt of birds c, d, e, g; third molt of birds b, i, k, l; fourth molt of birds k, l (compare Fig. 3).

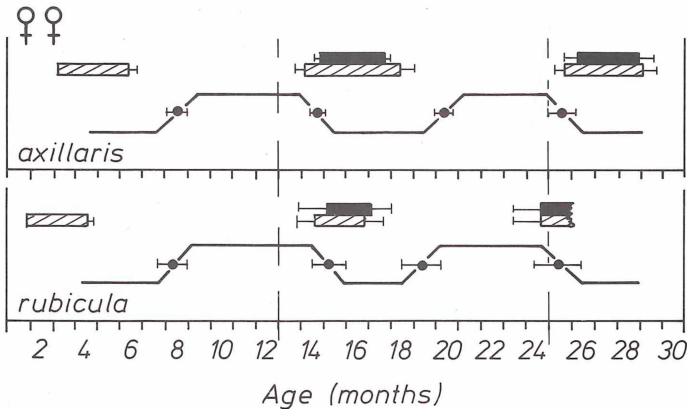


Fig. 5. Average time course of the follicular and molt cycles of the σ African (*axillaris*) and European (*rubicula*) stonechats shown on Fig. 1. For the calculation of the mean molt onsets and ends the following (presumably atypical) molts were ignored: *axillaris*: third molt of birds k, m, n, q; *rubicula*: second molt of birds p, q; third molt of bird s; fourth molt of birds q, s (compare fig. 3). — For further explanations see fig. 4.

between the males ($p < 0.003$; ANOVA). This difference is mainly due to the longer duration of the first sexually active phase ($p < 0.002$; t-test), resulting from an earlier onset of testicular growth ($p = 0.06$; Kruskal-Wallis-test, $p < 0.002$; Mann-Whitney U-test).

In both subspecies and sexes there was a tendency for the circannual period to be shorter than 12 months. The mean period (\pm SE) measured between successive onsets of gonadal growth was 348 ± 29 and 361 ± 13 days for the male and female *axillaris*, and 317 ± 25 and 329 ± 16 days for the male and female *rubicula*. Corresponding values for the period measured between successive onsets of postnuptial flight-feather molt are 354 ± 15 days for the combined data from male and female *rubicula*. None of the differences either between sexes or subspecies were significant.

4. Discussion

The results of the present study provide only little support for the hypothesis that equatorial environments provide stronger selective pressures for the evolution of circannual rhythms than temperate zone environments. Although there was a (almost significantly) smaller fraction of male European birds (*rubicula*) that exhibited circannual cycles than male African birds (*axillaris*), the majority of *rubicula* underwent clear cycles of testicular width and molt. Among the females no subspecies differences in the degree of expression of a rhythm could be detected. It is possible, of course, that under more extended experimental conditions a circannual rhythmicity would not persist as long in *rubicula*, as it does in *axillaris*, in which rhythms may continue for up to 7,5 years (GWINNER and DITTAMI 1990). However, since free-living European stonechats only rarely live longer than 2 years (e.g. only about 10% and 22% of the birds of populations in Germany and on Jersey Island respectively, were 3 years or older; GLUTZ VON BLOTZHEIM and BAUER 1988), the circannual rhythms demonstrated in Fig. 2 would provide an adequate life-long mechanism to control reproduction and molt.

It was proposed previously (GWINNER and DITTAMI 1990) that in tropical stonechats a major role played by the circannual mechanism may be the external and internal temporal adjustment of seasonal activities in an equatorial environment characterized by only minor and often irregular seasonal fluctuations. Such a function of circannual rhythms may indeed prevail in the tropical birds, but the finding that stonechats from temperate zones exhibit almost equally clear circannual cycles as the equatorial conspecifics suggests that the endogenous mechanisms may also have functional significance in birds exposed to pronounced external variations in photoperiod and temperature all year round. It has been proposed that circannual rhythms, due to their inertia, protect organisms from reacting instantaneously to external stimuli and thus provide a buffer system against environmental noise (GWINNER 1986, GWINNER and DITTAMI 1988). Such a function would be particularly significant for organisms with a tight annual time schedule, i.e. migratory birds that use much of their time for migration. Indeed, some data suggest that long-distance migrants show more pronounced circannual rhythms than short-distance migrants

(GWINNER 1986). European stonechats of the population we have studied do migrate (although only over distances of 1000 to 2000 km, ZINK 1973). In addition they are pressed for time due to the fact that 2 to 3 broods are carried out each year (GLUTZ VON BLOTZHEIM and BAUER 1988). Hence, there may be a severe need for an accurate timing of seasonal activities and this may have exerted selection pressure on the evolution of circannual rhythms. Apart from these considerations, however, it must be emphasized that circannual rhythms have also been demonstrated in non-migratory, single brooded species (GWINNER 1986), suggesting that other as yet unidentified factors may have played a role in the evolution of circannual rhythms.

In principle, there is a possibility that the circannual rhythms exhibited by an organism under a particular constant condition have no present-day function, but rather represent a phylogenetic relic from periods when the ancestors of that organism were exposed to selection pressures favouring their evolution. Applied to the case of the European stonechat this could mean that their circannual rhythms had originally evolved in tropical ancestors. Such a possibility is extremely unlikely, however, because the African stonechats are almost certainly derived from palaeartic species or subspecies that had invaded Africa possibly as late as the last glacial period (HALL and MOREAU 1970). The circannual rhythms of the European birds may, therefore, rather have to be viewed as an original, primitive character that could have facilitated the immigration of temperate zone birds into the tropics. Indeed, the properties of the circannual rhythms of the European birds are so similar to those of the African birds that only minor evolutionary adjustments would have been necessary for the temperate-zone birds to change to the pattern presently observed in equatorial conspecifics.

The few differences that do exist in the circannual patterns of gonadal size and molt may be due to special adaptations to the different environmental conditions and life styles of the two subspecies. This holds true for the (genetically determined; GWINNER and NEUSSER 1985) difference in the timing and duration of the postjuvenile molt which begins and ends earlier and lasts shorter in *rubicula* than in *axillaris*. We have argued elsewhere (GWINNER et al. 1983) that the earlier and faster postjuvenile molt in the European birds is related to the fact that these birds are migrants and so may have to complete molt at an earlier age in order to be ready for fall migration in time. The juvenile non-migratory African birds may be able to spend more time molting. Similar considerations may be applied to explain the shorter duration of postnuptial molt in *rubicula* as compared to *axillaris*. *Rubicula* is not only migratory but also multi-brooded (a trait that appears to be reflected in the longer duration of the males' sexually active phase). Hence, there may be a need for adult birds of this subspecies to molt faster than the nonmigratory single brooded *axillaris*. It is not yet clear to what an extent the subspecies differences found here in the caged stonechats reflect corresponding differences in the molting patterns of free-living conspecifics. However, differences of the kind reported here for caged stonechats have been found in free-living birds of other taxonomic groups with similar differences in migratory and reproductive performance (STRESEMANN and STRESEMANN 1966).

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Literatur

- ASCHOFF, J. (1955): Jahresperiodik der Fortpflanzung bei Warmblütern. *Studium Generale* 9: 742-776. — BAKER, J. R. & J. BAKER (1934/36): The seasons in a tropical rain-forest (New Hybrides). Part 2. *Botany J. Linn. Soc. Zool.* 39: 507-519. — BAKER, J. R. & R. M. RANSON (1938): The breeding seasons of southern hemisphere birds in the northern hemisphere. *Proc. Zool. Soc. London A* 108: 101-141. — BLAKE, G. M. (1959a): Control of diapause by an «internal clock» in *Anthrenus verbasci* (L.) (Col. Dermestidae). *Nature* 183: 126-127. — BLAKE, G. M. (1959b): Diapause and the regulations of development in *Anthrenus verbasci* (L.) (Col. Dermestidae). *Bull. Ent. Res.* 49: 751-757. — BROCK, M. A. (1975a): Circannual Rhythms — I. Free-running rhythms in growth and development of the marine cnidarian, *Campanularia flexuosa*. *Comp. Biochem. Phys.* 51A: 377-383. — BROCK, M. A. (1975b): Circannual Rhythms — II. Temperature-Compensated free-running rhythms in growth and development of the marine cnidarian, *Campanularia flexuosa*. *Comp. Biochem. Physiol.* 51A: 385-390. — BROCK, M. A. (1975c): Circannual Rhythms — III. Rhythmicity in the longevity of hydrants of the marine cnidarian, *Campanularia flexuosa*. *Comp. Biochem. Physiol.* 51A: 391-398. — BROWN, L. H. & P. L. BRITTON (1980): The breeding seasons of East African birds, EANHS, Nairobi. — CHAPIN, J. P. (1932): The birds of the Belgian Congo, Vol. 1. *Bull. American Museum Nat. History* 65: 1-756. — DITTAMI, J. P. & E. GWINNER (1985): Annual cycles in the African stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. *J. Zool.* (A) 207: 357-370. — GLUTZ VON BLOTZHEIM, U. N. & K. M. BAUER (1988): *Handbuch der Vögel Mitteleuropas*, 11: 446-509. Aula-Verlag, Wiesbaden. — GWINNER, E. (1986): Circannual Rhythms. Springer Verlag, Heidelberg. — GWINNER, E., J. DITTAMI & H. GWINNER (1983): Postjuvenile molt in East African and Central European stonechats (*Saxicola torquata axillaris*, *S. rubicula*) and its modification by photoperiod. *Oecologia* (Berlin) 60: 66-70. — GWINNER, E. & V. NEUSSER (1985): Die Jugendmauser europäischer und afrikanischer Schwarzkehlchen (*Saxicola torquata rubicula* und *axillaris*) sowie von F1-Hybriden. *J. Orn.* 126: 219-220. — GWINNER, E., V. NEUSSER, D. SCHMIDL, & L. BALS (1987): Haltung, Zucht und Eiaufzucht afrikanischer und europäischer Schwarzkehlchen (*Saxicola torquata*). *Gefiederte Welt* 5/6: 118-120 and 145-147. — GWINNER, E. & J. DITTAMI (1988): Adaptive functions of circannual clocks. In: I. ASSENMACHER & J. BOISSIN (eds.): *Endocrine Regulations as Adaptive Mechanisms to the Environments*. pp. 115-122. CNRS, Paris. — GWINNER, E. & J. DITTAMI (1990): Endogenous reproductive rhythms in a tropical bird. *Science* 249: 906-908. — HALL, B. P. & R. E. MOREAU (1970): An atlas of speciation in African passerine birds. *British Mus. Nat. History, London*. — IMMELMANN, K. (1971): Ecological aspects of periodic reproduction. In: D. S. FARNER J. & R. KING (eds.). *Avian Biology*, Vol. I. pp. 341-389. Academic Press, New York and London. — KAVALIERS, M. (1982): Seasonal and circannual rhythms in behavioral thermoregulation and in their modification by pinealectomy in the white sucker, *Catostomus commersoni*. *J. Comp. Physiol.* 146: 235-243. — MARSHALL, A. J. (1959): Internal and environmental control of breeding. *Ibis* 101: 456-478. — MARSHALL, A. J. (1960a): The role of the internal rhythm of reproduction in the timing of avian breeding seasons, including migration. *Proc. XII. Orn. Congr.* 1958. — MARSHALL, A. J. (1960b): Annual periodicity in the migration and reproduction of birds. *Cold Spring Harbor Symp. Quant. Biol.* 25: 499-505. — MARSHALL, A. J. & D. L. SERVENTY (1959): Experimental demonstration of an internal rhythm of reproduction in a trans-equatorial migrant (the short-tailed shearwater *Puffinus tenuirostris*). *Nature* 184: 1704-1705. — MOREAU, E. E. (1931): Equatorial reflections on periodism in birds. *Ibis* 1: 553-570. — MOREAU, R. E., A. L. WILK & W. ROWAN (1947): The moult and gonad cycles of three species of birds at five degrees south of the equator. *Proc. Zool. Soc. London*, pp. 345-364. — STEBBINS, R. C. (1963): Activity changes in the striped plateau lizard with evidence on influence of the parietal eye. *Copeia* 4: 681-691. — STRESEMANN, E. & V. STRESEMANN (1966): Die Mauser der Vögel. *J. Orn.* 107 (Sonderheft): 1-448. — VOOUS, K. H. (1960): *Atlas of European birds*. Nelson, London. — ZINK, G. (1973): *Der Zug europäischer Singvögel I*. Möggingen: Vogelzug-Verlag.

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