

Seasonal changes of locomotor activity patterns in ruin lizards *Podarcis sicula*

I. Endogenous control by the circadian system

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Received: 19 August 1993 / Accepted after revision: 25 January 1994

Abstract. The daily pattern of locomotor activity of the ruin lizard *Podarcis sicula* in its natural environment changes from unimodal in spring (with only one activity peak per day) to bimodal in summer (with two well-separated activity peaks per day) and it becomes unimodal again in autumn. In order to establish whether such seasonal changes in pattern might be at least in part controlled by endogenous temporal programs, lizards were collected at different times of the year and immediately after capture their locomotor behavior was tested in the laboratory under constant temperature (29°C) and in darkness. For some individuals tested in the laboratory the locomotor pattern previously expressed in the field was known. Seasonal differences in pattern have been unequivocally found to have an endogenous component, as most lizards in constant conditions retained the locomotor pattern shown in the field during the same season. Besides, in the bimodal lizards the freerunning period of locomotor rhythms (τ) was significantly shorter and circadian activity time (α) longer than in the unimodal ones. Altogether the data are compatible with the idea that both the interdependent changes of τ and α and the changes in locomotor pattern occurring seasonally in the circadian activity rhythms of *P. sicula* would depend on changes in the phase relationship between mutually coupled oscillators which drive these rhythms.

Key words: Circadian rhythms – Locomotor activity – Seasonality – Lizards

Introduction

Seasonal variations in the daily pattern of activity have been reported in most diurnal lacertid lizards from southern Europe (Gruber and Schutze-Westrum 1971; Busack 1976; Pough and Busack 1978; Bowker 1986; Henle 1988; Van Damme et al. 1990; Foà et al. 1992).

Generally, activity is sporadic in winter. In spring and autumn activity is more intense and without substantial interruptions throughout the day. In summer activity becomes bimodally distributed, with an early or mid-morning peak and a late afternoon peak, separated by a period during which activity is dramatically reduced. In most studies cited above, the term “activity” has been used to mean “presence” of lizards in the field. Not only individuals actually engaged in locomotor activity were included, but also immobile (for example during basking) animals. Other investigations have considered locomotor behavior separately: they have shown a seasonal alternation between the unimodal and bimodal patterns of locomotor activity (Perez Mellado and Salvador 1981; Perez Mellado 1982, 1983; Pollo Mateos and Perez Mellado 1989).

Since lizards are ectotherms, which can be active only within a limited range of body temperatures, it is clear that under favorable thermal conditions locomotor activity is more intense, while it is dramatically reduced during the hottest part of the day in summer, when lizards retreat to the shade or into their burrows to avoid overheating. Hence, seasonal differences in locomotor activity have been generally interpreted as a direct behavioral response of lizards to related changes in solar radiation and ambient temperature. In this context, however, one should consider the possibility that seasonal changes in locomotor behavior may not be completely controlled by the environment. Daily rhythms of locomotor activity are also controlled by the endogenous circadian system. They are entrained to the 24-h light cycle of the external day and, in ectotherms, also to the 24-h temperature cycle (Hoffmann 1968). Furthermore, seasonal changes in locomotor behavior are brought about, at least in part, by changes in photoperiod or thermoperiod working through the circadian system. In the fish *Lota lota* and *Couesius plumbeus*, for example, the length of the free-running period of the locomotor rhythm (τ) recorded in constant conditions was found to vary consistently depending on season (Kavaliers 1978 1980). Such seasonal differences in τ are independent of the annual cycle of

reproduction, as they were observed in sexually immature individuals. In four species of nocturnal rodents Pittendrigh and Daan (1976a) have shown that the pattern of activity in constant conditions is dictated by the photoperiod to which the rodents were previously exposed. In the birds *Zonotrichia atricapilla* and *Z. leucophrys* and the mice *Peromyscus maniculatus* and *Mus musculus*, also, the length of the freerunning period depends on previous photoperiodic conditions (Gwinner 1975; Pittendrigh and Daan 1976a). All this certainly indicates a flexibility of circadian programs that most probably derives from the multioscillator structure of the circadian system (Pittendrigh 1972, 1974; Pittendrigh and Daan 1976b). Seasonal changes in τ and circadian activity time (α) have been postulated to arise from changes in the phase relationship between mutually coupled oscillators which drive locomotor rhythms. This may allow the time course of activity to adjust to seasonal changes in the external day, and, at the same time, recognize local time throughout the year (model of "internal coincidence": Pittendrigh 1972). If such seasonal changes in circadian parameters were also to occur during long-term recording of locomotor activity in constant conditions, true endogenous circannual cycles of circadian rhythms could be demonstrated (for a review, see Gwinner 1986).

The present investigation examines the possibility that seasonal changes of locomotor activity patterns in lizards might be controlled at least in part by endogenous temporal programs. The object of the study was a population of ruin lizards *Podarcis sicula*. Seasonal changes in daily locomotor behavior were observed in the field.

Our main interests were to verify: (i) whether lizards collected at different times of the year would retain the same pattern of locomotor activity they showed in the field when tested under constant conditions in the laboratory; (ii) whether seasonal changes in τ and α of the locomotor rhythm could be detected.

Methods

Field observations. Observations of ruin lizards (*Podarcis sicula campestris* De Betta, 1857) were carried out at the field station of our Department, located 1.5 km from the Ligurian sea (Pisa, Italy), in an open area of reclaimed marshland with well-drained, sandy soils. The activity of many individual lizards was centered on a 150-m² flat meadow, incorporating the foundations of a dismantled poultry pen, in which perforated bricks and other debris provide shade and refuge. In order to obtain activity data at least roughly comparable with "pure" daily locomotor activity recordings of lizards tested individually in the laboratory, each daily observation was carried out on a single focal lizard, by recording continuously from sunrise to sunset, with the aid of 10 × 40 binoculars, time of day and duration of each bout of locomotor activity in the field. Segments of activity less than 30 s were discarded, while those between 30 and 60 s were approximated to the minute. At hourly intervals, soil temperature 4–5 m from the lizard was measured. All field work was performed on sunny days, with light or no wind. The field study was limited to adult male individuals, as they are particularly easy to keep in the laboratory for subsequent locomotor recording. The observations were carried out during April, May, June, July, September and October 1990. Each month two different lizards were observed, each one during 3 non-consecutive days. At

the end of the last day of observation each lizard was carried to the laboratory, in order to establish its locomotor activity pattern under constant conditions (see below). Additionally, daily recordings of the activity in the field of two lizards were repeated during April, May, June and July 1991, in order to examine seasonal changes of the locomotor activity pattern in the same individual.

Locomotor recording in the laboratory. The locomotor activity of individual lizards was monitored by tilt cages (30 × 15 × 11 cm) connected to an Esterline Angus event recorder. The tilt cages were placed inside environmental chambers, that were kept in constant darkness (DD) and at a constant temperature of 29°C. This temperature is within the range of temperatures considered optimal for activity in *P. sicula* (range 28–33°C: Licht et al. 1969). Food (*Tenebrio molitor* larvae) and water (with added Aminoplex-polivit) were supplied twice a week. The lizards were fed with the aid of an infrared viewer (Find-R-Scope, Mont Prospect, Ill) to avoid pulses of bright visible light. Lizards were allowed to freerun in DD for 10–20 days. After lizards previously observed in the field were transported to the laboratory, they were immediately put into the individual tilt cages for locomotor recording. For laboratory experiments additional lizards (with no field data) were used ($n = 69$). They were collected in groups of 10–14 individuals in August, October, November 1990, and April, June, July 1991 along the coast of the Ligurian sea (Marina di Vecchiano Pisa, Italy), 12 km from the field station. After capture, each monthly group of lizards was carried to the laboratory and put into the individual tilt cages for locomotor recording. In order to see whether summer bimodality displayed by lizards in the laboratory depended on their exposure to a constant temperature of 29°C, in July and October–November 1990 two control groups (9 and 10 per group, respectively) were tested in DD at a constant temperature of 25°C.

Data evaluation. Locomotor activity records were divided into 24-h segments, and consecutive days were mounted on a chart one below the other. The free-running period of the locomotor rhythm (τ) and the circadian activity time (α) were estimated by the eye-fitting method (Pittendrigh and Daan 1976a). Bimodality or unimodality of the locomotor pattern was first established by visual inspection: bimodal records are characterized by a double peak of locomotor activity regularly repeated in subsequent circadian cycles, while unimodal records are characterized by a single peak of activity per circadian cycle. In some records the nature of the locomotor pattern (bimodal or unimodal) was difficult to establish by visual inspection. In any case, spectral analysis (periodogram) was applied to

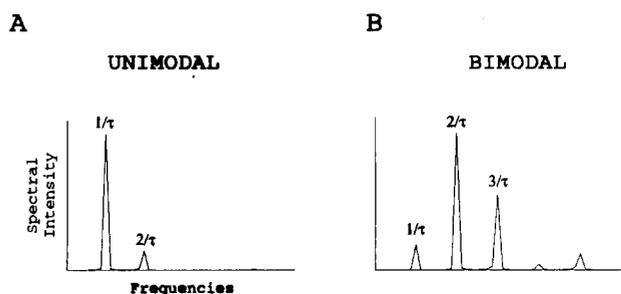


Fig. 1A, B. Spectral analysis of two time-series, derived from **A** an ideal unimodal and **B** an ideal bimodal distribution of activity. Scores for no activity (0) or different amounts of activity (1, 2, 3) were given each 10-min interval for eight consecutive circadian cycles either to obtain an ideal time-series with only one activity peak per circadian cycle (unimodal) or an ideal time-series with two distinct activity peaks per circadian cycle (bimodal). Both ideal distributions of activity were given a free-running period (τ) of 24 h. For further explanations, see Methods

detect all periodicities in the raw data (Vajani 1984). In order to do this, eight consecutive circadian cycles for each record (always starting from day 2 of locomotor recording) were transformed into a numerical time-series, following Rusak's method (Rusak 1977). Each 10-min interval of the raw record was given the following scores: no activity, 0; one or two pen deflections, 1; pen deflections filling up to half the segment, 2; pen deflections filling more than half the segment, 3. Spectral analysis applied to an ideal unimodal distribution demonstrated a single frequency-peak at $1/\tau$ (unimodal model, Fig. 1A). Spectral analysis applied to an ideal bimodal distribution of locomotor activity showed frequency-peaks at $2/\tau$ and $3/\tau$, which were higher than the frequency-peak at $1/\tau$ (bimodal model, Fig. 1B). When compared with the models, many of the data fitted very well either the ideal bimodal or ideal unimodal distribution (Kolmogorov-Smirnov test, $P > 0.50$). Between the two extremes, however, we found intermediate situations reflecting a "continuum" between the ideal unimodal and ideal bimodal situation. For convenience, each locomotor record was assigned to one of the following four classes: A, only one frequency-peak at $1/\tau$ is present (fitting the unimodal model of Fig. 1A); B, low frequency-peaks at $2/\tau$ and $3/\tau$ are present besides that at $1/\tau$; C, frequency-peaks at $2/\tau$ and $3/\tau$ are high, but the frequency-peak at $1/\tau$ is dominant; D, frequency-peaks at $2/\tau$ and $3/\tau$ are higher than that at $1/\tau$ (fitting the bimodal model of Fig. 1B).

We also examined (Mann-Whitney *U*-test, two-tailed) whether there were differences in τ and α (i) between lizards tested in different seasons; (ii) between lizards of the four different classes above.

Results

Field data on two focal lizards whose locomotor activity was recorded on sunny days in April, May, June and July unequivocally showed in both individuals a gradual change of the locomotor activity pattern from unimodal in spring to bimodal in summer (Fig. 2).

From April to October the locomotor activity of two different focal lizards per month was recorded for 3 days in the field. Lizards belonging to the same monthly pair

behaved similarly to one another. In April (Fig. 3A, left panel) and May (not shown) the locomotor pattern was unimodal. In June (not shown) and July (Fig. 3B, left panel) lizards showed a marked bimodal pattern, due to a dramatic reduction of the amount of locomotor activity between 1200 and 1600 hours. In September the locomotor pattern was weakly bimodal (Fig. 3C, left panel), while unimodality was resumed in October (Fig. 3D, left panel). Generally, a marked bimodal pattern was observed when recorded soil temperatures reached their highest levels (Foà et al. 1992; Tosini et al. 1992). Reduced movement around midday in summer is correlated with reduced areas of shade available to lizards within our observation site at that time of day (Avery 1993). The time interval between locomotor activity onset in the morning and locomotor activity cessation in the evening increases from April to July (Fig. 2, Fig. 3A–B, left panels) and decreases thereafter (September–October: Fig. 3C–D, left panels). At the end of the last day of field observation each focal lizard was transported to the laboratory for locomotor recording in constant conditions. In the laboratory all these lizards retained the pattern of locomotor activity previously shown in the field (middle vs. left panels of Fig. 3). Lizards tested in the laboratory either in late July or late September had a bimodal locomotor pattern. However, while the bimodal pattern in late July is a class D bimodal that fits the bimodal model (Fig. 3B, middle and right panels; and see example in Fig. 4D), the bimodal pattern in late September does not: the record of Fig. 3C is a class C bimodal (middle and right panels and see example in Fig. 4C).

In a further experiment, groups of 10–14 lizards (with no field data) collected in different months were tested in the laboratory immediately after capture. Such tests carried out on relatively large numbers of lizards revealed that, although most lizards show a bimodal activity pat-

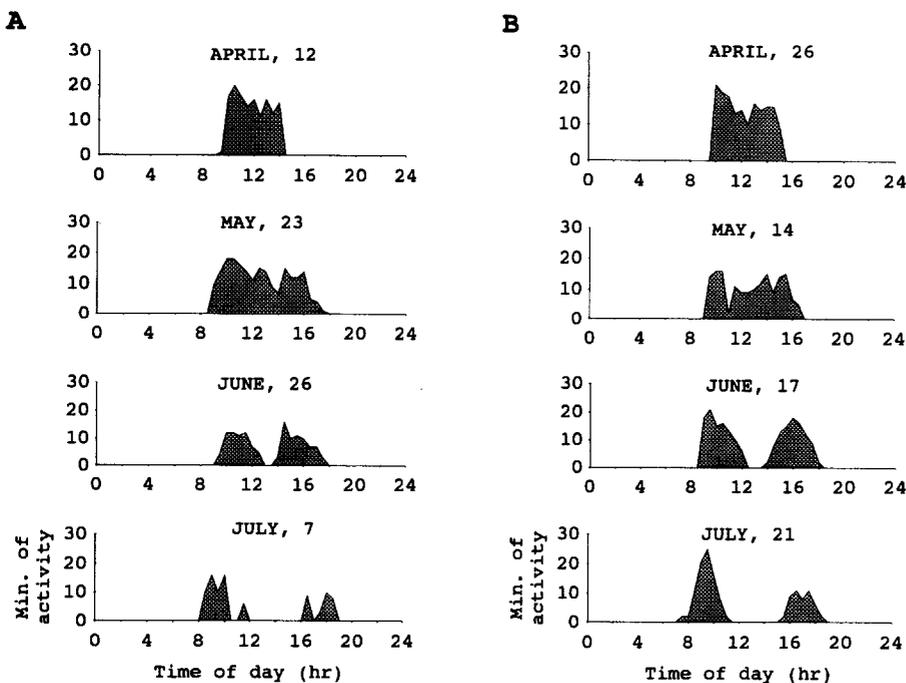


Fig. 2A, B. Locomotor activity of two focal lizards in the field. For each lizard (A and B respectively) activity was recorded during 4 days of different months. Minutes of activity per each half-hour interval from dawn to dusk (*ordinate*) are plotted over 24 h (*abscissa*). In both lizards a change of the daily locomotor pattern from unimodal in April to bimodal in July is evident

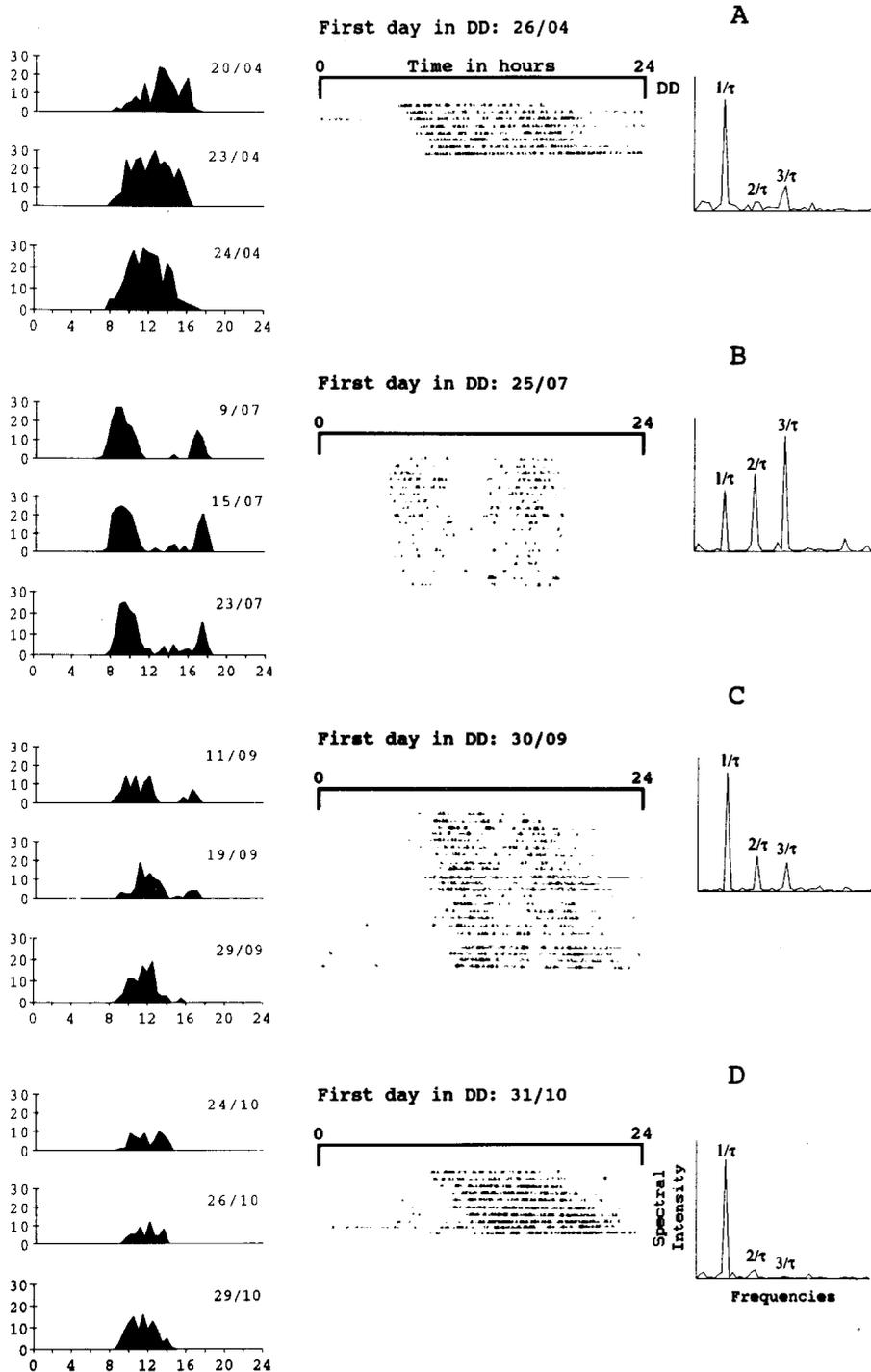


Fig. 3A–D. Locomotor activity of four individual lizards (A, B, C, D) recorded both in the field and in the laboratory. Each lizard was tested in a different month. For each lizard the *left panel* shows 3 days of locomotor activity in the field (data plotted as in Fig. 2), while the *central panel* reports 1–3 weeks of locomotor activity under constant temperature (29°C) and darkness in the laboratory. The *right panel* is the result of spectral analysis of the respective laboratory record. *Central panels:* each *horizontal line* is a record of 1 day's activity (0000–2400 hours), and consecutive days are mounted one below the other. Each lizard retained in the laboratory the same locomotor pattern previously shown in the field. Clearly, the locomotor pattern is different depending on season.

tern in summer, some bimodal individuals can also be found in April, October and (one individual) in November–December. Still, the monthly percentage of bimodal lizards gradually increases from spring to summer (peak: 91% in August) and decreases thereafter (trough: 7.1% in November–December) (Fig. 5). Spectral analysis further showed that the quality of the bimodal pattern varies markedly depending on season (Table 1). In fact, 14 out of the 16 lizards with a class D bimodal pattern (87.5%) were found between June and August. Conversely, 19 out of the 24 lizards with a class A unimodal pattern (79%) were found in the remaining months.

Mean values of the freerunning period of the locomotor rhythm (τ) and the circadian activity time (α) for each class of locomotor pattern are shown in Fig. 6. Bimodal lizards have a τ significantly shorter than unimodal ones ($P < 0.0001$, Mann-Whitney U -test, two-tailed). The τ of lizards with a class D bimodal pattern is significantly shorter than τ of lizards with a class C bimodal pattern ($P < 0.05$). α is significantly longer in bimodal lizards than in unimodal ones ($P < 0.0001$). τ in April (mean $\tau = 24.43 \pm 0.08$ h SEM) is significantly longer than τ in June ($P < 0.004$; mean $\tau = 24.13 \pm 0.05$ h SEM), July ($P < 0.02$; mean $\tau = 24.17 \pm 0.05$ h SEM) and August

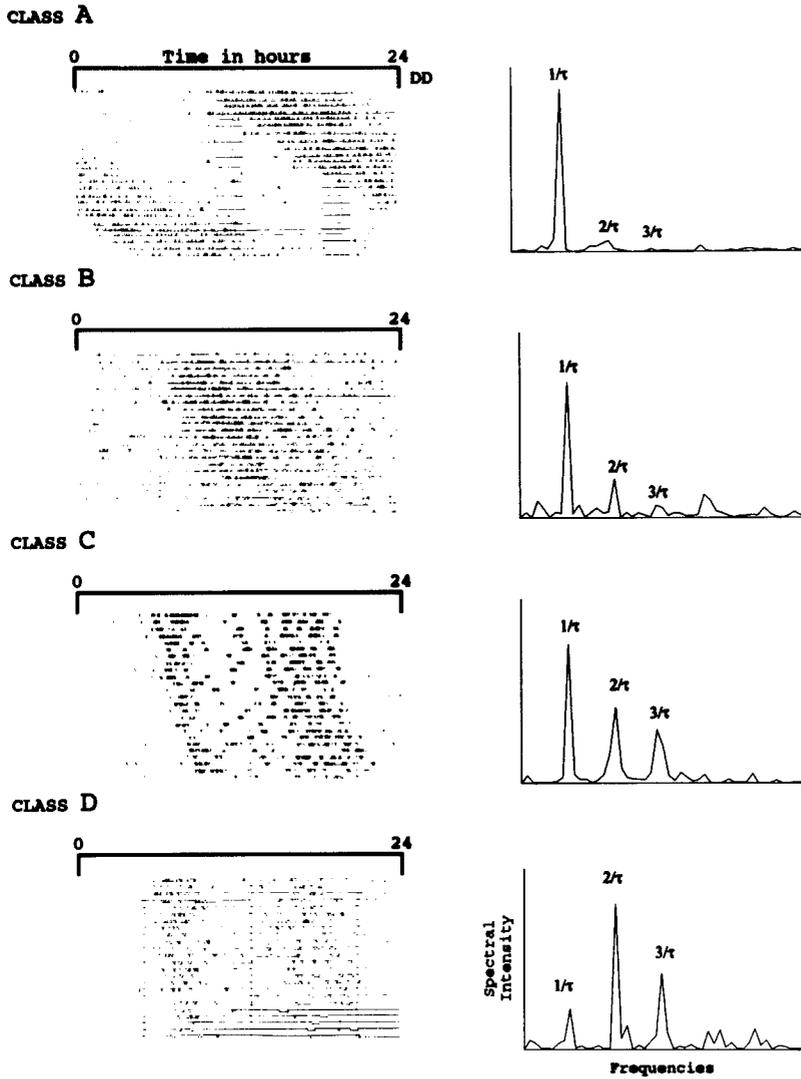


Fig. 4A–D. Locomotor activity records (left panels) and respective spectral analysis (right panels) in four individual lizards tested under constant temperature (29°C) and darkness. The examples are representative of the 4 classes of locomotor patterns revealed by spectral analysis. Class A Only one frequency-peak at $1/\tau$ (it fits the unimodal model of Fig. 1A). Class B Low frequency-peaks at $2/\tau$ and $3/\tau$ besides that at $1/\tau$. Class C High frequency-peaks at $2/\tau$ and $3/\tau$, but the $1/\tau$ frequency-peak is dominant. Class D Frequency-peaks at $2/\tau$ and/or $3/\tau$ are higher than at $1/\tau$ (it fits the bimodal model of Fig. 1B)

A

MONTH	UNIMODAL		BIMODAL		N tot
	CLASS A	CLASS B	CLASS C	CLASS D	
APRIL	2	3	5	0	10
JUNE	2	1	5	2	10
JULY	2	1	4	4	11
AUGUST	1	0	2	8	11
OCTOBER	6	2	4	2	14
NOV.-DEC.	11	2	1	0	14

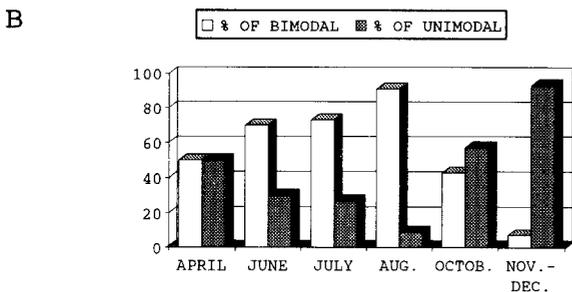


Fig. 5A, B. Locomotor pattern of lizards collected in different months (with no field data) and tested under constant temperature (29°C) and darkness immediately after capture. A In each month numbers of lizards for each class (A–D) of locomotor pattern revealed by spectral analysis are given. B Percentages of unimodal (class A + B) and bimodal (class C + D) lizards in each month

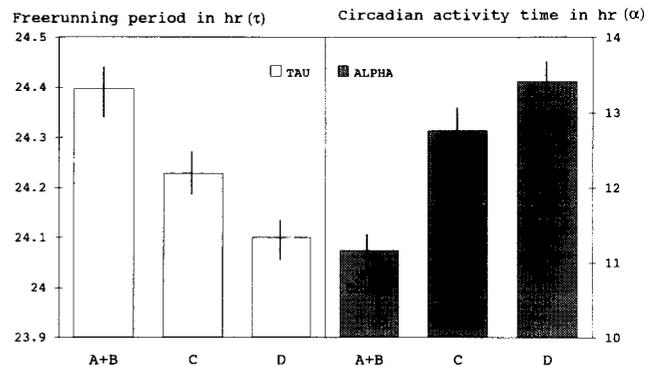


Fig. 6. Free-running period of the locomotor rhythm (τ) and circadian activity time (α) for each class of locomotor pattern under constant temperature (29°C) and darkness. As differences in τ and α between unimodal lizards belonging to class A and B were not statistically significant, A and B unimodals were grouped together for further comparisons. τ of the unimodal lizards (A + B) is significantly longer than τ of class C bimodals ($P < 0.05$, Mann-Whitney *U*-test, two-tailed) and class D bimodals ($P < 0.0001$). τ of class C bimodals is significantly longer than τ of class D bimodals ($P < 0.05$). α of the unimodals is significantly shorter than α of class C bimodals ($P < 0.001$) and class D bimodals ($P < 0.0001$)

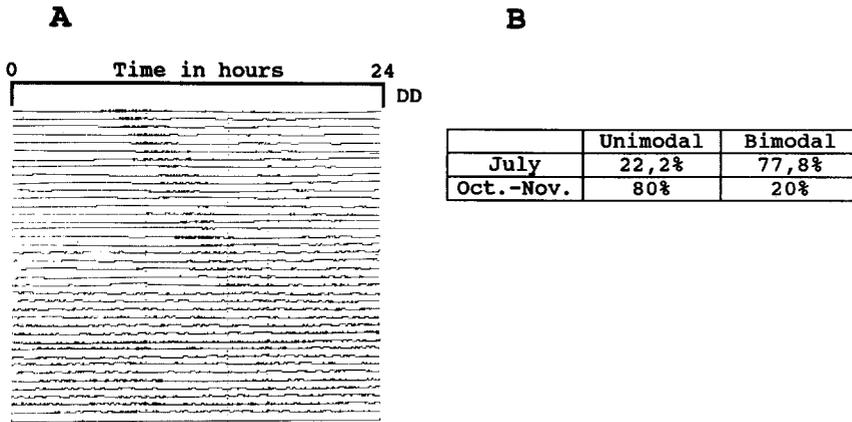


Fig. 7A, B. Locomotor activity of lizards tested under a constant temperature of 25°C and darkness. **A** Representative locomotor record of an individual captured and tested in July. Initially the lizard is rhythmic and shows a bimodal locomotor pattern typical of summer. Towards the end of the record, however, the main bout of activity becomes diffuse. **B** Percentages of bimodal and unimodal lizards found in July and October confirm the expected seasonal trends even in laboratory tests at 25°C

($P < 0.003$; mean $\tau = 24.1 \pm 0.05$ h SEM). Furthermore, τ in summer (June + July + August, mean $\tau = 24.14 \pm 0.03$ h SEM, $n = 34$) is shorter than in autumn (October + November, mean $\tau = 24.42 \pm 0.06$ h SEM, $n = 27$), while α in summer (mean $\alpha = 13.31 \pm 0.35$ h SEM) is longer than in autumn (mean $\alpha = 10.63 \pm 0.2$ h SEM). Both these differences are highly statistically significant ($P < 0.0001$).

Lizards collected in July or October were immediately tested in the laboratory in DD and at a constant temperature of 25°C. Each group showed the expected locomotor pattern for the respective month (Fig. 7B). After 10–20 days of locomotor recording, however, the main circadian bout of activity of most lizards became more diffuse (Fig. 7A). Such an effect was never observed in lizards tested at a constant temperature of 29°C.

Discussion

The daily pattern of locomotor activity of ruin lizards (*Podarcis sicula*) in their natural environment has been shown to change from unimodal in spring (with only one activity peak per day) to bimodal in summer (with two well-separated activity peaks per day) and to become unimodal again in autumn. The experiments reported here were performed to establish whether such seasonal changes in pattern could be controlled at least in part by endogenous temporal programs. Each month from April to September we examined the locomotor behavior in constant laboratory conditions of two different, freshly captured lizards, whose activity pattern in the field for the current season was individually known. Seasonal differences in pattern were unequivocally found to have an endogenous component, as these lizards retained under constant conditions in the laboratory the same locomotor pattern they showed in the field during the same season (Fig. 3). The existence of marked seasonal differences in the locomotor pattern under constant conditions was corroborated by the results of further experiments, in which groups of 10–14 lizards collected in different months (with no field data) were tested in the laboratory immediately after capture: the monthly percentage of lizards with a bimodal pattern increased from spring to summer and decreased thereafter (Fig. 5B).

The expression of a marked bimodal pattern in circadian rhythms of locomotor activity is independent of the level of constant temperature (29°C) used in laboratory experiments: most lizards tested in July under a constant temperature of 25°C were clearly bimodal (Fig. 7). “Sloppiness” of circadian rhythmicity toward the end of many locomotor records at 25°C is most probably due to a non-specific effect of such a low level of constant temperature on the general behavior of lizards. In fact 25°C, the highest body temperature that a lizard held at a constant ambient temperature of 25°C can achieve, is well below the range of body temperatures considered optimal for activity in *P. sicula* (28–33°C: Licht et al. 1969).

Spectral analysis of the laboratory data made it clear that while unimodal records have only one frequency-peak per circadian cycle at $1/\tau$, bimodal records have additional frequency-peaks at the $1/\tau$ submultiples $2/\tau$ and/or $3/\tau$; $1/\tau$ generally remains the dominant frequency-peak in the bimodal pattern exhibited by some of the lizards in spring or autumn (class C bimodals, Fig. 4C). As summer progresses, however, bimodality becomes more and more pronounced: the number of bimodal locomotor records with frequency-peaks at the $1/\tau$ submultiples being dominant over that at $1/\tau$ steadily increases from June to August (class D bimodals, Fig. 4D).

Seasonal differences in pattern under constant conditions are associated with systematic differences in the free-running period (τ) and circadian activity time (α) of locomotor rhythms. In summer τ is significantly shorter and α longer than in other seasons. τ is significantly shorter and α longer in the bimodal lizards than in the unimodal ones. Therefore, seasonal differences in both τ and α are mostly due to the fact that the percentage of bimodal lizards is much higher in summer than in the rest of the year (78% vs. 31% respectively). Moreover, since class D bimodal lizards, which are characterized by extremely short τ and long α , were found almost exclusively in summer, seasonal differences are further enhanced.

The pattern of changes in circadian parameters reported here is compatible with the multioscillator model developed for the circadian system by Pittendrigh and co-workers (Pittendrigh and Daan 1976b; Daan and Berde 1978). According to the model, locomotor rhythms are controlled by two circadian oscillators, or sets of oscillators, that are normally coupled to each other. Activi-

ty onset and activity offset are assumed to be phase points of the two (or sets of) oscillators, so that the interval (α) between them would be a measure of their mutual phase relationship. τ of the coupled system is malleable, changing as the phase relationship between the oscillators (that is reflected in α) changes. Interestingly, Underwood suggested that each activity bout of the bimodal pattern of various reptiles may be the expression of one of the two (or sets of) oscillators described in Pittendrigh's model (Underwood 1992). Pittendrigh further proposed that seasonal cycles in behavioral and physiological events (for example, pattern of activity or reproductive state) may depend on the mutual phase relationship between the constituent oscillators being subject to seasonal fluctuations (internal coincidence, Pittendrigh 1972).

Hence, both the transition of the locomotor pattern from unimodal to bimodal (and vice versa) and the interdependent changes in τ and α occurring seasonally in circadian activity rhythms of ruin lizards are readily explained as changes in phase relationship between mutually coupled oscillators which drive these rhythms. Such seasonal changes in circadian parameters in species inhabiting temperate zones demonstrate a flexibility of circadian programs that has important adaptive functions, as it may allow the time course of activity to adjust to the seasonal changes in the external day and, at the same time, recognize local time throughout the year (Pittendrigh 1972; Pittendrigh and Daan 1976b).

Retreat into the shade or burrows and the consequent dramatic reduction of the amount of movement around midday in summer, which renders the locomotor pattern of ruin lizards so typically bimodal, has been generally regarded more or less explicitly as being a direct behavioral response of these animals to the very high levels of ambient temperature at that time of day (Huey and Pianka 1977; Avery 1980; Ouboter 1981; Grant and Dunham 1988). Since, however, we have demonstrated that summer bimodality is retained in free-running activity rhythms under DD and constant temperatures of either 29°C or 25°C, such an interpretation is no longer acceptable. Bimodality in summer is not merely a behavioral adjustment that is independent of the underlying circadian oscillators, but is a feature of the circadian system that has most probably evolved as an adaptation to high levels of ambient temperature occurring predictably around midday. Changes in mutual phase relationship between constituent oscillators provide appropriate changes in τ and α that render the locomotor pattern unimodal again in autumn, when the adaptive necessity of a double-peaked pattern disappears with the lowering of ambient temperature.

It has been suggested that seasonal differences in τ of the locomotor rhythms of the fish *Lota lota* and *Couesius plumbeus* reflect the reorganization of the circadian system in response to the seasonal changes in the external day (Kavaliers 1978, 1980). Investigations in birds (*Zonotrichia atricapilla*, *Z. leucophrys*) and nocturnal rodents (*Peromyscus maniculatus*, *Mus musculus*, *Mesocricetus auratus*) have specifically shown that the pattern of activity and the values of τ and/or α in constant conditions are dictated by the length of the photoperiod to

which the individual animals were previously exposed (Gwinner 1975; Pittendrigh and Daan 1976a). The existence of such after-effects of photoperiod on circadian rhythmicity in constant conditions clearly supports the hypothesis that seasonal changes in τ , α and activity pattern are brought about by seasonally changing photoperiod length.

From the present short-term laboratory experiments in constant conditions we cannot decide whether the seasonal differences in circadian parameters of the locomotor rhythms of *Podarcis sicula* would result from after-effects of the different photoperiods (or thermoperiods; see Pittendrigh and Daan 1976b; Underwood 1992) experienced by the lizards in different seasons, or, alternatively, reflect the existence of a truly endogenous rhythm. In fact, seasonal differences in circadian parameters may be merely due to different photoperiod (or thermoperiod) lengths establishing different phase relationships between constituent oscillators which persist in constant conditions (after-effects), or depend on true endogenous circannual cycles of circadian rhythms, which need photoperiodic or thermoperiodic information only to be properly phased to the external year. Future investigations should test these hypotheses, either by examining whether the expected seasonal changes in circadian parameters occur in the same individual lizard during long-term locomotor recording in constant conditions, or whether the expected changes can be obtained through appropriate manipulation of photoperiod (or thermoperiod) durations in the laboratory.

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