

Synchronization of Activity Rhythms with the Tide in a Saltmarsh Collembolan *Anurida maritima*

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Summary. On a marine saltmarsh, the intertidal collembolan *Anurida maritima* (Guérin) has a well-defined tidal rhythm of activity on the mud surface between submerging tides: a large proportion of the individuals emerge from their underground refuges shortly after the retreat of the tide, forage there for a few hours, and retire underground at least 1 h before the return of the tide. This activity rhythm has a period of about 12.4 h and it persists in the field during sequences of non-submerging tides and in the laboratory away from the tides in constant light. In the field the level of activity is greatly reduced during the night. It is suggested that the function of this tidal rhythm is to enable individual *Anurida* to anticipate the return of the tide both during periods of regular, twice-daily tidal submergence and after a period of days when the habitat has not been covered by the tide.

Introduction

It is often assumed that the nature of the clock underlying biological activity rhythms, although of undeniable physiological interest, is of little direct relevance to the ecologist (see Enright 1975). In the natural environment, the zeitgebers can usually be relied upon: animals do not live in constant conditions. However, there are situations in which the nature and existence of the underlying endogenous control of activity rhythms could be of direct ecological importance. One example is provided by the activity rhythms of polar animals. It has been shown that in the continuous daylight of the arctic summer, locomotor activity rhythms tend to free-run, with periods that may be either longer (e.g. in *Cottus poecilopus*; Müller 1970) or shorter (e.g. in the burbot, *Lota lota*; Müller 1973) than 24 h. Bovey and Oertli (1974) reported that the activity rhythms of beavers free-run under the ice-cover of their lakes in winter.

A second situation in which natural zeitgebers might be absent and endogenous rhythms might therefore be of direct relevance, is provided by animals that live in the intertidal zone. An animal living above extreme high water neaps will experience sequences of submerging tides that will alternate with sequences of non-submerging tides: the relative duration of these sequences will depend, amongst other things, on the local tidal regime, predictable seasonal changes, and unpredictable weather effects. How, for example, is a terrestrial animal, living in the high intertidal zone and vulnerable to tidal flooding, to synchronize its locomotor activity with periods when its habitat is not covered

by the tide? After a period of tidal emergence, how is it able to predict when the next tidal submergence will occur? Comparable problems face marine animals living below extreme low water neaps.

Field observations on terrestrial saltmarsh arthropods suggest two possible solutions to this problem (Treherne and Foster 1979). A carabid beetle, *Dicheirotichus gustavi* Crotch, has a circadian locomotor rhythm which is suppressed during periods of submerging tides (Treherne and Foster 1977). It is possible that this is a widely used strategy, since Heydemann's (e.g. 1966, 1979) extensive studies indicate that most saltmarsh insects have circadian, rather than circatidal, rhythms of locomotor activity. A mite, *Bdella interrupta* Evans, adopts a more complex solution of switching between a rhythm of period 12.5 h during tidal submergence and an 11.5 h rhythm during tidal emergence (Foster et al. 1979). This appears to ensure that a peak of activity is maintained in daylight hours and is safely separated from the tides during periods of tidal submergence.

There is as yet no evidence that the most obvious solution, namely the maintenance of a 12.4 h circatidal rhythm during periods of tidal emergence, is adopted by any terrestrial intertidal animal. In this paper, we present evidence that this strategy is used by the intertidal collembolan, *Anurida maritima* (Guérin).

Anurida maritima is abundant in a wide variety of intertidal habitats throughout the holarctic (Imms 1906; Joose 1966). It has a catholic diet of dead animals (Imms 1906) and is considered by Dexter (1943) to be one of the most important scavengers of the intertidal zone. Unusually for a collembolan, it has no spring and cannot jump. Davenport (1903) reported that some intertidal Poduridae appear to anticipate the return of the tide, but made no observations on the behavioural rhythms of *Anurida*. We present here field observations and a preliminary laboratory investigation of the rhythmic locomotor activity of *Anurida maritima*.

Methods

Field observations were made at two sites on the edges of a drainage channel on Hut Marsh, Scolt Head Island, Norfolk, U.K. (see Foster and Treherne 1975; Treherne and Foster 1977). Site 1, the low marsh site, is between 1.2 and 1.6 m above Ordnance Datum (O.D.). Site 2, the high marsh site, is 600 m to the north, bordering the same drainage channel, and lies between 2.0 and 2.2 m above O.D. Site 1 is submerged about 580 times per year, i.e. by about 82% of the annual tides; site 2 is submerged about 300 times per year, i.e. by about 42% of the annual tides.

Anurida maritima lives in the soil to a depth of about 10 cm. At site 1 in late June and early July 1978 and 1979, most of the

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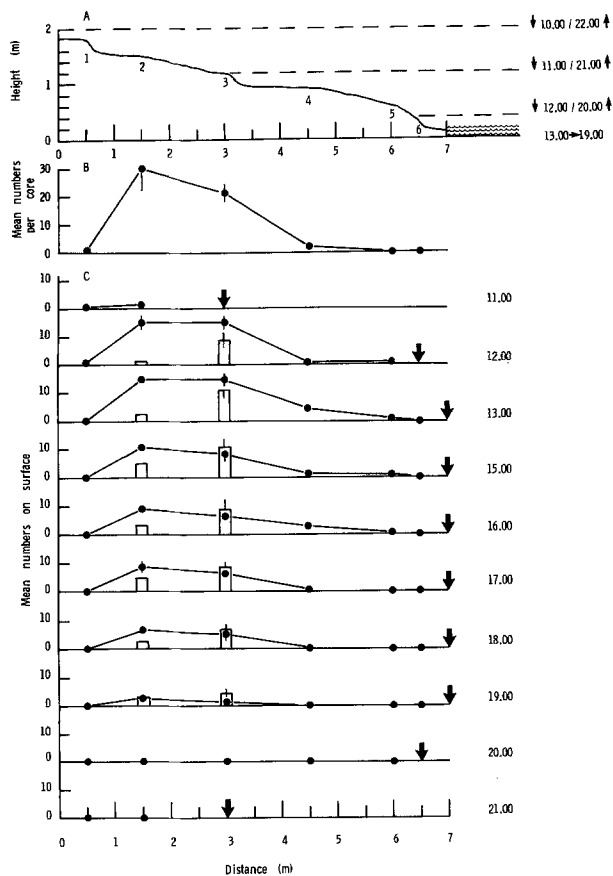


Fig. 1. **A** Diagrammatic section through Site 1, showing stations 1–6. Vertical scale: height in m above Ordnance Datum. Dotted lines indicate height of tide (↓ falling, ↑ rising) at times specified. **B** Distribution of *Anurida maritima* in soil. Mean numbers per core ($n=5$), 10 July 1978. **C** Distribution on soil surface in one intertidal cycle: 9 July 1978. Sample times given on right. Mean number within drainpipes (histograms) and outside drainpipes (filled circles) ($n=5$). Arrows indicate level of the tide. Vertical bars in this and subsequent figures indicate $\pm 1 \times$ S.E.M.

underground populations were in a zone between 1.1 and 1.6 m above O.D. (Fig. 1a, b). On 10 July 1978 at site 1, the peak average density was 33 ± 12 (5) (mean \pm s.e.m. (n)) individuals per core ($1,833 \text{ m}^{-2}$). On 9 July 1978, the peak average density at site 2 was 14.3 ± 3 (10) individuals per core (778 m^{-2}).

The locomotor activity of *Anurida maritima* under natural conditions was estimated by counting the numbers on the mud surface underneath 20×20 cm metal quadrats staked in the ground. At least 15 quadrats were inspected at each site on each sampling occasion. At night, a torch with a red filter was used. At both sites, the sampling quadrats were placed on the soil above the zone of maximum underground density of collembolans (e.g. between stations 2 and 3 at site 1: Fig. 1a).

Soil temperature was measured with a mercury thermometer with the bulb inserted 1 cm into the mud. Temperature and relative humidity at the mud surface were measured with a miniature thermocouple psychrometer (see Unwin in Corbet, Unwin and Prŷs-Jones 1979).

To obtain some idea of the proportion of the underground populations that come out onto the surface at low tide, 5 plastic drainpipes (15.3 cm diameter, 40 cm long) were placed vertically into the ground at each station at site 1, and paired with 5 circular indentations in the mud surface which enclosed the same area as the pipes. The numbers appearing within the pipes and within the circles were recorded during one intertidal period and, on the next day, the soil underneath the pipes was dug up and the collembolans washed out and counted (Fig. 1b).

To observe activity in controlled, non-tidal conditions, 100 freshly collected Collembola were placed on each of 4 sandwich boxes (surface area ca. 240 cm^2) filled to a depth of 3 cm with mud collected from the field. The mud surface was scored with a number of deep grooves, to provide refuges for the insects. The containers were kept in a broom cupboard at Wells Field Study Centre, Wells-next-the-Sea, Norfolk, in constant light (provided by a 60 watt bulb). The number of Collembola visible on the mud surface was counted at regular intervals. Temperature was not controlled, but it remained between 19 and 21°C throughout the course of the experiment, which lasted four days.

Observations on collembolan activity were analysed as periodograms (see Enright 1965) and by Fourier analysis using a Fast Fourier Transform (Rogers 1980). The latter programme requires 128 or 256 points of input, evenly spaced in time. Where necessary, these were produced from the raw data by linear interpolation. Output is in the form of a root-mean-square frequency-spectrum (e.g. Fig. 3b), with the ordinate expressed in arbitrary units and the abscissa in h^{-1} .

Results

General Description of Activity

The activity of the collembolan populations on the marsh surface during low tide periods between submerging tides followed a standard pattern (Fig. 1c). Individuals appeared on the mud within half an hour of the retreat of the tide, reached a peak of abundance within 2 to 5 h, and returned to their underground refuges at least an hour before the return of the tide. It is clear that individuals walk considerable distances; for example, some insects were observed at station 5, where there were no underground colonies.

A large percentage of the underground populations may make forays onto the surface during one intertidal period. At station 3, for example at 1300 h a mean of 11.2 ± 3.7 (5) individuals appeared at the surface within the area enclosed by the plastic pipes: this is just over half the total number (21.4 ± 2.4 (5)) of individuals that were disinterred the following day from the soil beneath. At station 2, the maximum number of individuals on the surface within the plastic pipes represented 15% of the total population, as revealed by sampling on the following day.

These forays onto the surface appear to be feeding excursions, since individuals were frequently seen congregating around recently dead larval and adult Diptera, small crabs, and polychaetes, stranded on the mud.

Direct Response to the Tide

Although individual *A. maritima* usually retreat underground well before the tide covers them, on very infrequent occasions individuals were observed walking on the mud surface as the tide rose around them. These insects reacted to the tide only when actually touched by the water, whereupon they accelerated rapidly up the slope, but were always eventually overtaken and floated off on the rising tide.

In a simple field experiment, five small portions (ca. 30×30 cm) of surface mud close to the animals' normal refuges were carefully dug out with a knife about 2 h before the expected tidal inundation. These mud platforms, on each of which a small number (5–20) of collembolans were still walking, were carried down to the bottom of the creek where the tide was beginning to rise, and inserted flush with the mud surface. These animals responded to the rising tide in the same way as the undisturbed individuals and were all eventually engulfed and carried off on the water. The mean rate of water movement across this gently

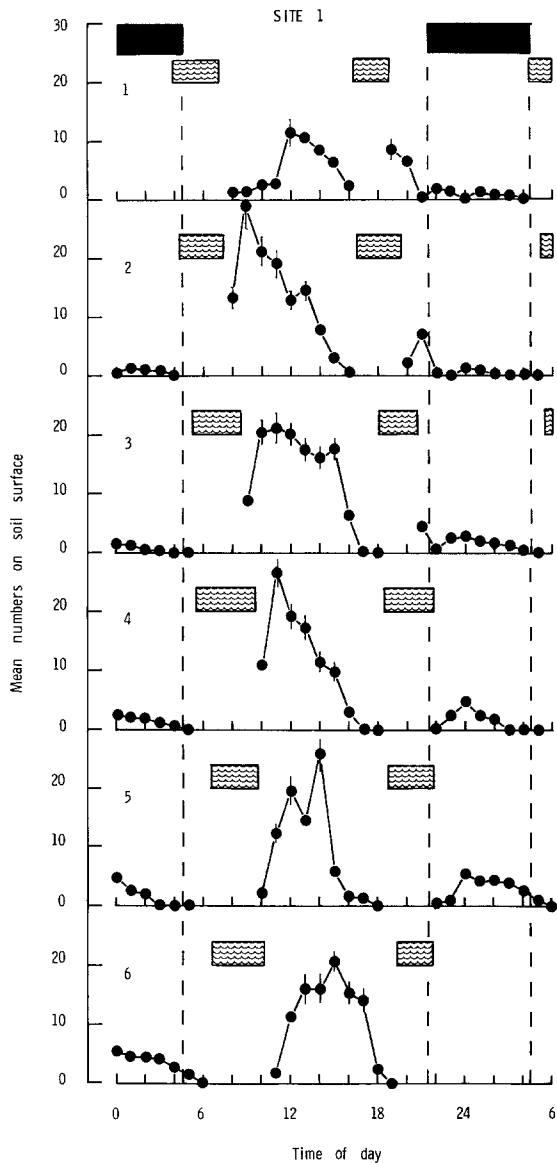


Fig. 2. Mean numbers of *Anurida* per quadrat on soil surface ($n=30$), 2 to 7 July 1978, Site 1. Hatched bars indicate period when tide covered the sample site

sloping mud surface was 45.3 ± 5 (5) cm min^{-1} , considerably faster than the accelerated uphill walking response of the collembolans (20.5 ± 0.7 (10) cm min^{-1}). Although this escape reaction might be more successful on a more vertical surface, these observations indicate that on gently sloping surfaces it is essential for the collembolans to anticipate the arrival of the tide.

Activity Patterns during periods of Tidal Submergence

During a 6-day sequence of submerging spring tides at the low marsh site, the collembolans appeared on the surface with a clearly defined rhythm of activity between high tides (Fig. 2). Activity was significantly reduced at night. A periodogram of these data shows clear peaks corresponding to periods of 12.5 and 24.8 h (Fig. 3a). Fourier analysis of the same data (Fig. 3b) produces essentially the same result, with peaks at 24.6 and 12.3 h. The peaks at 8.2 and 6.3 h represent sum and difference terms resulting from the interaction of the two principal frequencies.

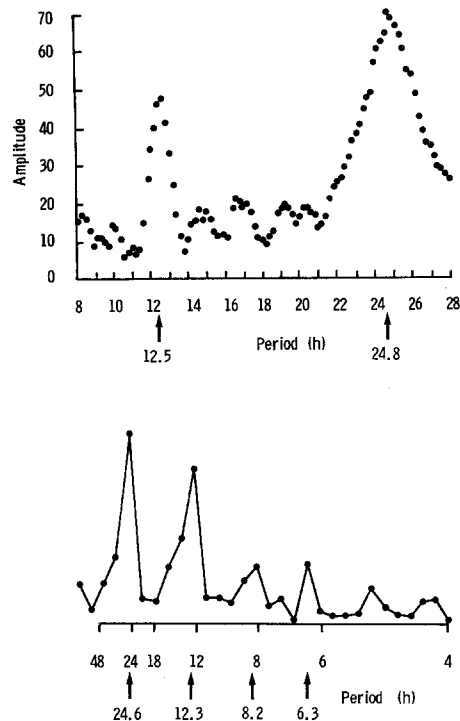


Fig. 3. Top: Periodogram of data illustrated in Fig. 2. for *Anurida* activity at Site 1 during a sequence of submerging tides. Bottom: Fourier-transform of the same data, using 128 points (interpolated from 120). Ordinate – root-mean-square output from the Fourier-transform programme (arbitrary scale); abscissa – period in hours (reciprocal scale). In this and subsequent figures, the high-frequency part of the spectrum has been omitted, as it contains little information. Arrows indicate the period for each peak

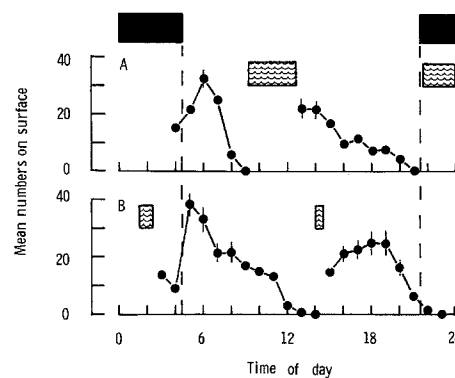


Fig. 4. Mean numbers of *Anurida* per quadrat on soil surface ($n=30$) at Site 1, A. on 11 July 1978 and B. on 15 July 1978

The pattern of activity between consecutive tides was similar to that described in Fig. 1: individuals usually retired from the mud surface within 0.5 to 1.5 h before the return of the tide. Although during this particular sequence, alternate activity peaks occurred at night and were small, it is possible for two large activity peaks to occur in one day, if the tides are phased appropriately (Fig. 4). This figure also indicates that individuals emerge promptly onto the soil surface, whether the preceding period of tidal submergence is long or short.

There was no significant correlation between temperature (either 1 cm below or at the surface) or relative humidity (measured at the surface) and any measured parameter of locomotor activity, i.e. integrated numbers, time to peak activity, or ampli-

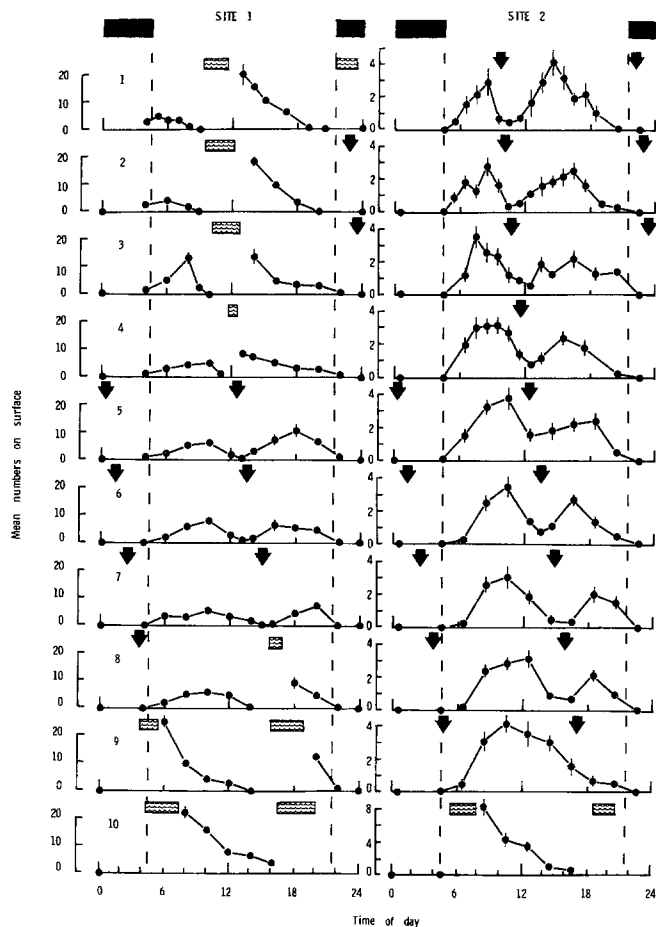


Fig. 5. Mean numbers of *Anurida* per quadrat on soil surface at Site 1 and Site 2 ($n=15$ at each site), 29 June to 8 July 1979. Hatched bars indicate period when tide covered the site. Vertical arrows show predicted times of the high tides that did not cover the sampling site

tude of peak activity. Although it was usually colder at night, it is not possible to establish unequivocally from these observations whether the reduced activity at night is simply an effect of temperature or whether darkness *per se* is also of importance. It seems unlikely that reduced temperature is the only factor: for example, during the night of day 3 the soil temperature never fell below 13°C and the peak activity was 2.6 ± 0.9 (30) individuals per sample, whereas during day 5, when the day-time temperature never exceeded 14°C , the peak activity was ten times greater (26.2 ± 3 (30) individuals per sample).

Activity Patterns During Periods of Tidal Emergence and Submergence

Collembolan activity was observed at both the high and low marsh sites over a 10-day period that embraced a sequence of emerging and submerging tides (Fig. 5). At the low marsh site, the pattern of activity during the periods of submergence (days 1–4 and 8–10) was similar to that observed at this site in the previous year (Fig. 2).

During the period of non-submerging tides (days 4–8) the bimodal lunar-day (“tidal”) rhythm continued. Figure 6 shows frequency spectra from Fourier analysis of (a) the whole 10-day period; (b) the initial period of submergence; and (c) the period of non-submergence. In all cases, the diel and “tidal” frequencies are clearly distinguishable. As shown in Fig. 6c, the “tidal”

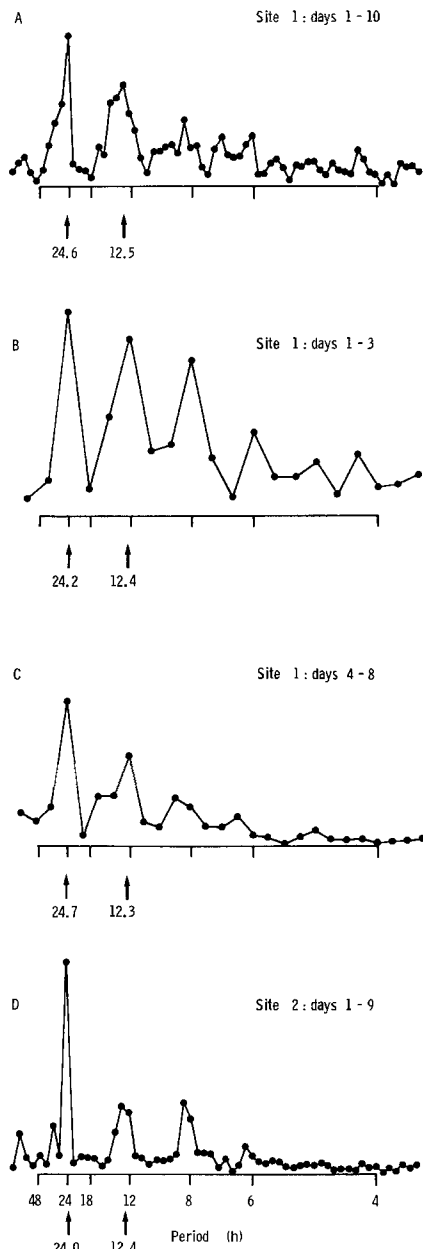


Fig. 6. Fourier transforms of data from Fig. 5: A Complete data from site 1, using 256 (240) points. B Site 1, initial period of submergence, using 128 (72) points. C Site 1, middle period of emergence, using 128 (96) points. D Complete data from site 2, using 256 (216) points

rhythm continues with no detectable change in frequency throughout the period of non-submergence, so that synchronization with the tides is preserved.

Similar results were obtained at the high marsh site (site 2): here the collembolan zone was covered the day before the observations began (28 June 1979), but the tides did not return again until day 10. During this 9-day period, the activity rhythm remained bimodal, with peaks at 24.0 and 12.4 h (Fig. 6d).

Activity Patterns in the Laboratory

Under conditions of constant dim light and in the absence of tidal coverage, the bimodal lunar-day rhythm persisted for a period of 4 days, after which the experiment was ended (Fig. 7).

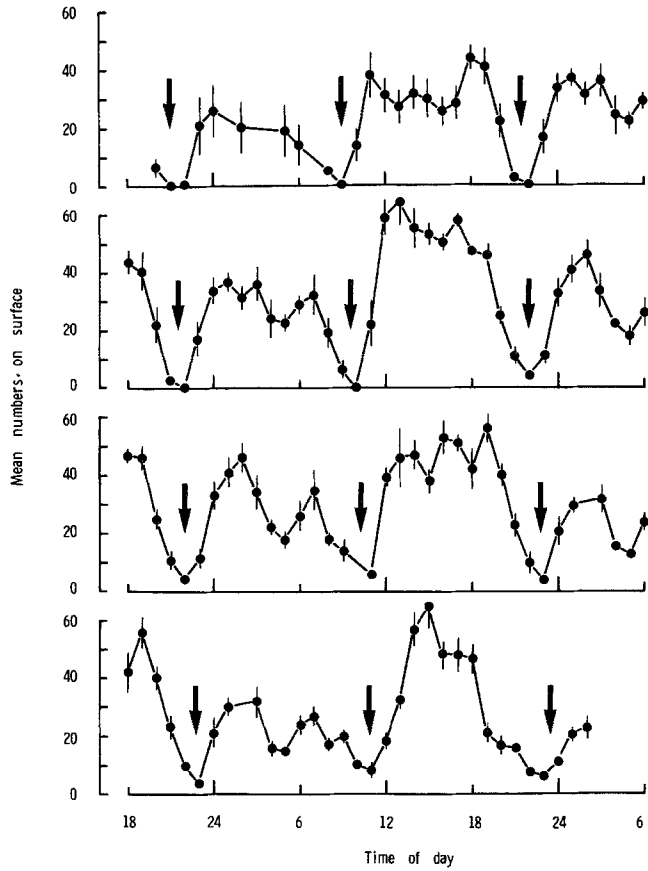


Fig. 7. Mean numbers of *Anurida* on soil surface in constant light in laboratory ($n=4$). Wells-next-the-Sea, 7 to 12 August 1978. Animals collected from saltmarsh at Wells, from mud about 1.2 m above Ordnance Datum. Arrows indicate predicted time of high tide at collection site

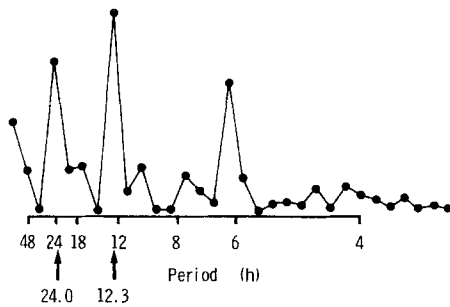


Fig. 8. Fourier transform of data from the laboratory experiment (Fig. 7), using 128 (99) points

The general pattern of activity showed some resemblance to that recorded in the field during periods of tidal emergence (Fig. 5): rather broad peaks of activity were interrupted by short retreats of the population underground, coinciding with the expected time of high tide. Fourier analysis (Fig. 8) correspondingly shows a principal period of 12.3 h; the 24.0 h diel rhythm is now weaker than the tidal one, suggesting that diel behaviour of these insects is more subject to direct environmental control, and therefore persists less strongly under constant laboratory conditions, than the circatidal rhythm.

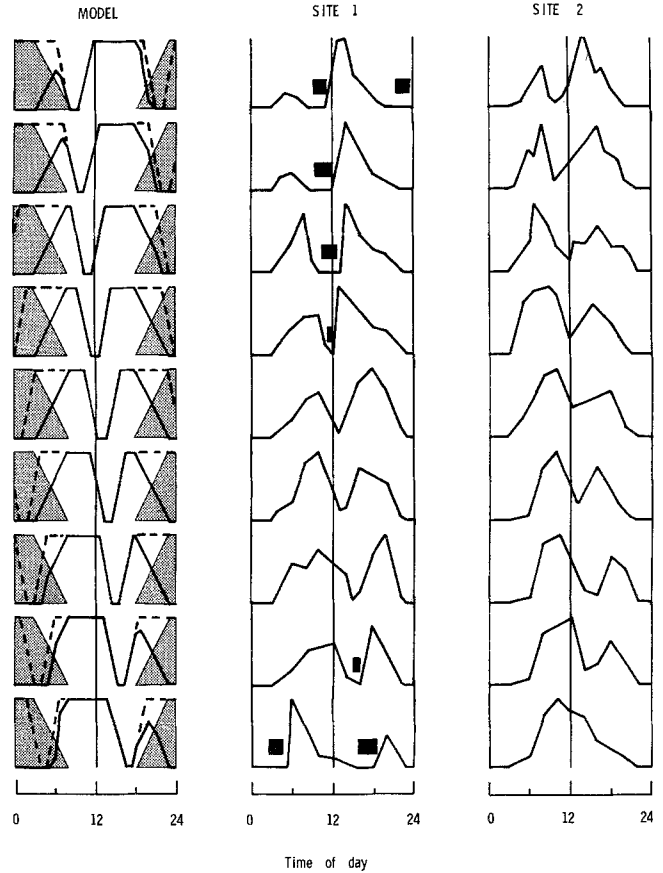


Fig. 9. Model of factors influencing locomotor activity of *Anurida maritima* in the field. Site 1, Site 2: collembolan activity on successive days (Fig. 5), expressed as % of peak activity for each day. Black bars indicate period of submerging tides. Model: dotted line indicates circatidal rhythm of above-ground activity, as revealed in constant light (Fig. 7); stippled zones indicate extent of suppressing influence of night-time on activity; continuous line is predicted activity, assuming this is a combination of the circatidal rhythm and the suppressing influence of night-time

Discussion

The present observations establish that *Anurida maritima* can anticipate the return of the tide during periods of regular, twice-daily tidal submergence. Davenport (1963) demonstrated that Collembola of the family Poduridae (sic), *Xenylla humicola* (Fab.) and *Archisotoma* (= *Isotoma*) *besselsi* (Packard), retreated from the surface of a New England beach about 1 h before the return of the tide, but there has been no previous unequivocal demonstration of this behaviour in *A. maritima*. The adaptive significance of this behaviour is clear: individuals cannot outrun the encroaching tide, and must therefore anticipate it, or risk being carried to uninhabitable zones or blown out to sea.

There are three possible general mechanisms by which an animal could synchronise its locomotor activity so as to avoid regular circatidal submergence. It might rely on a direct response to some feature associated with the rising tide, such as vibration of the substrate. It might make use of an endogenous "hour-glass" mechanism, such that, for example, retreat of the tide sets in motion a one-cycle pattern of activity: emergence onto the mud surface, followed 7-h later by retreat underground. Finally, the animal might have an endogenous oscillator which could ensure that it was continuously in phase with the tides.

The fact that the activity rhythms of *Anurida* can persist in the field in regions several hundreds of metres away from the high tides (site 2, Figs. 5, 6d), and in the laboratory half a mile from the sea (Figs. 7, 8), argues against the first two possible mechanisms and provides good support for the existence of an endogenous oscillator.

The observed activity rhythm of *Anurida* appears to be a combination of a circatidal rhythm and a diel rhythm of suppression during the night. The activity peaks are alternately suppressed and released as they move into and out of the hours of darkness (Figs. 2, 5). A very simple model produces an activity pattern generally similar to that observed in the field (Fig. 9). An obvious complication is the occurrence of submerging tides, which narrow the duration of the observed activity peaks. This model is similar to that proposed by Palmer and Round (1967) for the vertical migration rhythm in the benthic diatom *Hantzschia virgata* (see also Palmer, 1974). There are, however, two important differences. *Hantzschia* lives relatively low down in the intertidal zone, and has relatively short activity peaks: consequently there is never more than one activity peak expressed at a time. Secondly, since in constant conditions, the diatom's rhythm persists with only one peak expressed per 24 h, Palmer and Round conclude that this rhythm is a combination of two endogenous rhythms, a 12.4 h semi-lunar rhythm and a 24 h solar day rhythm. In contrast, the evidence suggests that the observed rhythm in *Anurida* is a combination of an endogenous 12.4 h rhythm and an exogenous rhythm of suppression during darkness.

In addition to the problem of synchronization with regular tidal submergences, *Anurida* must also cope with the more complex problem that confronts all terrestrial colonists of the upper intertidal zones; that is, how to predict the return of the first submerging tide after a period of tidal emergence. The solution apparently adopted by *Anurida* is simple and elegant: the established circatidal rhythm is overtly maintained throughout the period of emergence such that the populations are in appropriate synchrony with the first submerging tide, whenever it might occur. *Anurida* therefore, like the mite *Bdella interrupta* (Foster et al. 1979) maintains a rhythmic pattern of foraging on the surface during periods of both submergence and emergence, but the period of this rhythm, unlike that of the mite, does not change. This contrasts with the apparently less flexible and less efficient strategy of the carabid *Dicheirotrichus gustavi* (Treherne and Foster 1977) which has a circadian rhythm of activity that is suppressed during periods of submergence: it is therefore able to forage on the surface only during periods of tidal emergence.

It is clear that further work under controlled laboratory conditions is required to elucidate the exact nature of this activity rhythm and of the zeitgebers that control it. Preliminary laboratory experiments in Cambridge indicate that the locomotor activity rhythm of individual *Anurida* does persist in controlled conditions of light, temperature and humidity in a growth cabinet. However, the present observations provide good evidence that the locomotor activity of *Anurida maritima* can free-run in natural conditions during periods of emergence (Fig. 6). Natural free-running rhythms are extremely rare and have not apparently been reported before in insects. In addition, the present observations provide perhaps the best demonstration to date that the endogenous control of an activity rhythm can be of relevance not merely to an animal's physiology but also to its ecological organization.

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