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Ontogenetic differences in the circadian locomotor activity rhythm of the talitrid amphipod crustacean *Orchestoidea tuberculata*

Received: 3 August 1999 / Accepted: 26 May 2000

Abstract Adult talitrid amphipods often display a nocturnal activity pattern, which has been shown in a number of cases to be partly controlled by an endogenous rhythm of circadian period. Juvenile talitrids have been little studied in the past, but evidence from field studies indicates that they may display a different diel pattern of locomotor activity from that of adults. This study presents evidence from the field in south-central Chile that juvenile *Orchestoidea tuberculata* Nicolet show crepuscular activity peaks, contrasting with the nocturnal peaks shown by adult conspecifics. Under constant conditions in the laboratory, both juveniles and adults exhibit endogenous rhythms of circadian periodicity. However, the phasing of activity differs in juveniles and adults, corresponding to the differences observed in the field. It is suggested that differing phasing of peak locomotor activity may be a mechanism to reduce contact between juvenile and adult talitrids. Experimental evidence indicates a significant negative influence on survival of juveniles in the presence of adult conspecifics by intraspecific predation. Other factors influencing the timing of surface activity are also discussed.

Introduction

Talitrid amphipods are among the most abundant supralittoral and intertidal detritivores on temperate beaches throughout the world. They forage on the beach

surface, often during the night after burrowing by day and, as they show direct development, a range of size classes is typically present on the shore.

A number of field studies on the surface locomotor activity of talitrid amphipods from localities around the world have reported differences in the phasing of activity between adult and juvenile individuals (Geppetti and Tongiorgi 1967; Craig 1973; Jaramillo et al. 1980; Williams 1983; Scapini et al. 1992). However, this has usually been a passing observation, and differences in the activity patterns of adults and juveniles have not been studied experimentally. Geppetti and Tongiorgi used automatic pitfall traps to study the spontaneous surface activity of *Talitrus saltator* on a Mediterranean beach. Adults were found to have an exclusively nocturnal activity pattern, moving upshore from their strandline burrowing zone into the supralittoral dune area 2 to 3 h after midnight, and returning to the burrowing zone just before dawn. Juveniles showed a similar pattern of activity to the adults, but phased approximately 1 h later. The findings of Craig for the talitrid *Orchestoidea corniculata* on a Californian shore revealed slightly different patterns of locomotor activity. That author found that the population foraged downshore of the burrowing zone. It was also found that whilst adults were strictly nocturnal, juveniles emerged a little earlier, around sunset, and their activity peaked around dawn, after the adults had reburrowed.

Jaramillo et al. (1980) employed similar techniques to those of Craig (1973) to study activity of *Orchestoidea tuberculata* on a beach in central southern Chile. Results were, on the whole, similar to those of Craig. Adults were found to be strictly nocturnal and activity was concentrated in the intertidal zone. Juveniles were less strictly nocturnal than adults, often showing activity peaks close to dusk or dawn. Williams (1983) studied the locomotor activity of *Talitrus saltator* in the field in Britain. It was found that juveniles of that species emerged from the sand 2 to 3 h before adults and remained active on the beach surface for 1 h after the adults had reburrowed. Scapini et al. (1992) studied

Communicated by J. P. Thorpe, Port Erin

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surface locomotor activity of *T. saltator* on a Mediterranean beach. These authors described a lag in activity between adults and juveniles similar to that described by Geppetti and Tongiorgi (1967).

Although a number of experimental laboratory studies have aimed at elucidating the role of endogenous components in the control of rhythmic locomotor behavior in adult talitrid amphipods, to the authors' knowledge no such studies exist for juveniles. Early work on the solar orientation ability of *Talitrus saltator* from the Mediterranean (Pardi and Papi 1953; Pardi 1960) first suggested the existence of an internal timing mechanism of solar frequency. Since that time, the existence of an endogenous rhythm of locomotor activity with a circadian period has been demonstrated and investigated in some detail by a number of authors working on adults of various species of talitrid amphipods (e.g. Featherstone and McIntyre 1957; Wildish 1970; Bregazzi and Naylor 1972; Benson and Lewis 1976; Williams 1980, 1983). These studies were carried out under conditions of constant darkness and constant temperature. In all the above cases, there was a strong circadian component to the rhythm and activity was phased during time of subjective night.

The almost exclusively nocturnal surface locomotor activity shown by adult talitrids in previous studies has been attributed to two factors. Bowers (1964) and Rüppel (1967) suggested that the activity of diurnally-feeding surface predators, particularly birds, is an important factor favouring nocturnal activity in adult talitrid amphipods. Bowers also mentioned that conditions of temperature and humidity are also more favourable for surface activity during the night. It is known that talitrid amphipods are vulnerable to desiccation caused by high temperatures and low humidities (Morrit 1987; Brown and McLachlan 1990) and Scapini et al. (1992) favoured this as the most likely explanation for nocturnal surface activity in *Talitrus saltator* at their Mediterranean study site, since shore birds were relatively infrequent there.

Given that both predator avoidance and physiological demands favour nocturnal activity, it remains to be explained why juvenile talitrids show a more crepuscular, less exclusively nocturnal pattern than adult conspecifics. This problem is compounded by the fact that juvenile talitrids are more vulnerable to evaporative water loss than adults (Morrit 1987) and would therefore be expected, other things being equal, to adopt a similarly nocturnal activity pattern to that of adults. Jaramillo et al. (1980) proposed that the prolonged activity of juveniles compared to adults may be partly due to the lower vulnerability of juveniles to diurnally feeding predators (owing to their smaller size, lower visibility and higher mobility). Those authors and Scapini et al. (1992) also pointed out that, owing to their increased energy requirements for growth, juveniles may be obliged to extend the active foraging phase of their activity cycle. According to Dahl (1952) and Jaramillo et al., a certain amount of intraspecific predation seems

to occur in at least some species of talitrid amphipods. It is therefore possible that the advantages of differing phasing of juvenile and adult surface activity lie in minimising contact between the two groups and maximising survival.

Using a population of *Orchestoidea tuberculata* from a beach in central southern Chile, the present study aimed firstly to describe the temporal distribution of activity of juveniles and adults in the field using conventional pitfall techniques. Secondly, the endogenous basis of these activity patterns was investigated by means of actograph experiments under free-running conditions on adult and, for the first time, juvenile individuals. Finally, laboratory experiments were used to test the hypothesis that survival is adversely affected in mixed adult/juvenile groups of *O. tuberculata*. The results of these lines of investigation are discussed in the context of previous studies, with particular reference to the relationship between juvenile and adult activity patterns.

Materials and methods

Field sampling

All field sampling was carried out over 24 h periods on the beach at Mehuin, X Region, Chile (39°25'S; 73°13'W), a locality exposed to intense wave and swash action, and to a maximum tidal amplitude of only ~1.5 m. Sampling dates were 22–23 January 1995 (post-spring tide), 28 February–1 March 1995 (spring tide), 31 August–1 September 1995 (post-spring tide), 20–21 March 1996 (post-neap tide) and 17–18 June 1996 (neap tide).

Amphipods moving over the surface of the beach were trapped using either simple pitfall traps (1995 samples) or pitfall cross-traps (1996 samples).

Simple pitfall traps

Plastic jars 10 cm in diameter and 6 cm deep were installed on the beach surface along two replicate transects separated by 5 m. Within each transect, the traps were separated by 3 m, and transects extended from the upper beach levels to the highest levels reached by the swash zone. Throughout the sampling period, traps were removed and replaced as dictated by the extent of beach exposed by the tide.

Each trap was installed with its rim flush with the sand surface, and contained 3 cm of 10% formalin solution. Once installed, traps were guarded from a distance of 50 to 100 m to prevent disturbance by beach-users. Every 2 h the contents of the traps were emptied into pre-labelled plastic bags, and then refilled with formalin solution and replaced.

Pitfall cross-traps

The pitfall cross-traps were designed to indicate the mean direction of movement of the individuals trapped, but directional data were not used in the present study, which pooled all catch data. The design is based on the traps used by Scapini et al. (1992). Each trap consisted of two pieces of 9 mm-thick marine plywood, each measuring 120 × 120 cm. These two pieces were slotted together through cuts at their midpoints, thus forming a cross. During use the crosses were arranged on the sand surface with their axes at 45° to the slope of the beach. It was ensured that no gaps existed at any point between the sand surface and the lower edge of the cross. Plastic pitfall traps of 10 cm diameter and 6 cm depth were

installed at each of the four corners of each cross. The rims of the traps were set flush to the sand surface, and their edges were in contact with the wood of the cross in two places. Each trap was half-filled with 10% formalin. Thus, any invertebrates moving over the sand surface arrived at one of the quadrants and were guided into the trap in that corner of the quadrant.

The middle trap of the five cross-traps was installed at the previous high-tide mark (i.e. the usual *Orchestoidea tuberculata* burrowing zone). Two further crosses were placed at 10 and 20 m both up and downshore from the middle cross-trap, respectively. The downshore traps were removed and replaced as dictated by the rise and fall of the tide. Rather than an arrangement of traps directly upshore and downshore of each another, the traps were arranged along a line at 45° to the beach slope to minimise interference effects between traps, assuming the predominant axis of migration of amphipods to be up- and downshore.

Every 2 h, the contents of each trap were emptied into a pre-labelled plastic bag and kept for later analysis. Traps were replaced and refilled with formalin solution. At night, use of torches was kept to a minimum, and a red filter was used to minimise disturbance to active individuals. The traps were observed from a distance of 50 to 100 m during daylight to avoid possible disturbance by beach-users.

During all field sampling, the times of dusk and dawn were recorded, along with times of high tides.

Analysis of samples from pitfall traps

Orchestoidea tuberculata Nicolet was separated from other invertebrates trapped, then sorted into size classes. "Juveniles" were defined as those individuals with overall body lengths (apex of cephalon to distal tip of telson) of <8.5 mm, whilst "adults" were taken to be those individuals with overall body lengths >15 mm, following Jaramillo et al. (1980) working with *O. tuberculata* from the same locality. Individuals of intermediate body lengths were not included in the analysis, to avoid ambiguity.

For each time interval and each trap, the numbers of juveniles and adults were counted. Mean numbers caught per trap per time interval were calculated by summing numbers of individuals caught over the entire spatial range of the sampling.

Although the simple traps (1995) and cross-traps (1996) were designed to answer different questions, it seemed reasonable to pool the data for the present study, which sought to define only the diel pattern of variation of total catches. Moreover, the timings of the five sampling programmes permitted randomization of high-tide times within a pooled 24 h data set. The data from all five field experiments were therefore combined in a summary graph in the following way. The mean number of individuals caught per trap was calculated for each sampling interval during each trial. Each mean was then converted to a percentage of the maximum number caught in any sampling intervals during that trial. Finally, the results from all five trials were combined by taking the mean of each of the percentage figures for each sampling interval over a standard 24 h period.

Actograph experiments

Collection of experimental individuals

Amphipods for use in actographs were collected from Playa Universitaria, Mehuin (39°25'S; 73°13'W) 24 to 48 h before the start of the experiment. Both adults and juveniles were excavated by hand from their burrowing zones during daylight hours, and immediately placed in light-proof bags containing moist sand from the burrowing zone. Actograph experiments were started during the evening of the day of collection.

Experimental conditions

After transport to the laboratory the amphipods were transferred to glass containers measuring 25 cm in length, 15 cm in height and

7 cm in width, along with the damp sand from the burrowing zone to a depth of 6 cm. The containers were also provided with food in the form of furoid algae from the collection site, and cotton wool dampened with seawater to maintain humidity in the sand and air. A Perspex platform of 8 cm length, located in the mid section of the glass container, exactly fitting its internal width, provided a flat surface flush with the sand surface over which locomotor activity could be recorded. Throughout experiments, containers were kept in continuous darkness (DD) in a light-tight constant temperature room at 12 °C at Instituto de Zoología, Universidad Austral de Chile, Valdivia. For each experimental trial, 15 adults or 50 juveniles were placed in each container.

The actograph apparatus was designed and constructed at the School of Ocean Sciences, University of Wales, Bangor. Detailed circuit diagrams are available in Warman (1990). Surface activity of amphipods was registered by interruption of two infrared beams across each of four containers, the beams arranged to pass over the surface of the Perspex platform in the glass container. Every 15 min during the course of the experiment, the number of interruptions of each beam was downloaded to computer as a separate channel. Adult and juvenile experiments were run simultaneously and in duplicate in adjacent glass containers. The dates of the experimental trials were 4 to 8 October 1995 and 7 to 11 October 1996.

Statistical analysis of actograph results

Raw data downloaded from the actograph apparatus were first graphed to give a display of activity per 15 min interval throughout the experiment. These data were then used in a periodogram analysis, performed by the programme "perio" (Aagard 1993). This programme provides an output in the form of a periodogram which gives a graphical display of possible period lengths within a user-specified range, plotted against standard deviation (s-units). Superimposed on the graph are the 95% confidence intervals calculated for the same data in randomised order. A particular periodogram peak was taken to be statistically significant if it exceeded the upper 95% confidence limit at the particular period length. The presence of a statistically significant periodogram peak was taken to indicate periodicity in the data.

The form and phasing of activity was further examined by the construction of 24 h form-estimates. This was achieved by firstly summing every four values in the raw data to obtain 1 hourly activity and secondly dividing the data into 24 h blocks and summing values for corresponding times of day. Using this method it was possible to obtain average 24 h activity patterns for comparison with those obtained in the field.

Coexistence experiments

Adult and juvenile *Orchestoidea tuberculata* were collected from the intertidal zone as detailed for the actograph experiments above. Experimental individuals were kept in damp sand in the laboratory for a maximum of 24 h before initiating the experiments.

The experimental design proposed by Underwood (1986) for detecting intra- and interspecific competition was employed for investigating the effects of adult/juvenile interactions on survival of *Orchestoidea tuberculata*. One set of experiments was run from 19 to 27 January 1991. Individuals were placed in square plastic trays measuring 50 × 50 × 12 cm high, covered by gauze. Each tray was filled to a depth of 2.5 cm with damp sand from the burrowing zone. A further set of experiments was conducted from 5 to 11 January 1997 with plastic containers measuring 8 cm diam. × 8 cm height. Each container had a clear plastic lid with small holes to allow air exchange. Tissue paper soaked with seawater was placed in each container to maintain humidity, but there was no sand. In both sets of experiments, treatments were as follows (Treatment, T, no. of adults, a, and no. of juveniles, j): T₁, 0_a, 10_j; T₂, 0_a, 20_j; T₃, 10_a, 10_j; T₄, 10_a, 0_j; T₅, 20_a, 0_j.

Four replicate containers were used for each treatment, making a total of 20 containers for each experimental trial. Experiments were run at ambient room temperature (15 to 20 °C) and exposed

to the natural light/dark cycle. Every day at midday, for the duration of the experiments, the number of live individuals remaining in each experimental container was counted and recorded. For the 1991 experiments, this involved sieving the sand with seawater to separate burrowed individuals from the sand. No food was provided over the experimental periods.

Results

Figure 1 is a summary graph of the results of the field pitfall-trap sampling. The vertical axis shows the mean percentage of the maximum number of *Orchestoidea tuberculata* caught per trap and the horizontal axis shows sampling time. Times of high tide are more or less randomised across the pooled 24 h format. Adult *O. tuberculata* activity (Fig. 1A) was almost entirely

nocturnal, with no adults caught in the pitfall traps on any sampling occasion during the period 08:00 to 16:00 hrs. In contrast, juvenile *O. tuberculata* (Fig. 1B) showed two main peaks of catch, around dusk and dawn. Catches were low during the middle part of the night.

The locomotor activity of adult *Orchestoidea tuberculata* under free-running conditions in the laboratory from 4 to 8 October 1995 is shown in Fig. 2A. Activity was almost exclusively confined to the hours of subjective night. The periodogram (Fig. 2B) derived from these data shows a significant peak at a period length of ~24 h, indicating a circadian rhythm. The small, barely significant peak at ~12 h appears partially as a sub-multiple of the circadian peak, but also reflects the bimodality of the later circadian peaks. Figure 3 shows the results of a simultaneous experiment run with juvenile *O. tuberculata*. The raw data (Fig. 3A) and the periodogram (Fig. 3B), again indicate a circadian pattern of locomotor rhythmicity, but with the peaks during

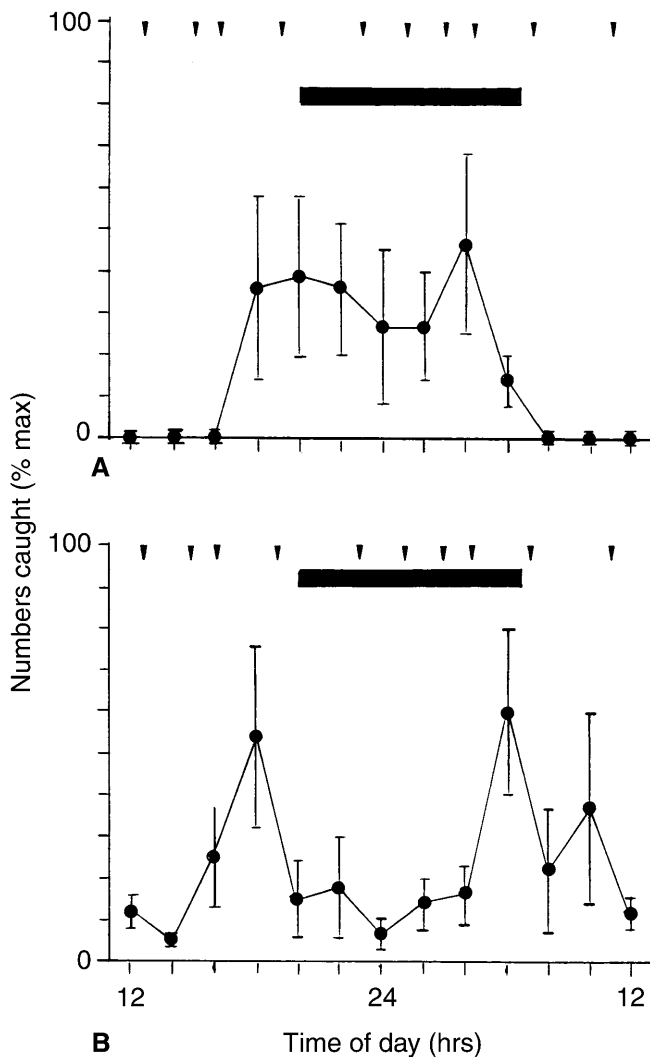


Fig. 1 *Orchestoidea tuberculata*. Mean \pm SE percentage maximum adults (A) and juveniles (B) caught in pitfall traps at 2 h intervals over 5 d sampling at Mehuin, Chile (Horizontal black bars mean duration of darkness; arrow heads indicate times of high tide) (see "Materials and methods - Field sampling" for detailed protocol and sampling dates)

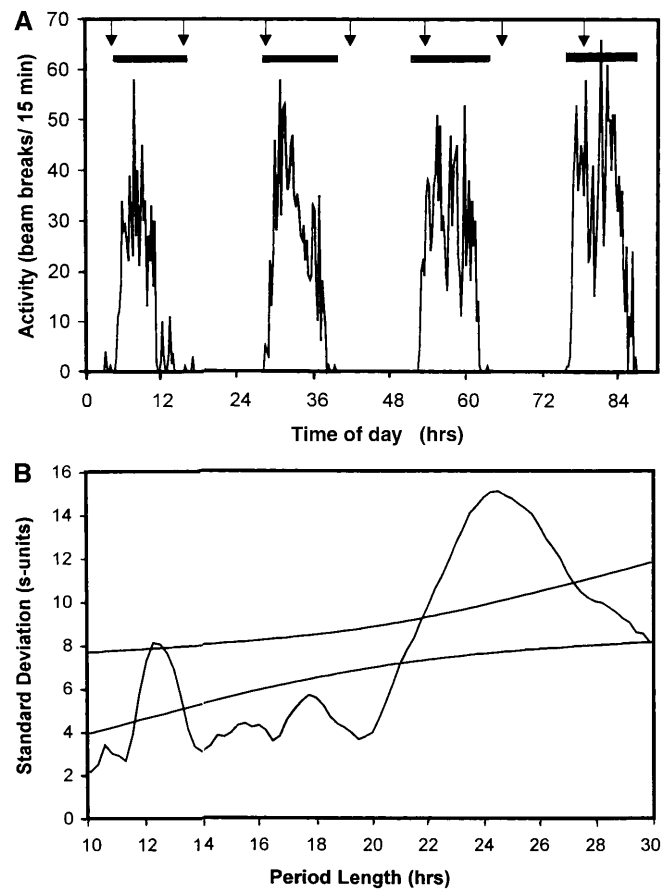


Fig. 2 *Orchestoidea tuberculata*. A Free-running locomotor activity rhythm of 15 adults in continuous darkness DD, from 4 to 8 October 1995; activity is shown as number of beam interruptions per 15 min (Horizontal black bars represent subjective night time; arrows indicate times of expected high tide) B Periodogram of data in A; periodogram statistic (SD) is plotted on vertical axis, period length is shown on horizontal axis; also included are 95% confidence limits of periodogram of data in a randomised state

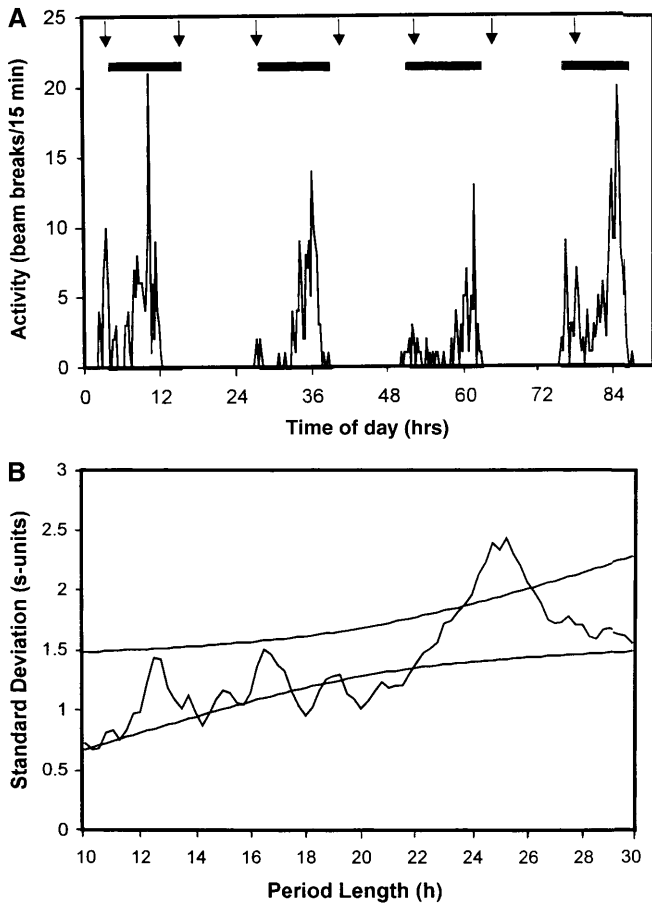


Fig. 3 *Orchestoidea tuberculata*. **A** Free-running activity rhythm of 50 juvenile *O. tuberculata* in DD from 4 to 8 October 1995. **B** Periodogram of data in **A**. Further details as in legend to Fig. 2

subjective darkness being more markedly bimodal than those expressed by adults. Moreover, the reduction of locomotor activity in the middle of the circadian outbursts of activity in juveniles appeared to coincide with the peaks of activity in adults (Fig. 3A).

Figure 4 shows hourly-form estimates (means of 4d) for both adult and juvenile locomotor activity, derived from the raw data sets in Figs. 2 and 3. Adult peak activity occurs during early hours of subjective night. In contrast, juvenile activity was less confined to the hours of subjective night, with a bimodal activity distribution. Activity peaks occurred before dusk and before dawn. There was a reduction in juvenile activity around the peak time of adult activity. Figure 5 shows a further hourly form-estimate (means of 4d) for adults and juveniles derived from raw data collected from 7 to 11 October 1996. This figure confirms that there is some complementarity between the endogenous activity peaks expressed by adults and juveniles, peak locomotor activity in adults again coinciding with reduced activity during the circadian peaks of juveniles. This figure shows that highest juvenile activity occurred after subjective dusk and around subjective dawn. Figures 4 and 5 together, therefore, suggest that whilst both juveniles

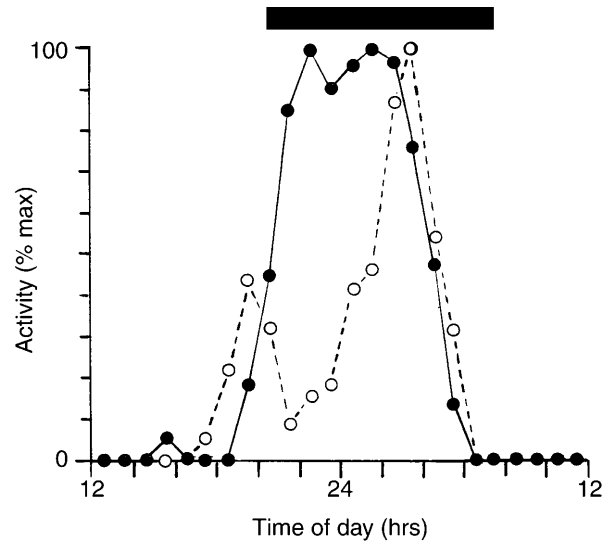


Fig. 4 *Orchestoidea tuberculata*. Twentyfour-hour form-estimate of percentage maximum locomotor activity of adults (●) and juveniles (○) under free-running conditions in DD from 4 to 8 October 1995 (Horizontal black bar subjective night)

and adults express circadian locomotor activity rhythms, with peak adult activity occurring during subjective night, juvenile circadian locomotor activity appears to be expressed in a more complementary crepuscular pattern.

Since the field (Fig. 1) and experimental (Figs. 4 and 5) data obtained indicated some complementarity between the daily locomotor activity patterns of adults and juveniles, co-existence experiments were carried out. These sought to test for direct competitive interactions between the two life stages following the protocol set out

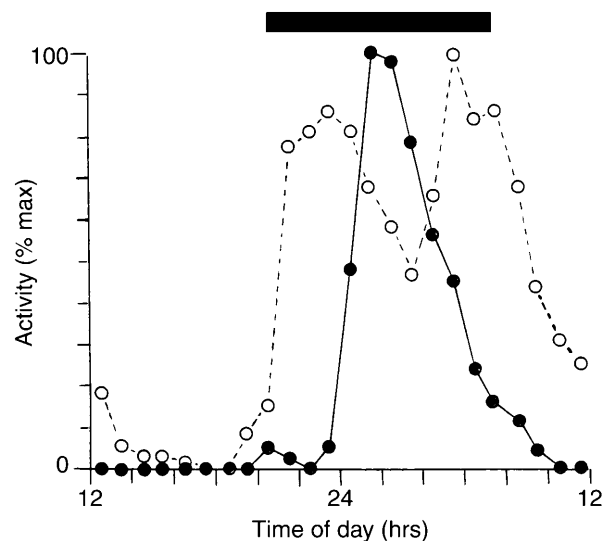


Fig. 5 *Orchestoidea tuberculata*. Twentyfour-hour form-estimate of percentage maximum locomotor activity of adults (●) and juveniles (○) under free-running conditions in DD from 7 to 11 October 1996 (Horizontal black bar subjective night)

Table 1 *Orchestoidea tuberculata*. Results of co-existence experiments in January 1991 and January 1997. Percentage survival of co-existing adults and juveniles is shown after 8 d in containers with damp sand (1991) or moist paper (1997), following rationale

Interaction effect	Treatments (T)	January 1991		January 1997	
		Mean % survival	<i>t</i> -test <i>p</i> -value	Mean % survival	<i>t</i> -test <i>p</i> -value
Adults on					
Adults	T ₄ vs T ₅	97.50/76.25	0.0026*	97.50/96.25	0.3652
Juveniles	T ₁ vs T ₃	75.00/47.50	0.0112*	100.00/65.00	0.0258*
Juveniles on					
Juveniles	T ₁ vs T ₂	75.00/83.75	0.1428	100.00/100.00	nd
Adults	T ₄ vs T ₃	97.50/95.00	0.2685	97.50/100.00	0.1780

in “Materials and methods – Coexistence experiments”. Table 1 shows the results of such experiments carried out in January 1991 and January 1997. In the 1991 experiments, mean percentage survival varied from 47.5% for juveniles in T₃ to 97.5% in T₄. The data indicate that adults had significant negative effects on survival of both adults and juveniles. In contrast, juveniles had no significant negative effect on the survival of either juveniles or adults. In the 1997 experiments mean percentage survival ranged from 100% for juveniles in T₁ and T₂ down to 65% for juveniles in T₃. In these experiments, adults had no significant effect on the survival of adult conspecifics, but had a significant negative effect on the survival of juveniles. Again juveniles had no significant effects on the survival of either juveniles or adults. No dead individuals or moulted cuticles were encountered during the daily observations of survivorship in these experiments, suggesting that the direct negative effects of adults on conspecifics, particularly juveniles, was by cannibalism.

Discussion

The results from the pitfall-trap samples in the field show a strictly nocturnal pattern of activity for adult *Orchestoidea tuberculata*, a finding which is in accordance with those of a previous study on this species (Jaramillo et al. 1980), and several studies on other talitrids (Geppetti and Tongiorgi 1967; Craig 1973; Williams 1983; Scapini et al. 1992). However, whilst some studies mention a lag between adult and juvenile activity peaks (Geppetti and Tongiorgi 1967; Scapini et al. 1992), or, as reported here, a less strictly nocturnal activity pattern in juveniles than adults (Craig 1973; Jaramillo et al. 1980; Williams 1983), earlier studies do not characterise the differences in activity phasing between adults and juveniles so fully as in the present study. In this study, whilst both adults and juveniles exhibited circadian locomotor rhythmicity under free-running conditions in the laboratory, juvenile surface-activity was seen to be clearly out of phase with that of adults. The nocturnal peak in adult activity coincided

outlined in ‘Materials and methods’ Co-existence experiments. *p*-values are from one-tailed Student’s *t*-tests (* significant at 5% level; *nd* no difference)

with a marked reduction in juvenile activity, which was expressed in a crepuscular pattern.

The present findings therefore suggest that, despite the benefits of strictly nocturnal emergence suggested by a number of authors (predator avoidance, avoidance of desiccation and heat stress) (Bowers 1964; Ruppel 1967; Jaramillo et al. 1980; Morrit 1987; Brown and McLachlan 1990; Scapini et al. 1992), there must be some additional adaptive advantage to juveniles in maintaining a crepuscular activity pattern. Scapini et al., suggested that juvenile *Talitrus saltator* have a higher energy requirement than adult conspecifics and must therefore extend their foraging phase into the dusk and dawn, despite the physiological stress and extra risk of interspecific predation that this might entail. This interpretation may partly explain the present observations, but it does not explain the reduction in juvenile activity that coincided with peak adult activity in this study.

In contrast, the coexistence experiments in the present study show that, at least under confined laboratory conditions, adult *Orchestoidea tuberculata* had a statistically significant adverse effect on the survival of juvenile conspecifics, probably by cannibalism. Dahl (1952) and Jaramillo et al. (1980) have previously reported intraspecific predation in talitrids, and this appears to be confirmed by the present study. Observations during the present study certainly suggest that local talitrid densities on beached wrack often exceed those within the experimental containers in the co-existence experiments, so it would not be surprising if the direct competition between adult and juvenile *O. tuberculata*, reported here under experimental conditions, also occurs in the field. Intense competitive pressure through cannibalism by adults could explain why juvenile activity on the beach surface is crepuscular rather than nocturnal, and is partly under endogenous control.

It is perhaps surprising that overall survival was lower in the January 1991 coexistence experiment, when sand was provided in the containers, than in the January 1997 experiment, when sand was not provided. Higher mortality of all groups in the 1991 experiments may have resulted from physiological or mechanical stress caused by daily sieving of the sand. Another possible factor

which could influence mortality is the sex ratio of adults used in the experiments. In neither case were adults sexed, but it is possible that adult males with their enlarged chelae are more significant predators on juveniles than females. A further set of experiments with known numbers of male and female adults should elucidate this matter.

Ontogenetic differences in overall locomotor activity observed in the field and recorded under free-running conditions in the laboratory may therefore be in part explained as a mechanism to minimise intraspecific predation. It is interesting to note that ontogenetic differences have also been observed in the direction of response to landscape cues in *Orchestoidea tuberculata* from the same population (Kennedy and Naylor 2000). Hence, the overall picture of locomotor behaviour of the population of *O. tuberculata* is complex. Both endogenous and exogenous cues combine to produce a markedly different pattern of activity for juveniles and adults. Each component of the population is subject to different selection pressures, and the behaviour pattern observed is presumably the product of these often conflicting pressures.

It is also relevant to mention in this context that the influence of endogenous cues affecting the occurrence of locomotor activity may often be overridden by exogenous cues such as temperature or inundation. An example is the almost total lack of emergence of adult *Orchestoidea tuberculata* on cold winter nights at the study site (Kennedy, personal observations) an observation also made by Scapini et al. (1992) in *Talitrus saltator* in the Mediterranean. Possible variations in emergence and endogenous rhythmicity related to the neap/spring tidal cycle also remain to be investigated.

Acknowledgements This research was funded by the European Union as part of a scientific cooperation initiative under Contract No. CII*CT930338. EJ acknowledges financial support from CONICYT (Project FONDECYT 88-904) while conducting some of the interaction experiments, and FONDAP Oceanografía & Biología Marina, Programa Mayor No. 3, Ecología y Conservación, while preparing this manuscript in Oman during February 1999. We also wish to thank M. Avellanal, H. Contreras, P. Quijon and P. Martínez for help during the field work.

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