Do parasites affect burrowing activity and emergence of sand hoppers, *Talorchestia quoyana* (Amphipoda: Talitridae)?

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Abstract: Sand hoppers (Amphipoda: Talitridae) are semiterrestrial crustaceans that feed upon stranded kelp. Their burrowing behaviour plays an important role in reintroducing nutrients into the sediment. The most abundant sand hopper on New Zealand's beaches is *Talorchestia quoyana* Milne-Edwards, 1840. It is host to a parasitic mermithid nematode, *Thaumamermis zealandica* Poinar, Latham and Poulin, 2002, which invariably kills its sand hopper host by emerging to complete its maturation and reproduction in a moist sand environment. The aim of the present study was to assess if the burrowing behaviour of *Ta. quoyana* showed pathologic consequences of infection by *Th. zealandica*. Two experiments were conducted to assess temporal variation in sand hopper burrowing in vitro. Parameters measured included the hour after sunrise and sunset that sand hoppers first emerged and the number of surface visits in the first hour after emergence. Across experiments, sand hopper burrowing behaviour showed considerable heterogeneity related to sand hopper length, sand hopper distribution, experimental series, and experimental moisture conditions. The presence of parasites was not a significant factor in determining sand hopper burrowing behaviour. The lack of pathological effect is surprising given the relative size of *Th. zealandica*.

Résumé : Les puces de sable (Amphipoda: Talitridae) sont des crustacés semi-terrestres qui se nourrissent de varech échoué. Leur comportement fouisseur joue un rôle important dans l'enfouissement des nutriments dans le sédiment. La puce de sable la plus abondante sur les plages de la Nouvelle-Zélande est *Talorchestia quoyana* Milne-Edwards, 1840. Elle sert d'hôte à un nématode mermithidé parasite, *Thaumamermis zealandica* Poinar, Latham et Poulin, 2002, qui finit toujours par tuer son hôte, la puce de sable, lorsqu'il émerge pour compléter sa maturation et sa reproduction dans un milieu de sable humide. Le but de notre étude est d'évaluer si le comportement fouisseur de *Ta. quoyana* montre des signes pathologiques lors d'une infection à *Th. zealandica*. Nous avons mené deux expériences pour évaluer la variation temporelle du comportement fouisseur de la puce de sable in vitro. Les variables mesurées incluent les heures de la première émergence des puces de sable après le lever et le coucher du soleil, ainsi que le nombre de visites en surface faites dans l'heure qui suit l'émergence. D'une expérience à l'autre, les puces de sable affichent des comportements très hétérogènes en fonction de leur longueur corporelle et de leur répartition, ainsi que de la série expérimentale et des conditions expérimentales d'humidité. La présence de parasites n'est pas un facteur significatif dans la détermination du comportement fouisseur des puces de sable. L'absence d'effets pathologiques est étonnante, étant donné la taille relative de *Th. zealandica*.

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Introduction

Sand hoppers (Amphipoda: Talitridae) are small, semiterrestrial crustaceans, common to temperate sandy beaches worldwide (Brown and McLachlan 1990). These supralittoral detritivores are associated with stranded wrack and kelp, feeding on and burrowing beneath the decomposing material (Brown and McLachlan 1990). Sand hoppers are primarily nocturnal, burrowing during the day to avoid desiccation and predators (Poulin and Latham 2002*a*). Their association with detritus combined with their burrowing activity introduces nutrients into the sand, supporting sediment bacteria and meiofauna (Brown 2001). Their spatial ecology has been examined (Inglis 1989; Marsden 1991*a*; Richardson et al.1991; Scapini et al. 1992; Poulin and Rate 2001), and while their distribution is not uniform across the shore, this patchiness is unrelated to kelp biomass (Marsden 1991*b*). Other biotic factors, such as parasites, have been identified as important to interpreting sand hopper spatial ecology (Poulin and Latham 2002*a*).

Temporal variation in sand hopper burrowing shows patterns consistent with age and sex (Cardoso 2002; Ugolini 2003) but may also reflect the influence of parasites. In other systems, pathological consequences of infection have been observed to result in differences in activity and fitness levels between infected and uninfected individuals (e.g., Fredensborg et al. 2004; Ferreira et al. 2005). Additionally, infected individuals may be expected to show the effects of reduced fitness by foraging at different times as a possible by-product of competitive exclusion by uninfected individu-

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als. Given the ecological importance of sand hoppers in sandy shore nutrient cycles, the presence of pathological reductions in activity or intraspecific competition could have implications that extend beyond the behaviour of individual sand hoppers to encompass the ecology of the species, the community, and the ecosystem (Thomas et al. 2000). Hence, this avenue requires further investigation.

The most common sand hopper found on the New Zealand coastline is *Talorchestia quoyana* Milne-Edwards, 1840 (Morton and Miller 1973). This species is abundant and recognised as the most important macrofaunal consumer of kelp (Inglis 1989). Three species of symbionts are associated with *Ta. quoyana*: a digamasellid mite, a rhabditid nematode, and a mermithid nematode, *Thaumamermis zealandica* Poinar, Latham and Poulin 2002 (Poulin and Rate 2001; Poinar et al. 2002). The digamasellid mite and the rhabditid nematode are external symbionts with no detectable effect on the host and are deemed to use sand hoppers strictly as a means of dispersal (Rigby 1996a, 1996b; Pugh et al. 1997; Poulin and Rate 2001). In comparison, the mermithid *Th. zealandica* is a large parasite found within the body cavity of *Ta. quoyana* (Poinar et al. 2002). When measured, these worms have been found to exceed 200 mm in length despite host length rarely exceeding 20 mm (Poulin and Latham 2002a, 2002b).

The life cycle of *Th. zealandica* involves a single host (*Ta. quoyana*) and a free-living stage (Poinar et al. 2002). The infective stage of the parasite penetrates the body wall of the sand hopper, where it grows over many months before emerging to complete its postparasitic maturation, killing the host in the process (Poinar et al. 2002). The adult worms require a moist sand environment for emergence (Poinar et al. 2002). This has been suggested as a causal factor for parasite manipulation of host burrowing depth (Poulin and Latham 2002a). There is evidence of a possible physiological mechanism, as elevated haemolymph osmolality has been found in infected individuals, possibly triggering a "thirst" response as described by Williams et al. 2004. However, it has recently been established that the role for parasites in this system may not be as pronounced as first thought and indeed may show variation dependent upon environmental conditions or possibly ecological conditions within the host and parasite population (Currey and Poulin 2006).

Currently, the pathological effect of parasite infection on sand hopper activity is unstudied in this system. A reduction in host activity levels as a pathological consequence of infection is plausible given the relative size of the parasite. This could affect host fitness if resources are limited and infected individuals are less competitive. The well-documented patchiness of sand hopper distribution (Inglis 1989; Marsden 1991a; Richardson et al.1991; Scapini et al. 1992; Poulin and Rate 2001) offers the possibility of localized competition across the sandy shore. Hence, pathological changes in behaviour may have diverse and wide-ranging effects on host population ecology.

This system was investigated by laboratory experimentation to assess the nocturnal and diurnal burrowing activity patterns of sand hoppers. Recording the time after sunrise or sunset at which the sand hoppers emerged (hour of emergence) and the number of surface visits in the hour after first emergence (emergence frequency) allowed the testing of the following hypotheses: (*i*) infected sand hoppers show less burrowing activity (as measured by emergence frequency) than uninfected conspecifics; and (*ii*) the reduced fitness of infected sand hoppers renders them less competitive, and hence their surface activity will not coincide with that of uninfected individuals of similar size and gender.

Materials and methods

Naturally infected sand hoppers were used for this experiment, as previous attempts to obtain the parasite's eggs or infective stages for experimental infections have failed (Poulin and Latham 2002a). Sand hoppers with parasites are not distinguishable from uninfected conspecifics, and their infection status was only apparent once they were dissected. Hence, all observations were conducted without prior knowledge of sand hopper infection levels.

Sand hoppers identified as *Ta. quoyana* were collected from an abundant population on Long Beach (45°45′S, 170°39′E), north of Dunedin, on the South Island of New Zealand. The Long Beach shoreline is sandy, with a gentle slope and exposed to moderate wave action. Sand hoppers were located in the sand beneath wrack and debris at the strandline. The sand hopper density on this 4 km long beach has been estimated at 200 individuals·m^{-2} in the 10 m wide zone they occupy parallel to the waves (Poulin and Latham 2002a). A total of 160 sand hoppers were taken from the beach in a targeted collection effort for laboratory experimentation.

Sand hoppers were obtained from the field in four bimonthly collection trips during May, July, September, and November of 2002. Samples were taken across the Austral winter, spring, and summer periods in an attempt to obtain sand hoppers with parasites at varying stages of development. Medium- and large-sized sand hoppers, those most likely to harbour parasites (Poulin and Latham 2002a), were collected by hand from the top 30 cm of sand underneath decaying patches of kelp at the strandline. The sand hoppers were stored in containers with moist sand for return to the laboratory. Additional materials required for the experiment, such as seawater, moist sand, and kelp, were also collected and stored in airtight containers at this time.

Back in the laboratory, 20 small, cylindrical plastic containers (4 cm diameter by 5.5 cm high) were filled to two-thirds capacity with sand. One sand hopper and a small (~1 cm^2) piece of kelp were added to each container. The 20 containers were placed in four rows with five containers in each and covered with clear plastic. The nocturnal and subsequent diurnal emergence behaviour of the sand hoppers was then observed and recorded over a 24 h period. This comprised the observation-based experiment. To assess the impact of sand moisture level on burrowing activity, a variant of the experiment was replicated with 20 different sand hoppers the following day. In this second series, 10 of the containers were treated with additional sea water (5 mL per container) to allow comparison of burrowing activity under normal and moist conditions. These quantities were selected as they reflected the typical range of sand moisture levels in which sand hoppers were found in their natural habitat. This was termed the moisture treatment experiment. After each

Table 1. Summary data for all sand hoppers (*Talorchestia quoyana*) and the mermithid parasites (*Thaumamernis zealandica*) collected from infected sand hoppers in both experiments.

Experiment	Moisture level	Total no. of sand hoppers	Length (mm, mean ± SE)	Male	Female	Juvenile	Prevalence of infection (%)	Prevalence of multiple parasites (%)	Length of the longest parasite per sand hopper (mm, mean ± SE)	Total parasite length per sand hopper (mm, mean ± SE)
Observation-based	Normal	79	12.5±0.4	29	30	20	19.0	3.8	87.3±16.5	99.1±21.9
Moisture treatment	Normal	29	11.0±0.6	6	12	11	6.9	0.0	25.0±21.0	25.0±21.0
	High	29	11.2±0.6	6	9	14	10.3	3.4	74.3±10.3	80.0±13.5
Total		137	11.9±0.3	41	51	45	14.6	2.9	79.2±13.1	88.9±17.2

experimental series, the sand hoppers were collected and processed (see below). In total, with four collection trips and two separate experimental series per trip, there were eight sets of 20 sand hoppers observed for a 24 h period during this study.

The behaviour of the sand hoppers was recorded with a Panasonic closed circuit, low-light, black and white video camera (model No. WVBP314E) attached to a tripod that was set so all containers were equally visible. To obtain footage of sufficient quality for analysis, the laboratory was lit with a single 45 W red light bulb during the nocturnal period and a single 45 W white light bulb during the diurnal period. Arthropods generally cannot perceive red light (Gross 1913), and thus the use of the red light bulb, an approach commonly used in arthropod studies (Casey 1987), did not interfere with the normal nocturnal activity of the sand hoppers. The lights were triggered by an electric time switch to approximate the natural photoperiod. The footage was recorded on VHS tape using a Panasonic time-lapse video cassette recorder (model No. AG6124) for playback on a television monitor. The footage was viewed to derive measures of activity for both the nocturnal and diurnal recordings. The measures derived were (*i*) the hour after sunset in which the sand hopper first emerged for nocturnal observations, (*ii*) the hour after sunrise in which the sand hopper first emerged for diurnal observations, and the total number of surface visits in the first hour after emergence in both the (*iii*) night and (*iv*) day, thus providing four parameters in total for each sand hopper. These parameters were termed the nocturnal hour of emergence, diurnal hour of emergence, nocturnal emergence frequency, and diurnal emergence frequency, respectively, and were selected as a means of assessing patterns in burrowing activity and temporal stratification of habitat use.

Once the sand hoppers were recovered from the samples, their length was measured (from the anterior end of the cephalon to posterior tip of the telson), they were sexed, decapitated, and preserved in 70% ethanol. Sex classification was determined by the presence of specialized gnathopods in mature males. These specialized gnathopods were indistinguishable in sand hoppers <10 mm in length; thus to prevent juvenile male misclassification, all sand hoppers <10 mm in length were classified as juveniles. To determine each sand hopper's infection status, they were dissected under a dissecting microscope using fine forceps. The number of mermithid worms per host (if any) was recorded, and the length of each straightened worm was measured to the nearest 1 mm. This measurement facilitated the derivation of total worm length, the sum of the lengths of all worms in a sand hopper, and the length of the largest worm in a sand hopper.

The resulting behavioural data were analysed with generalized linear models and linear regression models using SPSS (Version 9.0, SPSS Inc., Chicago). All tests were two-tailed. Parameters assessed included nocturnal and diurnal hour of emergence to assess temporal stratification and nocturnal, diurnal, and difference in emergence frequency (nocturnal minus diurnal) to quantify patterns in activity. Nocturnal and diurnal emergence frequency required square-root transformation, while difference in emergence frequency did not. Sand hopper emergence frequencies (noc-

Table 2. Burrowing activity summary data, including the hour of emergence (i.e., number of hours after sunset or sunrise when a sand hopper was first observed emerging) and emergence frequency (i.e., number of surface visits within an hour of first emerging) for nocturnal and diurnal observations for sand hoppers *Talorchestia quoyana* in each experiment.

Experiment	Moisture level	Hour of emergence (mean ± SE)		Emergence frequency (mean ± SE)	
		Nocturnal	Diurnal	Nocturnal	Diurnal
Observation-based	Normal	4.1±0.3	1.0±0.0	17. 6±1.3	13.8±1.1
Moisture treatment	Normal	2.7±0.4	1.5±0.3	11.5±1.7	12.3±2.1
	High	1.9±0.3	1.5±0.4	14.0±0.8	15.9±3.4
Total		3.4±0.2	1.3±0.1	15.5±1.0	14.0±1.1

Fig. 1. The relationship between sand hopper (*Talorchestia quoyana*) length and nocturnal emergence frequency in the observation experiment.
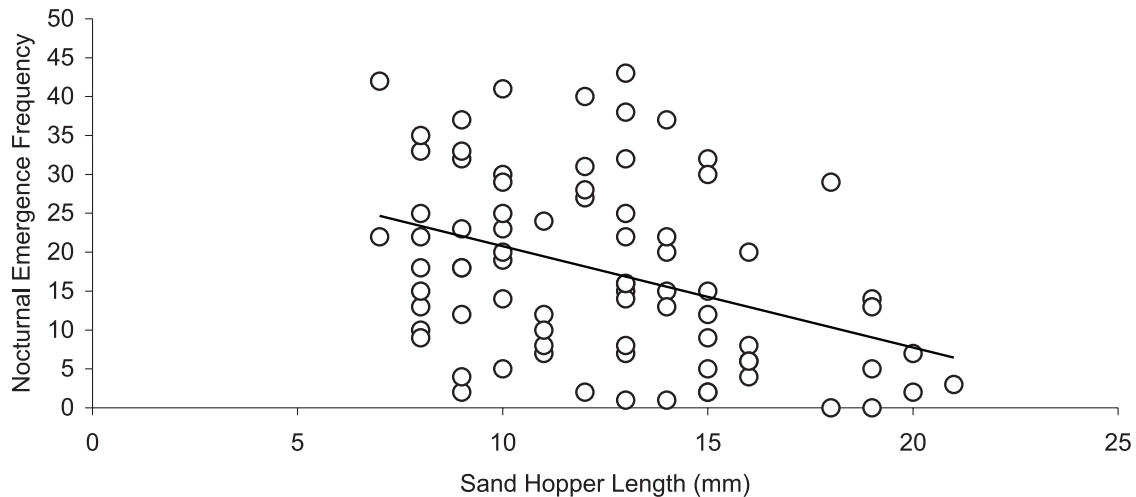
turnal, diurnal, and nocturnal minus diurnal) were investigated using analysis of covariance (ANCOVA), while nocturnal hour of first emergence was analysed using linear regression models because of the nature of each dependent variable. In both cases, sand hopper length was treated as a covariate. Factors included in the models were parasite infection status (presence or absence of mermithid parasites in each sand hopper), sand hopper sex, experimental treatment (if any), and experimental series. Two-way interactions between factors were also included in the models but are reported only when statistically significant ($P = 0.05$). Relationships underlying significant factors were assessed with product–moment correlation and descriptive statistics. Diurnal hour of first emergence showed insufficient variation for linear regression analysis. Additionally, low parasite prevalence rendered separate regression or ANCOVA analysis of longest and total worm length per host in the infected sand hoppers as inappropriate. Thus these parameters are interpreted with descriptive statistics only.

Results

During this study, 160 sand hoppers were observed in groups of 20 for a 24 h period as part of two separate experiments. In total, this investigation entailed 192 h of behavioural observation. Of the 160 sand hoppers initially collected, 23 escaped during the experiments. This prevented their dissection, and hence they are excluded from

further analysis. One uninfected juvenile sand hopper, from the high moisture condition within the treatment experiment, showed unusual behaviour. It emerged 8 h later than the last of the other sand hoppers in the diurnal observations and had a diurnal emergence frequency of 95 within an hour, six times the mean emergence for the same period. It has been included in the summary for completeness (Tables 1 and 2), but has been excluded from further statistical analysis.

The selective sand hopper collection methodology resulted in large sand hoppers being collected and an even distribution across sex (Table 1). The prevalence of infection showed variation between experiments, as did the length of parasites (Table 1). Across experiments, the nocturnal hour of emergence was consistently later than its diurnal counterpart (Table 2). This pattern was most pronounced in the observation-based experiment. For both experiments, 93% of diurnal emergences took place in the first hour. Nocturnal emergence frequency was marginally higher than diurnal emergence frequency in the observation-based experiment, but this pattern was reversed in the moisture treatment experiment (Table 2).

The factors affecting nocturnal emergence frequency in the observation-based experiment were assessed with an ANCOVA. Sand hopper length was the only significant factor identified ($F_{[1,60]} = 9.184$, $P = 0.0036$). This assessment was supported by a negative relationship between sand hopper length and nocturnal emergence frequency

Fig. 2. The variation in diurnal emergence frequency (mean ± SE) with the presence or absence of parasites and under different moisture treatments.
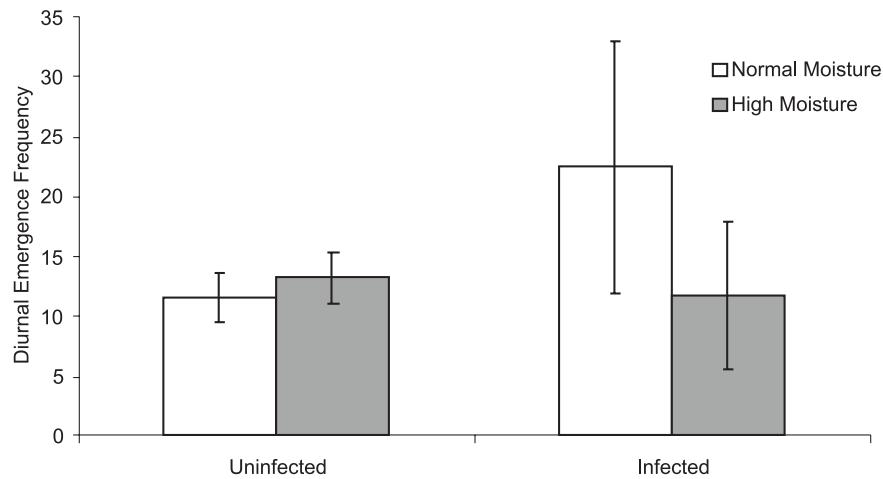
Fig. 3. The difference (nocturnal – diurnal) in emergence frequency (mean ± SE) across sand hopper sex and under different moisture treatments.
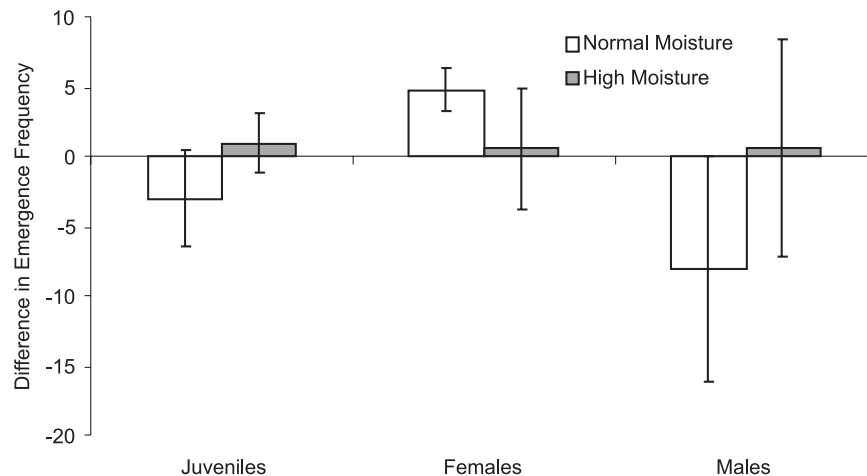
(product–moment correlation: r_{78} = 0.385, P = 0.0005; Fig. 1). Diurnal emergence frequency and the difference between nocturnal and diurnal emergence frequencies for the observation-based experiment were also assessed with an analysis of covariance; however, no significant factors were identified for either parameter (all P > 0.10).

In contrast with the observation-based experiment, the analysis of covariance assessment of nocturnal emergence frequency in the moisture treatment experiment identified no significant factors (all P > 0.20). The analysis of diurnal emergence frequency in the moisture treatment experiment identified the experimental series as a significant factor ($F_{[3,38]}$ = 4.636, P = 0.0074). This relationship was seen as a reduced diurnal emergence frequency over subsequent experimental series. Diurnal emergence frequency was elevated for infected individuals in the normal moisture treatment (Fig. 2). This factor was marginally significant ($F_{[1,38]}$ = 3.488, P = 0.0695).

Three significant factors were identified in the difference between nocturnal and diurnal emergence frequencies for the moisture treatment experiment: experimental series ($F_{[3,38]}$ = 8.690, P = 0.0002), sand hopper sex ($F_{[2,38]}$ = 3.420, P = 0.0431), and the interaction of these two factors

($F_{[5,38]}$ = 2.485, P = 0.0483). The difference in emergence frequency varied across experimental series, with nocturnal emergences more frequent in the high moisture series 4 samples and diurnal emergences more frequent in the normal moisture series 2 samples. Difference in emergence frequency varied across the sexes, with nocturnal emergences more frequent by females and diurnal emergences more frequent by males (Fig. 3). The significant interaction between experimental series and sand hopper sex was due to a large difference in emergence frequency for males in series 2.

Linear regression analysis identified experimental series and sand hopper length as significant factors in determining the nocturnal hour of sand hopper emergence in the observation-based experiment (Table 3). By comparison, sand hopper sex and parasite infection were not significant (Table 3). Nocturnal hour of emergence did show variation across experimental series, reaching a peak in series 2 (Fig. 4). Despite its importance as a factor in predicting the hour of emergence, there was no clearly defined relationship between sand hopper length and the nocturnal hour of emergence (product–moment correlation: r_{78} = 0.171, P > 0.10).

For the nocturnal hour of sand hopper emergence in the moisture treatment experiment, linear regression analysis

Table 3. An assessment of factors relevant to nocturnal hour of emergence by linear regression in the observation-based experiment.

Effect	R^2	R^2 change	F change	df	P
Experimental series	0.1675	0.1675	4.8966	3	0.0037
Sand hopper length	0.2452	0.0777	7.4107	1	0.0081
Sand hopper sex	0.2889	0.0437	2.1515	2	0.1239
Parasite infection	0.2947	0.0057	0.5614	1	0.4563

Table 4. An assessment of factors relevant to nocturnal hour of emergence by linear regression in the moisture treatment experiment.

Effect	R^2	R^2 change	F change	df	P
Moisture treatment	0.0441	0.0441	2.3066	1	0.1351
Experimental series	0.3111	0.2670	6.0705	3	0.0014
Sand hopper length	0.3138	0.0027	0.1811	1	0.6724
Sand hopper sex	0.3220	0.0083	0.2677	2	0.7663
Parasite infection	0.3333	0.0113	0.7277	1	0.3984

identified experimental series as the only significant factor (Table 4). Sand hopper length, sex, parasite infection, and moisture treatment were all found to be not significant (Table 4). Once again, the nocturnal hour of emergence varied across experimental series and in series 4 was elevated in the high moisture treatment, a stark contrast to series 1, 2, and 3 (Fig. 5).

Discussion

The present study tested two hypotheses that attempt to account for variation in host behaviour arising from the pathological consequences of parasite infection. These hypotheses predicted that infected sand hoppers would demonstrate reduced burrowing activity (as measured by emergence frequency) and be active at different times of the day as a result of competitive exclusion (as expressed in the first hour of emergence). No evidence was found to support either hypothesis across both the nocturnal or diurnal observations, suggesting that despite its size, this mermithid parasite does not demonstrate a detectable pathological effect of infection on its sand hopper host.

The present investigation did, however, provide some intriguing results. In both experiments, there was no apparent difference in nocturnal and diurnal activity levels, yet a striking difference was detected regarding when these activities occurred. The observation that emergence frequencies were very similar for nocturnal and diurnal observations, despite some variation across experiments, was unexpected for a study investigating behaviour with a nocturnal species. Two possible explanations may account for this pattern. The present study focused on sand hopper activity in the first hour after emergence. Differences between nocturnal and diurnal activity levels may only be apparent after this first hour of activity. Investigation of nocturnal and diurnal activity after the first hour of emergence would clarify this pattern. A second possible source of similarity in emergence frequencies may be the unnatural laboratory conditions required for the experiment. While every effort was made to simulate natural conditions, there is a possibility that the experimental conditions may have affected sand hopper behaviour.

Across experiments, the nocturnal hour of emergence was consistently later than the diurnal equivalent. The reason for this pattern is not immediately apparent but may arise as a result of physiological requirements for moisture. Moisture requirements have been identified as an important factor in sand hopper burrowing behaviour (Brown and McLachlan 1990); hence, dehydration may be a factor in determining when sand hoppers are most active. During daylight hours, early activity would reduce thermal stress and dehydration, while early nocturnal activity would confer no such benefit. This may account for the difference in when activity is occurring.

The key factors contributing to the unusual patterns in both the timing and intensity of sand hopper burrowing activity were sand hopper length, experimental series, and experimental treatment. The inverse relationship between sand hopper length and emergence frequency is a possible byproduct of reduced metabolic rate associated with increased body mass, a relationship found in many species and across taxonomic groups (Schmidt-Nielsen 1984), including arthropods (West et al. 2000). The importance of sand hopper length as a factor in their nocturnal hour of emergence shows consistency with the findings of other studies on sand hoppers (Cardoso 2002; Ugolini 2003). The differences across experimental series and treatment are unsurprising; they may arise from the effects of variables like sand moisture level, environmental conditions at the time of collection, and contrasts between kelp patches. This variation is clearly indicative of the heterogeneity across spatial and temporal scales that are a common aspect of sand hopper behavioural ecology (Poulin and Rate 2001). Future investigations could begin to address the complexities of this heterogeneity and unravel its constituent patterns. Seasonal and life-cycle-based patterns would be of particular interest.

Considerable heterogeneity was also displayed through the variety of observed emergence behaviours. Hence, the simple classification of emergence behaviour employed in this study may not fully capture the differences in activity levels displayed by individual sand hoppers. Sand hopper emergence events did vary in activity level; some sand hoppers remained near their burrow entrance, while others

Fig. 4. The variation in the nocturnal hour of emergence (mean ± SE) across the different experimental series for the observation experiment.
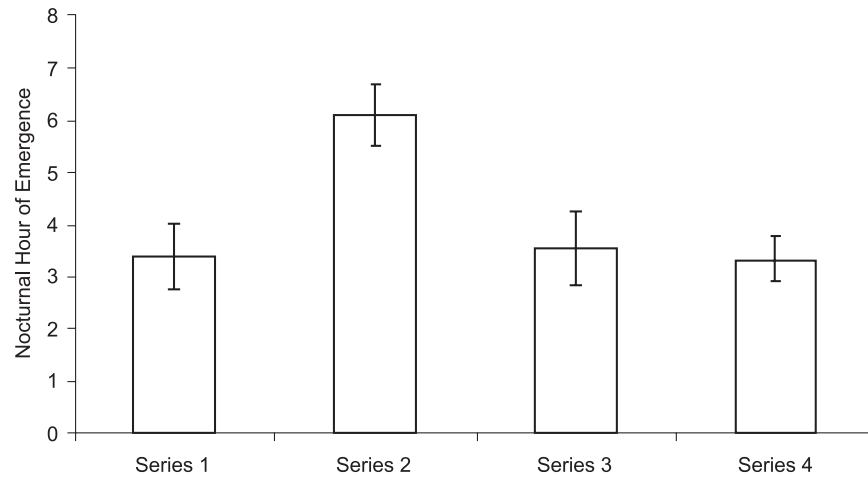
Fig. 5. The variation in the nocturnal hour of emergence (mean ± SE) across the different experimental series and moisture treatments.
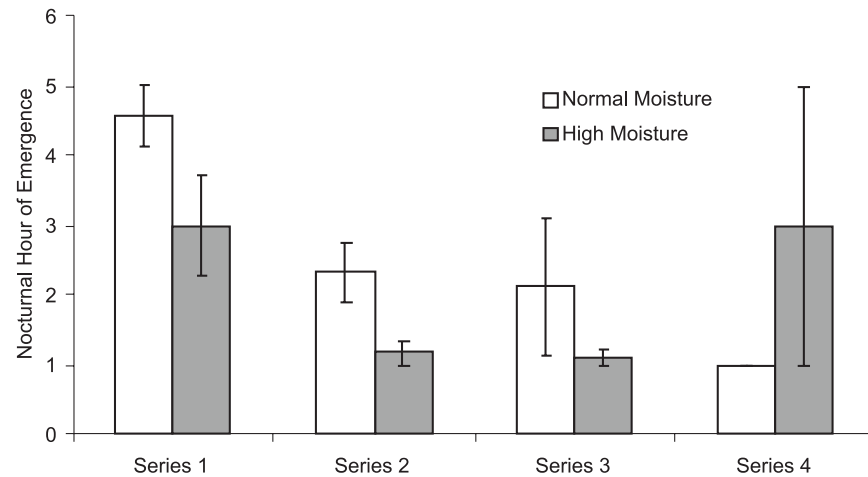
emerged fully and moved around their container for extended periods (R.J.C. Currey, unpublished data). Emergence event activity level showed continuous variation but appeared to be positively correlated with emergence frequency (R.J.C. Currey, unpublished data). Thus emergence frequency may tend to underestimate the difference in activity levels. Through an empirical approach, an examination of this surface activity may refine our understanding of the relationships detected in the present study.

One area that may warrant further consideration is the effect that sand hopper escapes may have on the data obtained for the remaining individuals. Escapes have the potential to introduce bias into the data, especially relating to measures of activity such as emergence frequency. This bias can arise because escaping individuals are likely to represent a subset of the more active sand hoppers. While this is a concern, it was found that across both experiments in the present study, nocturnal emergence frequency showed marginal reductions in the samples with elevated escape rates, while diurnal emergence frequency was unchanged. Thus, the overall effect of sand hopper escapes should not introduce an unacceptable level of bias into the emergence frequency data.

In future investigations of this system, an assessment of

burrowing in the field may offer further insights in temporal stratification of burrowing activity. Through the use of pitfall traps around the fringes of stranded wrack and debris and the employment of hourly sand hopper collections, it would be possible to assess the abundance, demographic profile, and infection status of sand hoppers emerging at different times. This approach has the possibility of detecting patterns consistent with competitive exclusion. If that was to occur, further laboratory investigations should be considered based on the present study but with multiple, identifiable sand hoppers placed in each container. This could permit the direct observation of competitive behaviour. The use of field and laboratory observations in tandem as described offers the opportunity to both identify patterns in natural behaviour and isolate the factors underlying these patterns (Currey and Poulin 2006).

Through the course of this investigation, we observed no detectable pathological effect of the mermithid parasite *Th. zealandica* on burrowing activity or emergence behaviour of the sand hopper host *Ta. quoyana*. This conclusion is surprising given the relative size of the parasite compared with the host and given its apparent effect on burrowing depth and haemolymph properties (Poulin and Latham 2002*a*;

Williams et al. 2004). Nocturnal and diurnal activity levels were very similar, again surprising in a nocturnal species, yet this emergence activity occurred at different times after sunset and sunrise, respectively, showing the possible influence of physiological constraints. Sand hopper length combined with spatial and temporal heterogeneity accounted for the variations in both burrowing activity and emergence timing. Examining the sources of heterogeneity is an important issue for future investigations of this system.

Acknowledgements

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