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Circadian rhythms of heart rate in freely moving and restrained American lobsters, *Homarus americanus*

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While circadian rhythms of locomotion have been reported in the American lobster, *Homarus americanus*, it is unclear whether heart rate is also modulated on a circadian basis. To address this issue, both heart rate and locomotor activity were continuously monitored in light-dark (LD) cycles and constant darkness (DD). Lobsters in running wheels exhibited significant nocturnal increases in locomotor activity and heart rates during LD, and these measures were significantly correlated. In DD, most lobsters exhibited persistent circadian rhythms of both locomotion and heart rate. When heart rate was monitored in restrained lobsters in LD and DD, most animals also demonstrated clear daily and circadian rhythms in heart rate. Overall, this is the first demonstration of circadian rhythms of heart rate in *H. americanus*, the expression of which does not appear to be dependent on the expression of locomotor activity.

Keywords: daily; nocturnal; locomotion; circadian rhythm; *Homarus americanus*; heart rate; lobster; laboratory experiment

Introduction

It is well established that many crustacean species synchronize their activities to the light:dark (LD) cycle. For instance, daily rhythms of locomotor activity have been found in the New Zealand rock lobster (*Jasus edwardsii*; Williams and Dean 1989), the western rock lobster (*Panulirus longipes*; Morgan 1978), the Rock crab (*Cancer irroratus*, Rebach 1985), the Spiny lobster, *Panulirus argus* (Kanciruk and Herrnkind 1973), as well as crayfish (*Astacus astacus*; Bojsen et al. 1998 and *Procamabrus clarkii*; Pollard and Larimer 1977). In many species, these daily rhythms are often manifested by nocturnal increases in activity.

The American lobster, *Homarus americanus*, is another species that likewise exhibits daily rhythms and is considered to be nocturnally active (Zeitlin-Hale and Sastry 1978; Cooper and Uzmann 1980; Ennis 1984; Karnofsky et al. 1989) though a recent study suggests that local environmental factors may modify this tendency in the field (Golet et al. 2006).

A variety of physiological measures are also synchronized with daily LD cycles in several crustacean species. For instance, metamorphic molt (Waddy and Aiken 1999), the concentration of several hormones (Fanjul-Moles 2006), changes in brain serotonin levels (Wildt et al. 2004), and the control of visual sensitivity (Arechiga et al. 1973;

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Page and Larimer 1975) are all modulated by LD cycles. Furthermore, significant nocturnal increases in heart rate have been recorded in several crustacean species, including two species of crayfish (*A. astacus*; Bojsen et al. 1998; and *P. clarkii*, Pollard and Larimer 1977), the shore crab, (*Carcinus maenas*; Aagaard et al. 1995), the Norway lobster (*Nephrops norvegicus*; Aguzzi et al. 2004), and the American lobster (O'Grady et al. 2001).

When daily rhythms in LD persist in constant environmental conditions, they are termed circadian rhythms and indicate the presence of an endogenous circadian clock. Circadian clock controlled rhythms of locomotor activity in crustaceans have been reported in two species of crayfish (*Procambarus clarkii*, Page and Larimer 1972; *Astacus astcus*, Viccon-Pale and Fuentes-Pardo 1994) and the American lobster (Jury et al. 2005). Other crustacean behaviors may also be controlled by endogenous circadian clocks. For example, ovigerous *Homarus gammarus* females exhibit an endogenous circadian rhythm in the larval release behavior (Ennis 1973; Branford 1979).

Reports of circadian control of crustacean physiological attributes are more limited. In *P. clarkii*, the daily rhythms of heart rate persist in constant conditions with periods of ""24 h and are thus influenced by a circadian clock (Pollard and Larimer 1977). While LD cycles modulate heart rate in the American lobster over a 24-h period (O'Grady et al. 2001), whether these daily rhythms persist in constant conditions is unknown. The main goal of this study is to determine if the heart rate rhythms persist in constant conditions to determine if these rhythms are controlled by an endogenous circadian clock.

Another issue of interest concerning the regulation of heart rate in crustaceans involves the relationship between heart rate and locomotion. Heart rate and locomotion appear to be closely and positively correlated in some crustacean species. Bojsen et al. (1998) found that a tight coupling exists between heart rate and locomotor activity in the crayfish *Astacus astacus* when studied in their natural environment over the course of several days. In addition, both short-term (minutes; Larimer and Tindel 1966) and long-term (days; Pollard and Larimer 1977) fluctuations in locomotion and heart rate were positively correlated in the crayfish, *P. clarkii*. In the American lobster, a passive treadmill system has been used to study the relationship between walking and changes in ventilation and heart rate (O'Grady et al. 2001). Nocturnal increases in locomotor activity were shown to lead to an increase in nocturnal heart rate. In addition, this study indicated a small but statistically significant positive correlation between average speed of walking bouts and heart rates over short time frames (minutes). However, heart rate and locomotion were not measured for over 24 h. An additional goal of the present study was to determine if heart rate and locomotion are positively correlated over longer periods of time (days, weeks) in *H. americanus*. While it seems likely that heart rate and locomotion will be positively correlated in this species, there is an apparent dissociation of heart rate rhythms from locomotor rhythms in the shore crab (Aagaard et al. 1995) in that locomotor activity rhythms need not be expressed in this species in order to allow the expression of heart rate rhythms. This finding has not, to our knowledge, been investigated in any other crustacean species.

We report here that the heart rate of American lobsters is modulated both exogenously (by light dark cycles) and endogenously by the circadian system. Furthermore, when we physically restrained lobsters in order to inhibit their locomotion, heart rate rhythms were still observed in both LD and constant darkness (DD), suggesting that locomotion is not a requirement for the expression of these endogenous rhythms of heart rate.

Methods

Animals and environmental conditions

All lobsters (7 male; 13 female) were intermoult adults (78–94 mm carapace length) purchased from a local supplier and promptly placed in one of the two 115 L recirculating seawater marine tanks (Oceanic 55, Jewel Industries Inc., Chicago, IL) in a ‘‘light-tight’’ room at Plymouth State University, Plymouth, NH. Seawater was obtained from the University of New Hampshire Marine Coastal Laboratory in Newcastle, NH. Water temperature was recorded continuously (HOBO, Onset Computer Corporation, Bourne, MA) and maintained at 17 ± 2ºC. Salinity was measured using a hygrometer and was maintained between 28 and 36 ppt by the bi-weekly addition of distilled water. The pH level of the water was maintained between 7.5 and 8.0 by the addition of Sea Buffer (Aquarium Systems, Mentor, OH) weekly as necessary. All lobsters were initially exposed to a 14:10 light:dark (LD) cycle. Light was provided using 2 broad spectrum 20 W fluorescent lights (Simkar Corp., Pittsburgh, PA). The light level at the surface of the water was '""25 lux (LunaPro light meter, Gossen Germany). A HOBO Light/Temperature data logger (Onset Computer Corporation, Bourne, MA) recorded the duration and timing of the photoperiod continuously throughout the experiment. Animals were not fed for the duration of the experiments. Starvation over a period of weeks does not appear to change locomotor activity rhythms in lobsters (Jury et al. 2005) or crayfish (Styrishave et al. 1995).

Locomotion and heart rate recording

Locomotor activity was collected using ‘‘running wheels’’ as previously described (Jury et al. 2005). Briefly, these running wheels were constructed from 5-gal plastic buckets with 30 cm inner diameter and width of 10 cm. They were perforated on all surfaces with approximately 500 holes (6 mm diameter each) to allow for ample water circulation and to provide increased traction for the lobsters. The wheel rotated around a hollow, 1 cm diameter plastic axle fixed to a PVC stand. Two small magnets were attached 180 degrees from each other on the outer surface of the wheel. Locomotor activity of the lobsters was detected when the magnets passed near a reed switch located on one leg of each stand. For a more detailed description see Jury et al. (2005). All locomotor activity was recorded using a computer based data collection system (*Clocklab*, Coulbourn Instruments, Allentown, PA). When the lobsters were first placed into the wheels, several days passed before the lobsters showed obvious signs of locomotor rhythmicity. After this time, heart rate was monitored in all of the animals. To monitor heart rate, two small holes were created superficial to the heart in the dorsal carapace about one centimeter apart. Two wires were then placed into the holes and secured into place with three layers of tape and cyanoacrylate. The wires ran through small diameter plastic aquarium tubing (the tubing was secured to both the lobster and the central axle and served to protect the wires as well as to provide strain relief) and exited the running wheel through the central axle. The wires were connected to impedance converters (model 2991, UFI, Morro Bay, CA.). Analog signals from the impedance converters were digitized (Powerlab 200A/D converters, *iWorx*, Dover, NH) and stored on a computer for later analysis.

Experimental procedure

Experiment 1: freely moving animals in LD and DD

The purpose of this experiment was to examine the relationship between the LD cycle and heart and locomotor activity in freely moving lobsters. Lobsters (two male/four female, 450–670 g, 82–94 mm carapace length) purchased in the winter (January) were placed into running wheels after heart-monitoring wires were secured and subjected to a 14:10 LD cycle for 10–14 days. The running wheels were arranged in the tank so that the lobsters were visually isolated from one another. Subsequent to the LD cycle, a 13-day period of DD ensued.

Experiment 2: freely moving and restrained animals in LD

The purpose of this experiment was to examine the relationship between the LD cycle and heart rate in restrained lobsters. Lobsters (1 male/5 female, 440–620 g, 83–93 mm carapace length) were purchased in the fall (October) and had both their heart rate and locomotor activity monitored in LD for 10 days as above. The lobsters were then subjected to an additional 10 days under the same LD conditions with the addition of a plastic partition in each running wheel. The plexiglas partition kept the lobsters confined to the bottom half of the running wheel. This prevented the wheel from turning and greatly reduced their ability to move. The running wheels were arranged in the tank so that the lobsters were visually isolated from one another.

Experiment 3: freely moving and restrained animals in LD and DD

The purpose of this experiment was to determine if heart rate rhythms would persist in restrained animals in DD. Lobsters (4 male/4 female, 454–513 g, 78–87 mm carapace length) were purchased in the early spring (late-March). Six of the eight lobsters were restrained under 30 cm x 6 cm white plastic baskets (‘‘immobilization chambers’’) and heart rate was monitored as above. These chambers were used to decrease the room that the lobsters had to move in (lobsters in the RWs could move somewhat laterally while the animals in the immobilization chambers could not). While the tops of these chambers were solid, the sides were mesh and were readily pervious to sea water. Half bricks were placed in the chambers with the lobsters in order to further reduce their overall ability to move. These lobsters were also visually isolated from one another. The remaining two (control) lobsters were placed in running wheels and both locomotor activity and heart rates were monitored as above. For the first phase of the experiment, lobsters were immediately exposed to a 14:10 LD cycle for 30 days. In the second phase of the experiment, the lobsters were subjected to DD for 10 days.

Data analysis

Average heart rates were calculated at 5-minute intervals for each lobster using a ‘‘macro’’ program that we developed using Powerlab (Version 3.6.1). Some lobsters occasionally broke or chewed through the heart rate or locomotor activity wires. This occurred in ""20% of the animals and the wires were replaced within 24 h. This loss of data (always 524 h) appears as gaps in the activity records and was not included in the analysis. Both locomotor and heart rate data were analyzed both visually in actogram form and statistically for significance of circadian rhythmicity using Chi-Square periodogram analysis (*p*50.01; Sokolove and Bushell (1978) performed by *ClockLab* (Coulbourn Instruments, Allentown, PA). All summary statistics are presented as mean ± SEM. When lobsters from different experiments were exposed to exactly the same conditions (i.e. LD), the data were pooled to increase *N* and strengthen analyses. Possible significance of differences between means was assessed using Student’s *t*-test (Statview, Abacus Concepts, Berkley, CA.). Regression analyses were also calculated using Statview. Significance was assessed at the *p*50.05 level.

Results

Experiment 1: heart rate and locomotion in LD and DD

Locomotor and heart rate activity from two unrestrained lobsters in running wheels and sequentially exposed to LD and DD are presented in Figure 1. In LD, both lobsters showed 24 h rhythms in locomotion and heart rate. Overall, 93% (13/14) of the lobsters in

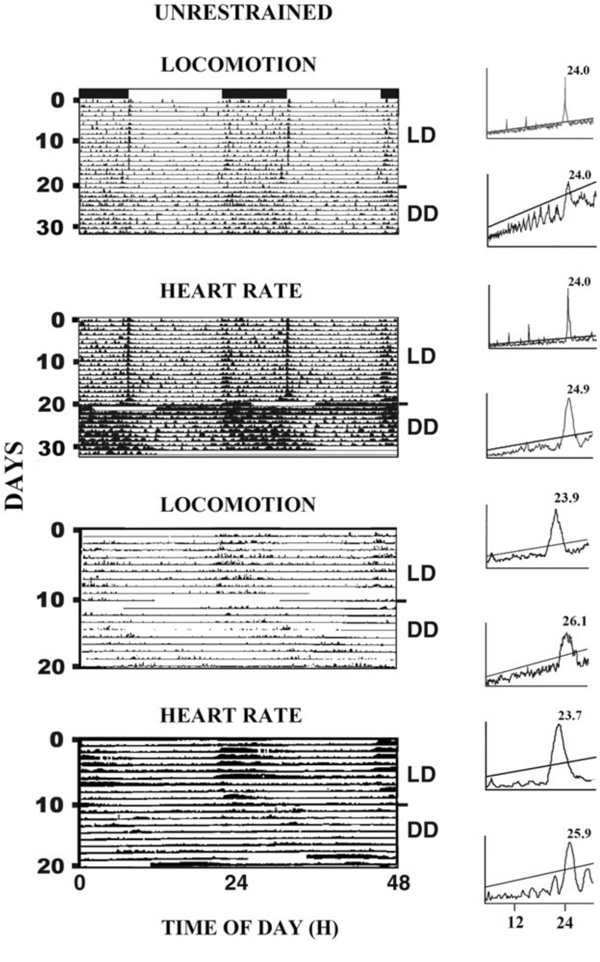

Figure 1. Representative actograms (left panels) and associated Chi-square periodograms (right panels) of locomotor and heart rate activity simultaneously recorded from two unrestrained lobsters in running wheels. Lobster 1: top two panels; Lobster two: bottom two panels. Actogram data are double-plotted to improve visualization of results. LD ¼ Light/Dark; and DD ¼ Constant darkness. The dark rectangle represents the dark phase of the LD cycle and the light rectangle represents the light phase of the LD cycle. Chi-square periodograms: peaks above sloping line indicate statistically significant values (*p*50.05). The values above the periodogram indicate the highest significant peak (*Tau*).

LD from Experiments 1, 2, and 3 exhibited significant locomotor rhythms (*Tau* ¼ 23.86 ± 0.1 h) and 71% (10/14) exhibited significant heart rate rhythms (*Tau* ¼ 23.55 ± 0.18 h). Activity amounts were significantly higher in D *versus* L in all of the animals exhibiting significant rhythms (Figure 1; Student's *t*, repeated measures, *p*50.05). When some of these animals were later exposed to DD, the temporal patterns of activity persisted with periods of ""24 h (Figure 1). Overall, 88% (7/8) of these lobsters in DD (Experiments 1 and 3) showed significant free-running rhythms of locomotion (*Tau* ¼ 24.58 ± 0.40 h), while 63% (5/8) showed significant heart rate rhythms (*Tau* ¼ 25.00 ± 0.38 h) under constant conditions. When the *Taus* of animals that exhibited significant heart rate and locomotion periodicities were compared, there was no statistical difference detected between the periods of heart rate and locomotion in either LD (*t*(8) ¼ 1.28, *p* ¼ 0.24) or DD (*t*(4) ¼ -0.17, *p* ¼ 0.99).

Experiment 2: the effects of physical restraint on heart rate in LD

The effects of physical restraint on heart rate rhythms of lobsters exposed to LD are presented in Figure 2. Daily rhythms of both heart rate and locomotor activity were displayed while the animals were unrestrained. When the animals were prevented from turning the wheel with the addition of a plastic partition, daily heart rate rhythms persisted in some (Figure 2; top) but not all (Figure 2; bottom) animals. Significant daily heart rate rhythms persisted in 33% (2/6) of the animals (*Tau* ¼ 23.79 ± 0.29 h).

Experiment 3: The effects of physical restraint on heart rate in DD

The heart rates of two restrained lobsters from Experiment 3 are presented in Figure 3. In LD, both lobsters exhibited 24 h rhythms in heart rate activity. Heart rates can be seen to be higher in D than in L. 83% (5/6) of the restrained lobsters in LD exhibited significant heart rate rhythms (*Tau* ¼ 24.12 ± 0.17 h). When constant conditions were effected the heart rate rhythms of both lobsters persisted in DD (Figure 3). 83% (5/6) of the restrained lobsters also exhibited significant heart rate rhythms in DD (*Tau* ¼ 24.12 ± 0.4 h).

Heart rate and locomotor activity comparisons

The average heart rate and locomotor activity from eight unrestrained lobsters from Experiments 1 and 3 are presented in Figure 4. In LD cycles, both heart rate and locomotor activity were higher in D than during L. In addition, there was a positive correlation between heart rate and locomotor activity ($R^2 > 0.41$, *p*50.0001; Figure 5).

Discussion

Circadian rhythms of heart rate

Our results are the first to demonstrate clear circadian rhythms of heart rate in the American lobster, *H. americanus*. Over 70% of the animals used in this study exhibited significant heart rate rhythms with periods of ""24 h in constant conditions. Circadian clock controlled rhythms of heart rate have also been reported in the crayfish (Pollard and Larimer 1977). Other field and laboratory studies of various crustaceans

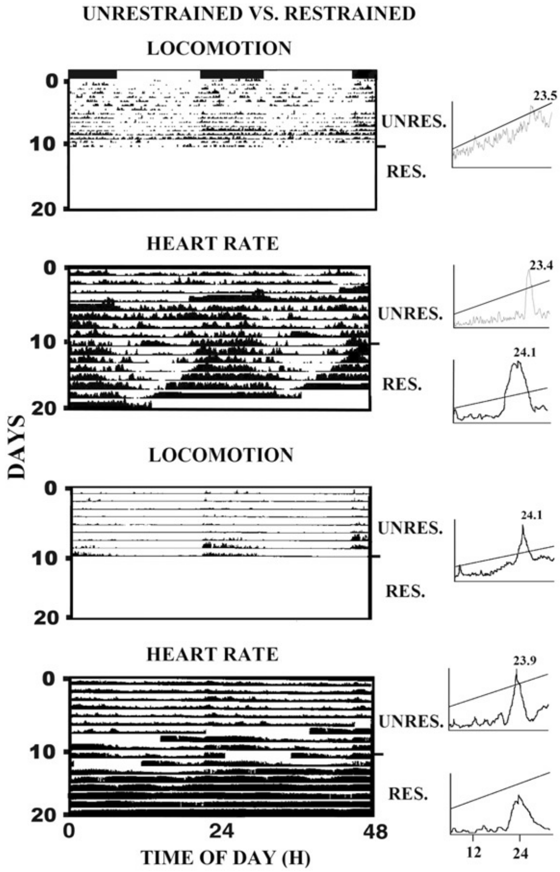

Figure 2. Representative actograms (left panels) and associated Chi-square periodograms (right panels) of locomotor and heart rate activity of two lobsters exposed to LD cycles housed in running wheels. UNRES ¼ lobsters were able to turn running wheels; and RES ¼ restrained (lobster prevented from moving significantly or turning running wheel).

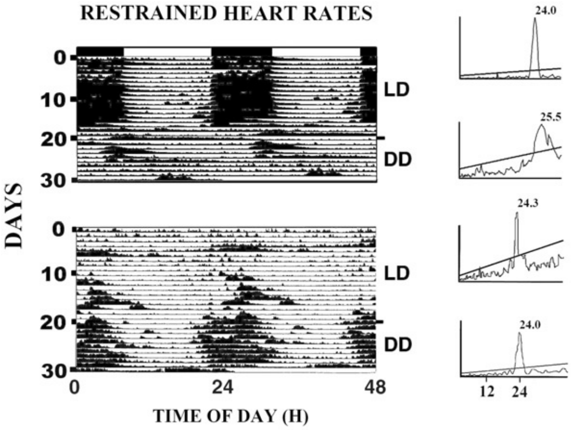

Figure 3. Representative actograms (left panel) and Chi-square periodograms (right panel) of heart rate activity in two lobsters exposed to LD and DD cycles and housed in ‘‘immobilization chambers’’.

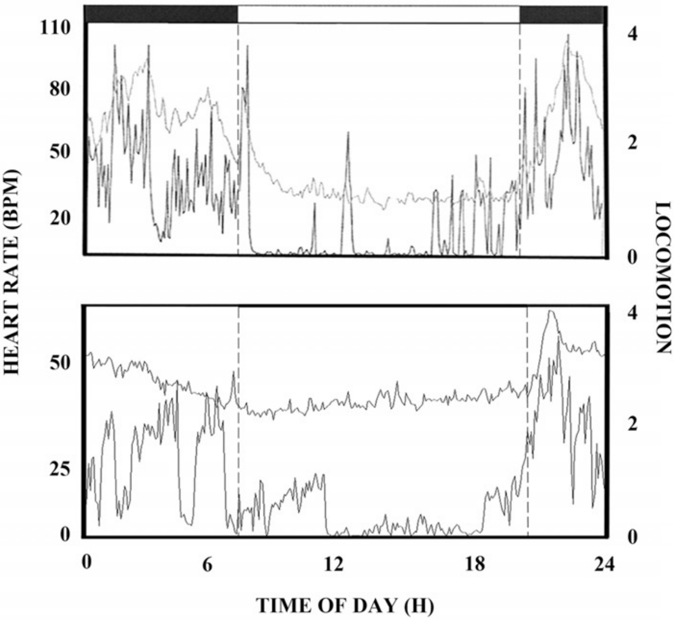

Figure 4. Heart rate (top curve in each panel) and locomotor activity (bottom curve in each panel) *vs*. time of day in lobsters (*n* ¼ 6 from Experiment 1 -top panel; *n* ¼ 2 from Experiment 3 -bottom panel). Values represent cumulative 5-min interval averages for all lobsters over a 10 day LD period.

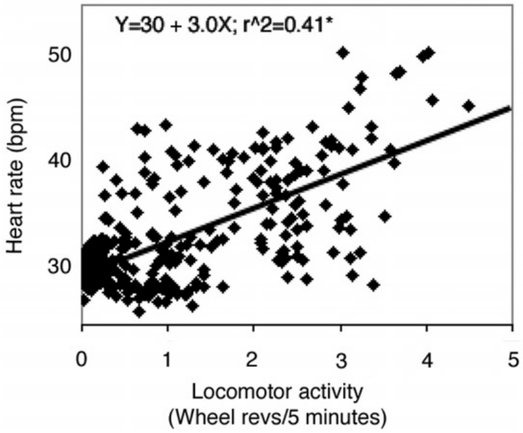

Figure 5. Scatterplot of locomotor activity (X axis – wheel revolutions/5 min) *vs*. heart rate for six lobsters (from Experiment 1) in an LD cycle. Data were averaged over a 10-day period by time of day. * $p > 0.0001$.

indicate circadian clock control of larval release behavior (Branford 1978), visual physiology (Arechiga et al. 1973; Page and Larimer 1975), cell proliferation (Goergen et al. 2002) and concentrations of a variety of hormones (Fanjul-Moles 2006). Taken together, these results suggest that endogenous oscillators are widely used among crustacean species for the temporal partitioning of physiology and behavior.

Daily heart rate rhythms

Our results are also the first to show long-term daily rhythms of heart rate activity in *H. americanus.* We found that both heart rate and locomotor activity increased during the dark phase of LD. A previous treadmill study had demonstrated shorter term (24 h) LD modulation of heart rate in this species (O'Grady et al. 2001). Significant daily rhythms in heart rate are also seen in several other crustacean species (*P. clarkii*, Page and Larimer 1972; *C. maenas*, Aagaard et al. 1995; *A. astacus*, Bojsen et al. 1998; and *N. norvegicus*, Aguzzi et al. 2004).

Several researchers have also documented a sudden increase in heart rate and locomotion during the D to L transition in several crustacean species (Pollard and Larimer 1977; Rebach 1985; Arechiga and Rodriquez-Sosa 1997; Li et al. 2000; Schapker et al. 2002). In the crayfish *P. clarkii* this increase has been shown to be directly induced by the lights-on transition and is thus not endogenously controlled by a circadian clock: that component of its activity did not persist in constant conditions (Pollard and Larimer 1977). While in the present study, some animals did express this kind of reaction to light (7/20; Figures 1 and 4 – top panels), in most cases (Figures 1 – bottom only, 2, 3, Figure 4 – bottom panel), neither heart rate nor locomotion increased significantly immediately after the D to L transition. This lack of a lights-on effect was also observed in all individual animals in a previous treadmill study (O'Grady et al. 2001) though the grouping of locomotion and heart rate data into 1-h bins could have obscured these shorter-term changes. Interestingly, *H. americanus* has been shown to consistently increase its heart rate over the short-term (minutes) in response to other environmental changes such as temperature (Jury and Watson 2000), salinity, or shadows (Dufort et al. 2001). By combining the data into 5-min bins (our study) or 1-h bins (O'Grady et al. 2001) these types of transient changes could be missed. However, while this apparent light-induced peak of heart rate is apparent in some animals in the current study, it is also likely that this response represents more of an exogenously induced ''startle response'' (Page and Larimer 1972), rather than endogenous modulation, since the peak of activity does not appear to persist in constant conditions (Figure 1 – top panel).

LD rhythms and nocturnality of locomotion

Our study also provides further documentation that the American lobster, like many other crustaceans (Arechiga et al. 1993), is primarily nocturnally active. Nocturnal increases in locomotor activity have been found in the New Zealand rock lobster (Williams and Dean 1989) as well as in the crayfish (Bojsen et al. 1998), the European lobster (Smith et al. 1998, 1999), and the rock crab (Rebach 1985) among many others. While our findings of a preference for nocturnal increase in activity are consistent with other studies on this species (Cobb 1969; Lawton 1987), two recent studies suggest that they may not always be nocturnal, especially in the field. A recent laboratory study by Jury et al. (2005) indicated that most, but not all, animals were primarily nocturnally active. Furthermore, a study conducted on animals in the field suggested that while ""60% were nocturnal, fully 10% preferred to move during the daylight hours (Golet et al. 2006). The authors of the field study suggested that social interactions may be nearly as important as LD cycles for determining the temporal partitioning of the day for some individuals. With this in mind, it is possible that the animals in the present study might have exhibited less preference for nocturnality if they were allowed to see other conspecifics during the day as they certainly can in the field.

HR and locomotion are correlated

Our results also suggest that heart rate and locomotion are positively correlated, at least when these measures are averaged over 5-min intervals and collected over long periods of time. There are several other specific similarities between these two measures that go beyond a statistical correlation. Our unforced walking experiments show that heart rate increases considerably during bouts of locomotion in lobsters (Figure 4). Furthermore, both heart rate and locomotor activity were higher in D than in L and the visual similarities in the temporal patterns of heart rate and locomotion within individuals are often strikingly similar (Figures 1, 2 – bottom). In addition, there were no statistical differences detected between the HR and locomotor periods. Taken together, our results suggest a close temporal relationship between the timing of heart rate modulation and the timing of locomotion modulation: changes in heart rate are positively correlated over both short term (minutes) and long term (days). These findings were similar to a previous study on *P. clarkii* (Pollard and Larimer 1977). While it is possible that separate circadian clocks modulate these two outputs in these two species, the simplest explanation of these results is that a single endogenous timing system controls these two outputs.

The similarities in the temporal patterns of locomotion and heart rate may vary somewhat between crustacean species and individuals. In the American lobster, heart rate and ventilation rates increase considerably during bouts of locomotion but only a ‘‘small, but significant positive correlation’’ was observed in 3/5 animals (O’Grady et al. 2001). Our findings appear to support a more robust correlation between locomotion and heart rate but the analysis time frame appears to be an issue between these two studies. O’Grady et al. (2001) found that, in some animals, heart and ventilation rates increases sometimes preceded locomotion by 5–10 s (O’Grady et al. 2001). Similar dissociations between heart rate and locomotion were seen after bouts of walking as it took just over an average of 6 min for heart rate to return to pre-walking rates. Likewise, Rose et al. (1998), using a ‘‘forced’’ walking paradigm and continuously monitoring both heart rate and locomotion, found that the size of the increase in heart rate was not always directly related to walking speed when analyzed at time scales of seconds. Since we grouped our heart rate and locomotor data into 5-min bins, we would not be able to pick up differences at these time scales. Likewise, in some shore crabs (8/20) there was an apparent dissociation between heart rate and locomotion over short time periods: heart rate increased only after locomotion increased while in other animals heart rate increased 1–3 min in advance of locomotion (Aagaard et al. 1995). However, in others, simultaneous increases in both heart rate and locomotion were observed within the same minute in 20 of 28 individuals (Aagaard et al. 1995). In *A. astacus* (Bojsen et al. 1998) and the Australian crayfish (*Cherax tenuimanus*; Villareal 1990) heart rate and locomotion appear to be more tightly coupled. Changes in locomotion explained between 38–47% of the variation in heart rate in *A. astacus* (Bojsen et al. 1998). This range is similar to the present study where changes in locomotion explained """40% of the variation in heart rate. Overall, the reported degree of association or dissociation between locomotion and heart rate appears to be dependent, at least in part, on the time scales that are used by investigators to compare these two measures as well as whether the animals are walking voluntarily or are forced (Rose et al. 1998).

The effects of restraint on heart rate rhythms

In the present study, the prevention of overall locomotor activity using two different methods did not suppress either daily or circadian patterns of heart rate changes in lobsters. In LD cycles, heart rates of most restrained lobsters still increased with the onset of the darkness even though locomotor activity was inhibited (Figure 2). Likewise, in DD, circadian rhythms of heart rate persisted in most restrained animals (Figure 3). These findings suggest that locomotion is not a requirement for expression of heart rate rhythms in the American lobster. Similarly, nocturnal increases in heart rate were also observed in immobilized shore crabs (Aagaard et al. 1995). Interestingly, while Aagaard et al. (1995) found that immobilized *C. maenas* exhibited a higher percentage of heart rate rhythms *versus* freely moving individuals, our results were equivocal on this issue. Taken together, the results from our present study and the Aagaard et al. (1995) study suggests that crustacean heart rate rhythms may not only be an outcome of increased metabolic needs during more active times but is also more directly influenced by an endogenous circadian clock. The location and mechanism of this clock remains to be elucidated.

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