FACTORS INFLUENCING RATE AND DIRECTION OF LOCOMOTION IN <u>GONIABASIS</u> <u>LIVESCENS</u>, A FRESH WATER SNAIL

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ABSTRACT

Whitman, Deborah L. Factors influencing rate and direction of locomotion in Goniabasis livescens, a fresh-water snail. Rate and direction of snails' movements were studied in relation to environmental and internal cues. The snails do have patterns to their rate of movement, but not to direction of movement. Directional movement seems to be based on environmental factors that do not have daily cycles, or on no environmental factors at all. Rate of movement patterns were also found not to be affected by environmental factors that vary on daily cycles. The patterns observed seem to be influenced by internal cues or rhythms, instead.

INTRODUCTION

Annual and diurnal rhythms are the most frequent topics of studies in locomotory patterns. Both of these are presumed to be somewhat influenced and regulated by environmental factors (Cloudsley-Thompson, 1961). For fresh-water, aquatic animals in shallow waters however, the potential responses to environmental factors are not very clear. Some cues such as tidal rhythms and vertical migrations of plankton which are available to other aquatic animals are unavailable to animals in shallow, fresh-water habitats. However, in shallow water, both light intensity and water temperature are much more prone to variability than at greater depths, and these two parameters may be important cues in affecting the locomotory patterns of such animals as the fresh-water snail, Goniabasis livescens.

Other environmental factors may affect the locomotion of G. livescens in ways that do not produce patterns of movement through time, but merely manifest correlations between the factor in question and the properties of the snail's movement. These would be factors which do not fluctuate reliably on a daily basis, such as wave movement and possibly food availability.

Thirdly, if patterns do appear to exist in the locomotion of an animal, but these patterns do not appear to relate to environmental cues, one may then look to "internal" cues the animal may be using to determine its patterns of movement. The most obvious factor here would be the need to fulfill a nutritional requirement, although other possibilities such as seeking a site to mate or lay eggs may be hypothesized for less frequent movement patterns. If one can successfully disprove such a hypothesis of internal cues, overiding internal rhythms may be looked to as the cause of such locomotive patterns (Herme, 1963). These would be internal rhythms which are not related to cues in any way.

If neither cyclic rhythms nor correlations with other environmental factors are found, one may tentatively conclude that the movement is not affected by the cues tested and may be random.

Based on some initial observations of G. livescens in the field, I was curious about what types of factors might be affecting the snail's movements. In calm waters, they leave a distinctive trail behind them, and my initial observations of their movements as indicated by these trails led me to believe that their locomotory behavior did have some pattern to it. Based on those observations, I chose two properties of their movement, the direction and rate of movement to study.

Because I suspected the movements of the snail of containing some type of pattern, I focused on those factors which would ellicit a patterned movement response, chiefly: a) light intensity b) water temperature c) internal cues, especially hunger, and tried to determine their importance as cues used by G. livescens in determining rate and direction of movement.

My first objective was to conduct a 24-hour observation of the snails in their natural habitat, taking measurements of light intensity and water temperature as well as the rate and direction of snail movement during that time period. Using this data, I first looked for established patterns or rhythms and then looked for correlations between the parameters and environmental factors measured. Following this, I intended to determine if the amount of time since the last feeding would affect the rate of a snail's movement to test the "hunger" hypothesis.

MATERIALS AND METHODS

24-Hour Observational Period

The study site was chosen due to the high population of G. livescens located there. It is a small beach at the University of Michigan Biological Station on Lake Douglas, near Pellston, Michigan. The beach is located about ¼ mile from the main part of camp, just off the Pine Point Trail. The site was located about 30 to 80 meters from the shoreline. The depth of the water only ranged from 17 to 26 cm. because the site is located on a large shoal that extends well out into the lake before dropping off. This provided a fairly stable shallow water depth in which G. livescens are abundant and easily located. To the right of the site about 10 meters, a small "peninsula" intruded about 40 meters, very slightly secluding the study site.

The study was conducted over 24 hours running from 7:00 pm August 2 to 7:00 pm August 3, 1980. A few hours before the study began, 60 snails were collected from the study site and marked numerically with tester's paint. The shells were dabbed with acetone to dry them before painting, to increase the life expectancy of the markings. The snails were then returned and allowed to reorient to their environment for three hours before observations were begun.

The 24 hour observation time was divided into six sampling periods of four hours each. Observations were carried out for the first two hours of each time block; no observations were carried out during the second two hours. At the beginning of each sampling period, the location of each snail being followed was flagged, and its direction and distance of movement was noted at that time. If a trail was present, the distance was taken as the length of the trail. If no trail was present (usually due to strong wave activity) the distance moved was taken as the net distance from the last point at which the snail was observed. This was probably a slight underestimation in many cases, but only rarely would that be signifigantly so. The first hour of each sampling period was used in this way.

The second hour of each sampling period was used to return to the same snails and flag their new position, noting direction and distance of movement at this time. From my initial observations, I had not expected to be able to follow an individual snail for much longer than one hour, thus the one hour time intervals were designed to compensate for this. However, due to very calm weather, I was able to follow the snails over the two hour "non-observational" periods as well, and was actually able to follow six individuals for the full 24 hours. At each sampling period approximately 14 individuals were flagged. When flagging the snails, the snail's number and sample period number were noted on the flag to avoid confusion.

A final observation was taken at 7:00 pm on August 3 so that a total of 13 samples were taken over the 24 hours, with intervals of one to three hours between the samples. For each sample period, measurements of light intensity and water temperature were also taken.

"Hunger" Experiment

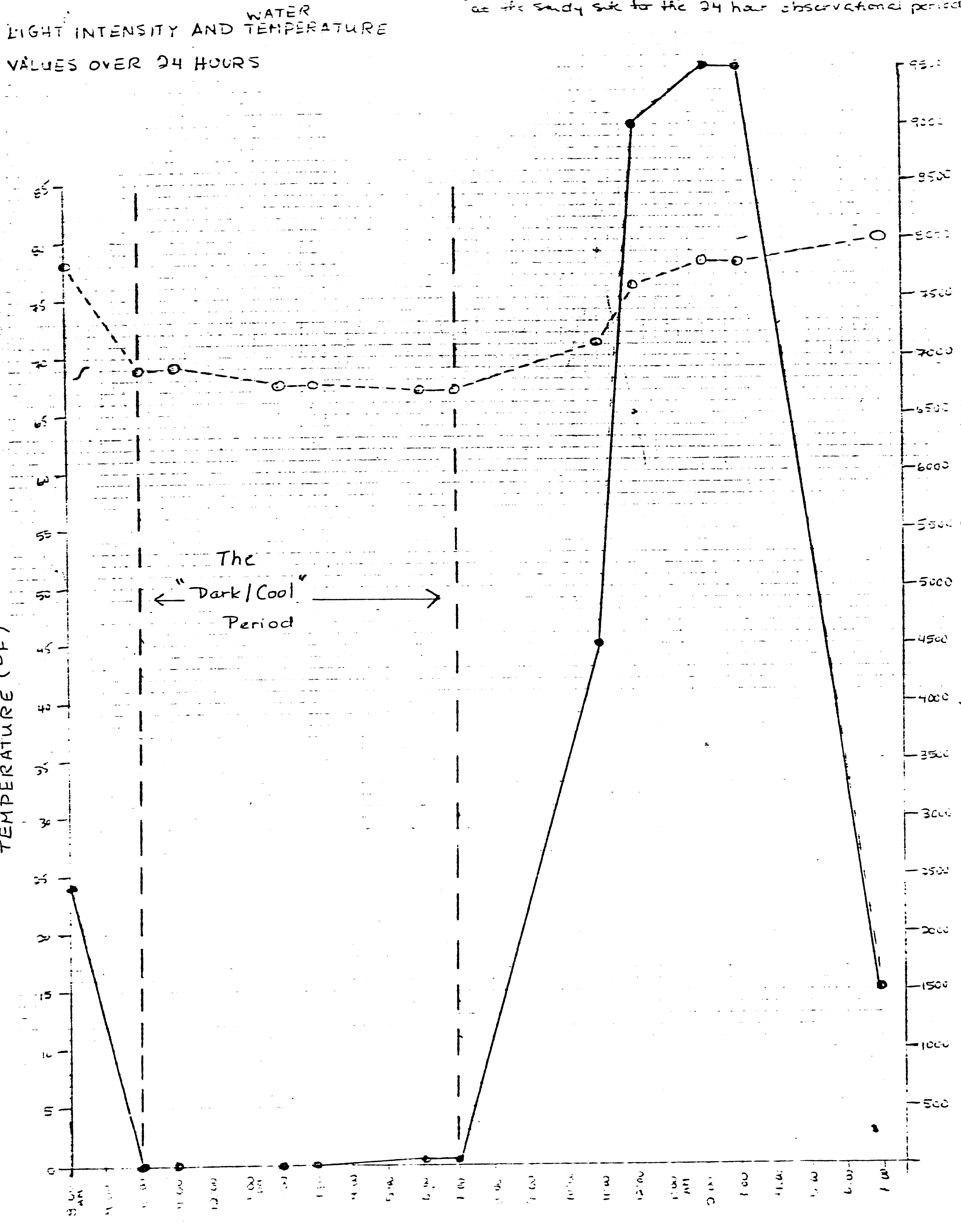
To test the hunger hypothesis, an indoor set up was erected in Lakeside Lab near the boatwell. A large metal tub (approximately 2.5 m X 1 m X 1 m deep) was filled with about 5 cm of sand and 10 cm of lake water. Finally, a thin top layer of sand was applied that was taken from the top layer of sand at the study site. Presumably, this top layer of sand contained the nutritional requirements of G. livescens because they feed on diatoms and other ~~phyto~~periphyton found on the surface of the sand. A microscopic inspection of this top layer showed that the snails were indeed receiving from it, a variety of diatoms and other phytoplankton.

The subjects for this hunger experiment were obtained just in front of the volleyball court about two meters away from shore. Only animals that had been making trails were chosen, to assure that they had been eating recently. It is generally accepted the G. livescens feed constantly while in motion (Baker, 1928). Six of these "recently fed" snails were taken to the lab, ~~and~~ marked, and placed in the experimental set-up. Their rate of movement was calculated over a four hour period. Following this, the snails were placed in filtered lake water (filtered through a micropore with .45 μm filter paper) and starved for 20 hours. The four hour experiment was repeated after the starvation period to campare the rate of movement before and after starvation. Light intensity, water temperature and time of day were held constant throughout both experimental runs.

RESULTS

Before examining the locomotion results themselves, it will be helpful to be acquainted with the patterns of the light intensity and water temperature over the sampling period. Figure 1 shows that samples number 2 through 7 (approximately 10:00 pm to 7:00 am) represent the facultative "darker" and "cooler" sampling periods. The light/warm and

Figure 1. Values for light intensity and water temp. at the study site for the 24 hour observational period



dark/cool periods shown in Figure 1 are used throughout the paper in comparisons with locomotory rhythms.

Direction of Movement

Based on Figure 22 there does not appear to be a daily cycle or pattern to G. livescen's direction of movement with respect to shore. The sample numbers 2 through 7 represent the time of lowest light intensity and water temperature as seen in Figure 1. If the direction of movement was being affected by those parameters, one would expect to see a different pattern of directional movement in these samples with respect to the others. This is not observed in Figure 2 however. Instead, the overall direction of movement tends to be away from the shoreline, and the few variations in this occur in no pattern at all (samples number 5, 6 and 9).

This point is further emphasized in Figure 3. Here the direction of movement is based on compass readings, and no daily pattern seems to exist from these graphs. Again, if light and temperature were playing an important role here, one would expect the directional movement in samples 2 through 7 to be different from the other samples, and this is not the case.

One interesting point in Figure 3 is that the overall highest frequency of directional movement is to the Southwest (which incidently is away from shore). This might tend to suggest that the snails may be moving out of the study site, however I marked about 60 snails three days before the 24 hour observation period, and 10 of those were recovered the day of the ovservation period. I had removed about 40 of the 60 marked snails into the lab, so the percentage of recovery was actually rather high. Also, the markings had been put on without using acetone, and it is very possible that some previously marked snails no longer bore markings after three days. In addition to this, it can be noted that at the end of the 24 hour observation period, 33 of the 60 snails marked for the observations

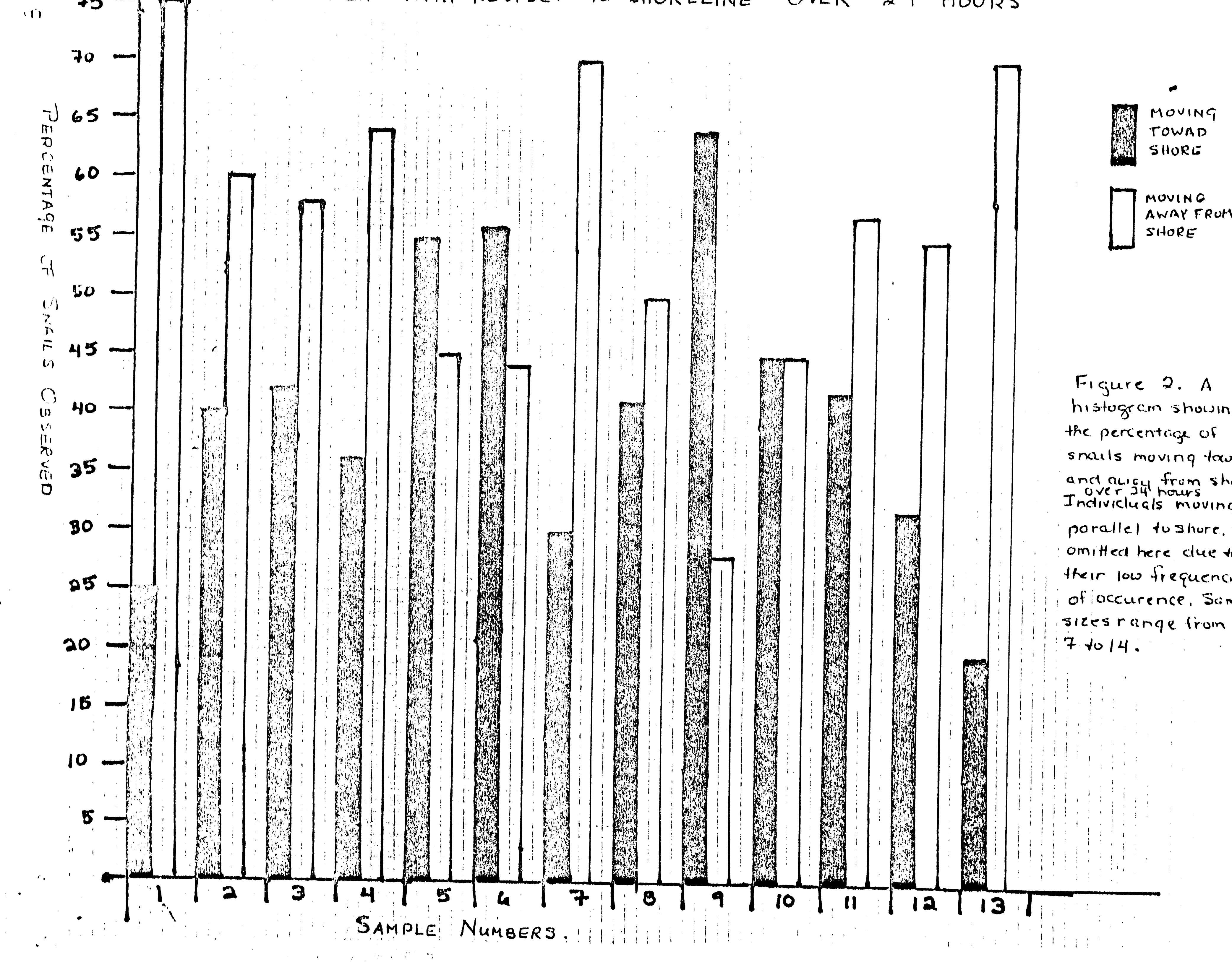


Figure 2. A histogram showing the percentage of snails moving towar and away from shor over 24 hours. Individuals moving parallel to shore, ar omitted here due to their low frequency of occurence. Samp sizes range from 7 to 14.

MOVEMENT WITH RESPECT TO COMPASS DIRECTION OVER 24 HOURS

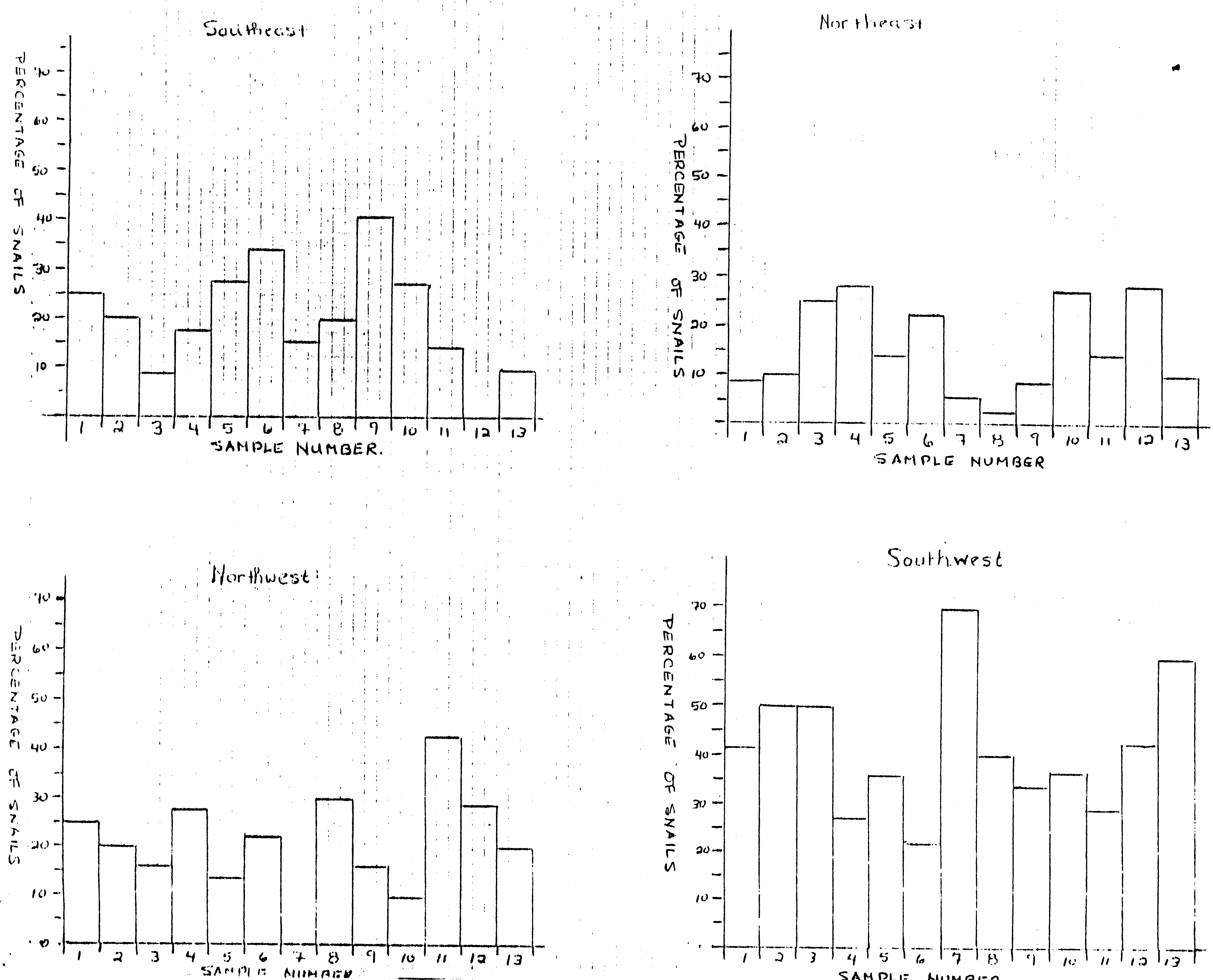


Figure 3 - Histograms showing the percentage of snails moving toward each of the 4 …

were recovered at the study site. Based on these data, the snails do not seem to be leaving the study area permanately.

Rate of Movement

Figure 4 shows the rate of movement over 24 hours for the six snails that were followed for the entire sample period. Unlike the directional data, some type of locomotory pattern is suggested by these data. Each individual snail has a long period where the rate of movement is slow, followed by one or two shorter periods of one to four hours each of more rapid movement. These peaks and lulls in rate of movement do not occur at the same time of day for each snail. Notice that snails number P_{22} and P_{11} have their highest rate of activity in the dark/cool hours, while snails number W_{20}, W_{39} and P_{36} reach their peak activity around midday, and snail number P_{26} does not reach its peak rate of locomotion until the warmest and brightest part of the day. Less complete examples of this phenomea can be examined in Table I for other snails seen over the 24 hour period. However, I was unable to follow the other snails for the full 24 hours, which makes the data less complete for these individuals. If the pattern of movement rates were controlled by light intensity and water temperature, one would expect the peaks and lulls to approximately coincide for each snail, but this is not what is observed.

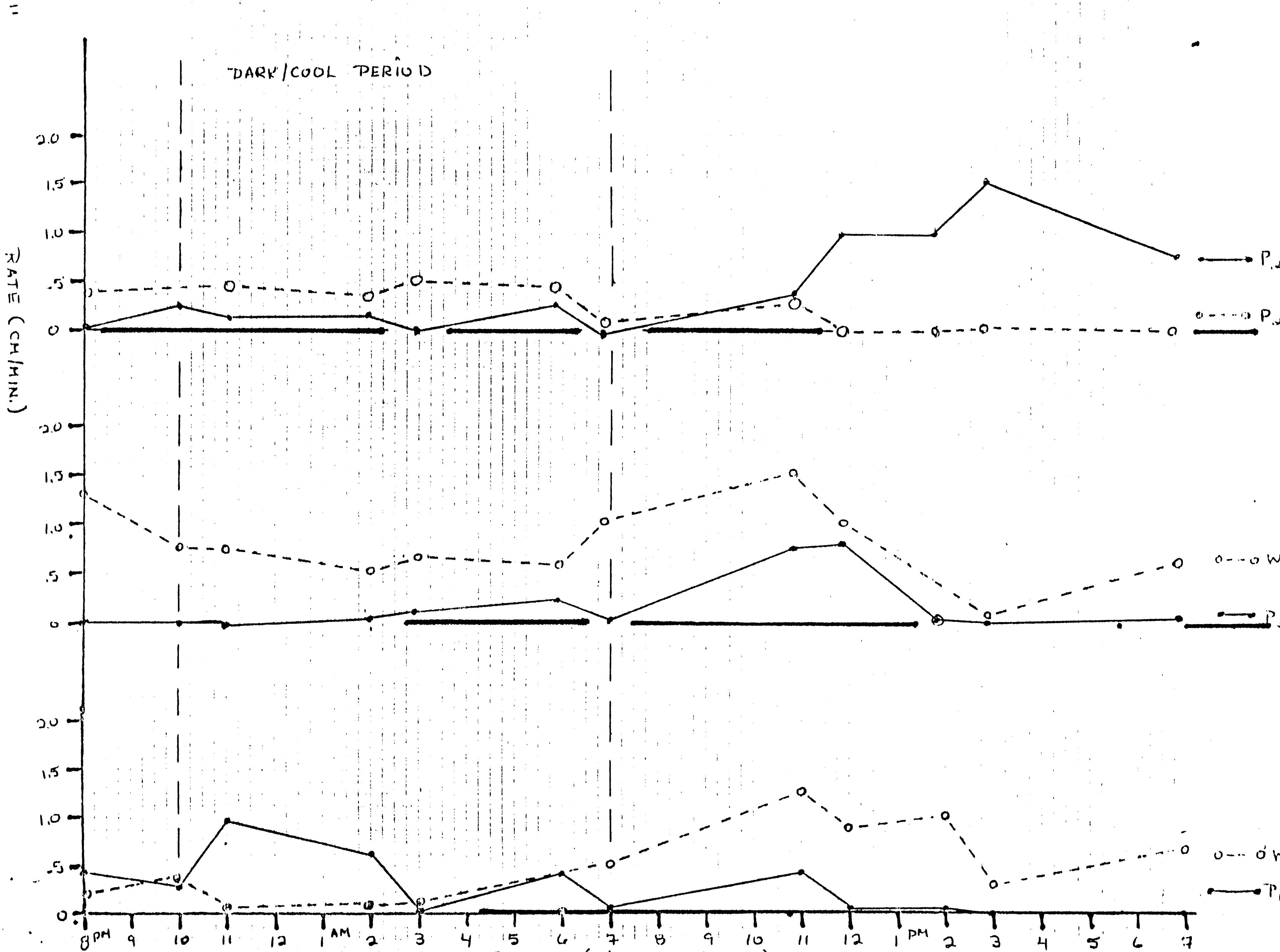
Overall, there does appear to be a slightly higher rate of movement in the light hours, however when the "dark/cool" samples are compared to the "light/warm" samples by the Mann-Whitney-U test, there is not a significant difference in the rate of movement at the two intervals (U=12, tabular value=5, $p > .05$).

Hunger Experiment

The hunger experiment was run once, using six snails. The graphs depicting the results are found in Figure 5. The mean rate of movement over four hours before the starvation period was $.298 \pm .204$, and the

RATE OF MOVEMENT OVER 24-HOURS.

Figure 4. A graphic representation of the rate of movement for six individual snails over 24 hours.



Snail # \ Interval	1	2	3	4	5	6	7	8	9	10	11	12	13
R32		.61	.58	.42	.79	.46							
W39		.21	.35	.06	.08	.16	.01	.55	1.26	.90	1.08	.34	.70
P11		.43	.32	.98	.66	.04	.44	.04	.46	.04	.04	0	.01
W25		.39				.14	.35	.94					
P37		.27	.13	.47	.47	.09	.26	1.3					
P36		0	.01	0	.03	.10	.23	.08	.77	.82	0	0	.01
P3		.01	.01										
W20		1.34	.79	.77	.57	.70	.44	1.08	1.56	1.06	.01	0	.61
R10		1.00	.86	.36	.03	0	.02	.02	.64	.95			
P22		.42	.51	.48	.35	.54	.45	.05	.30	0	0	.02	0
P26		0	.25	.16	.18	0	.29	0	.39	1.01	1.01	1.56	.77
W32		.02	.45	.23	.17	.16	.01	0					
P24				.35									
R5										1.16	.02	.17	.27
P7								.04	1.0	.75	1.2	.88	.01
P30								0	.72	0	0	0	.51
W31								1.31					
P6										.47	0	.02	.02

Table I. A list of the rates moved by each snail sampled over the 24 hour period.

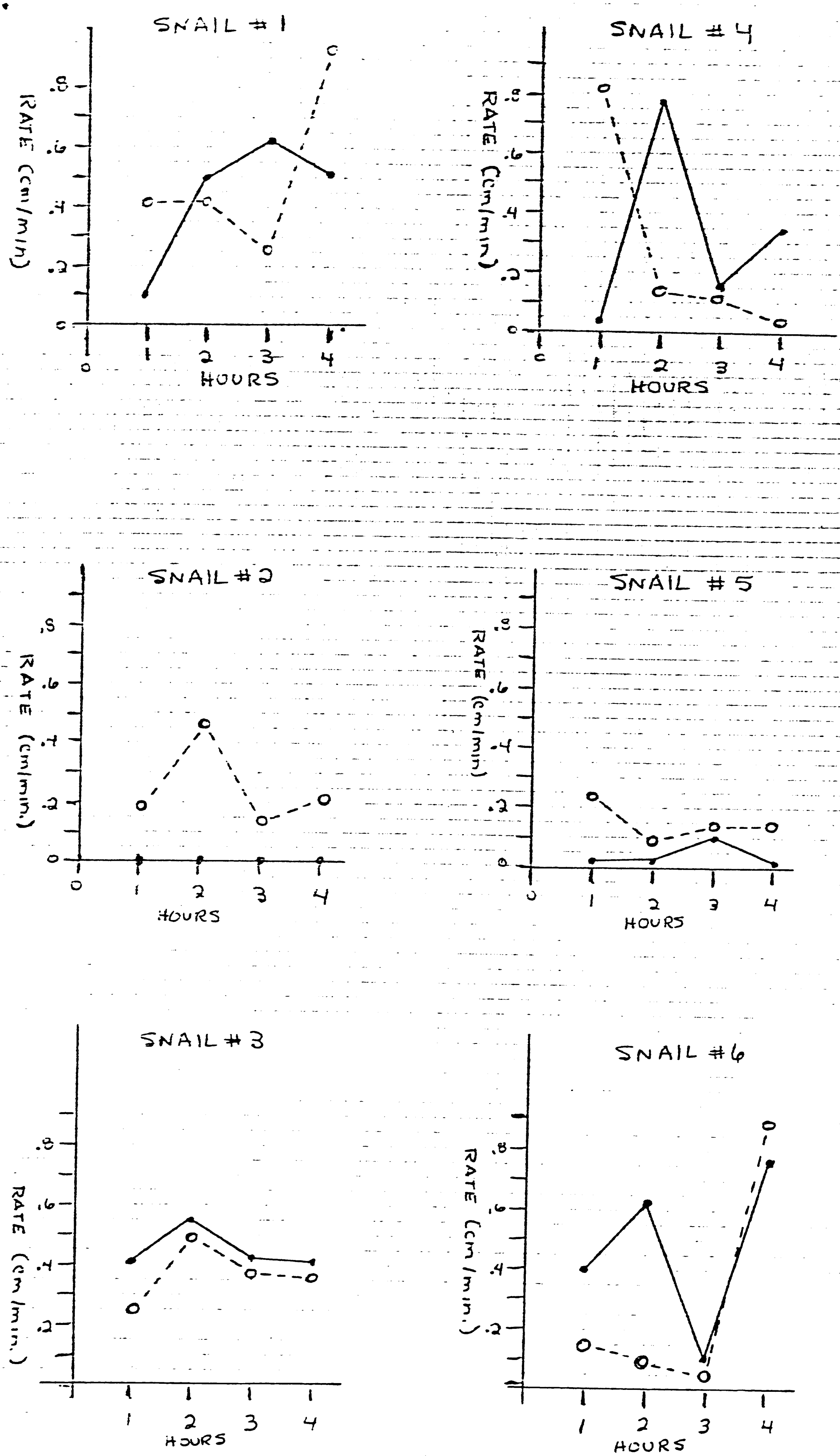


Figure 5. A graphic representation of the rate of movement before and after a 20 hour starvation period. Graphs are for six individual snails.

o - - - o Rate after starvation

●——● Rate before starvation

mean rate of movement after the starvation period was $.308 \pm .123$. As analyzed by the Mann-Whitney-U test, these do not represent significantly different rates of movement (U=17, tabular value=5, $p > .05$). An analysis was also done on the rate of movement for the first hour of the experimental periods. The mean rate of movement in one hour before starvation was $.160 \pm .197$, after starvation the rate was $.344 \pm .242$. These were also found not to be signifigantly different rates of movement according to the Mann-Whitney-U test (U=9, tabular value=5, $p > .05$). Again the dramatic differences exibited by individual snails should be noted. Snail #2 moved faster over the entire four hours after starvation, while snail #3 moved faster over the entire four hours before starvation, and still other snails exibited differing combinations of comparative "before/after" values.

DISCUSSION

Based on the results of Figures 2 and 3, one would not expect the directional movement of G. livescens to be affected by parameters which run on daily cycles--such as light intensity and water temperature. There are no daily patterns observed in the directional data, however the data do suggest that some type of effect is being expressed because of the overall trends observed away from shore in a Southwest direction. This may indicate that other factors which are not cyclic on a daily basis may be affecting the directional locomotion. Based on the recovery rates for the marked snails, one would expect the snails to reverse this directional trend at some time and return towards shore. Perhaps factors such as changes in food availability or wave strength and direction could be hypothesized as the controlling factors here. Wave patterns do not seem to be cyclic on a daily basis in Douglas Lake, and during the 24 hour observation period, my tentatige observations seem to indicate that the waves were coming from a constant direction (north) at all times except in periods of total calm. Changes in food availability are less certain, because phytoplankton is abundant in the lake. It seems reasonable however, to suppose that wave movement might affect the location of the areas of highest concentration of phytoplankton. Thus, one might even expect a combination of the effects of wave activity and food abundance may be controlling factors here. Obviously further investigation would be needed to substantiate this, but my data does seem to suggest the action of such factors.

Rate of Movement

The rate of movement data are most interesting from the standpoint that the patterns exhibited differ so markedly from snail to snail. There are definitely patterns of rapid movement followed by a slower period of movement, but the fact that the periods of rapid movement do not even come close to coinciding suggests that the determining factors are not environmental. The lack of a statistically significant difference between the rate of movement during the cool/dark and light/warm hours further suggests that factors that vary on daily cycles are not of importance here. In this case, one may suspect that one or more internal cues are being used by the animal to determine its rate of movement. This data originally suggested the hunger hypothesis in order to test for one type of potential internal cue.

What is most surprising about this data is that it is in opposition to most of the established hypotheses on molluscan activity. Mollusca are not assumed to exibit marked rhythms in their activity levels. They supposedly tend toward arhythmicity, or at the very least, prolonged activity (Cloudsley-Thompson, 1961, citing Calhoun, 1944). Cloudsley-Thompson do suggest that snails may exibit "exogenous" rhythms based on light intensity and temperature, but that these rhythms disappear under constant conditions. My results seem to be in opposition to both of these hypotheses.

Obvious patterns do exist in the rate of movement of G. livescens, but those patterns do not seem to be related to light intensity and water temperature at all. Based on Cloudsley-and Thompson's assumptions, it would have been very interesting to have seen if G. livescens exhibited patterns in its rate of movement under constant conditions over 24 hours, to prove even more conclusively that light and temperature do not play an important role here. Time, did not permit such a study this summer, so I leave that to be more fully explored by myself or others at a later date.

It was interesting to note that at least one paper written after the Cloudsley-Thompson book also brought out results differing from the results in the book. The findings of F. Herme indicated that land snails do exhibit daily rhythms of activity, and that those patterns are affected by light intensity and temperature, but that they also seem , at least in part, determined by overiding rhythms (F. Herme, 1963). The implication in her paper seems to be that the "overiding rhythms" are not affected by any cues at all, but are integral parts of the animals' developmental or learned behaviors. Such an overiding rhythm will be discussed later as potentially related to the locomotory patterns of G. livescens.

Hunger Experiment

The results of the hunger experiment do not uphold the hypothesis that the patterns observed in rates of movement are caused by internal hunger cues. However, due to the small sample size used, and some logistical problems with test itself, I am unwilling at this point to consider this hypothesis adequately disproven.

It is entirely possible that the process of starvation for 20 hours would not have a significant effect on a snail's feeding (moving) rate because snails are able to go for weeks at a time without food. Thus, if one is hypothesizing that hunger would cue the snail to eat, a

20 hour period without food may not be sufficient stimulus to throw off its already established feeding pattern. This presents a serious question about the validity of the test as it was conducted. A more valid test would be to starve several snails for varying periods of time, and to then compare the change in rate of movement before and after the starvation periods. This would give an indication if a threshold exists below which a daily feeding pattern is not altered.

If however, my data is foreshadowing the results of a more thorough study on this matter, one might then begin to consider the possibility of "overiding rhythms" ~~that~~ such as Heme discusses. Again, the outstanding factor to test here would be how firmly the patterns remain under constant conditions. Such overiding rhythms are a potential explanation for the locomotory patterns of G. livescens for which I was unable to test, and will leave to be tackled later.

Before closing, it should be noted that in speaking of the patterns or rhythms observed, I made the assumption that they occured on a daily (over the course of 24 hours) period. The samples ranged over 24 hours, so I am fairly certain that rhythms of under 24 hours are not present here, but it is entirely possible that the pattern I observed varies over longer periods of time. Diurnal rhythms are most often looked for, because the environmental factors often vary on daily cycles. But because I do not seem to be dealing with environmental factors that vary on daily cycles here, it would not necessarily be true that the rhythm length need to be 24 hours. Especially if the hunger hypothesis holds up, there would be no reason why a 24 hour cycle would be favored for feeding (unless the food availability varies over 24 hours which I do not believe is true in their shallow environment). A more thorough study would include multiple 24 hour observation periods to test if the patterns I observed in my observation period are repeated, and at what intervals they are repeated.

In summary, the directional movements of Goniabasis livescens do not seem to exhibit daily patterns, but they may exhibit non-cyclic paterns. Based on that information, one may hypothesize that if they are indeed affected by environmental factors, it would be by factors that do not vary in daily cycles such as wave direction and possibly food availability. This explanation seem to be the most consistant with my results, although it certainly warrants further investigation.

The rate of movement of G. livescens, on the other hand, shows definite daily (or perhaps slightly longer time interval) rhythms that do not coincide with environmental factors that have daily cycles. These patterns would seem to be controlled by some sort of internal rhythm, either by internal cues such as hunger, or by overiding internal rhythms. This study was unable to successfully disprove either of these possibilities, and that task must be left to later studies.

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