This is to certify that the

thesis entitled

Movement Patterns in the
Land Snail Anguispira alternata

presented by

Miranda Alderson Karson

has been accepted towards fulfillment
of the requirements for

Master's degree in Zoology

Major professor

Date 12/6/99

MOVEMENT PATTERNS IN THE LAND SNAIL *ANGUISPIRA ALTERNATA*

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology

1999

ABSTRACT

MOVEMENT PATTERNS IN THE LAND SNAIL *ANGUISPIRA ALTERNATA*

By

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This study examined the relationship between daily and long-term patterns of movement in the land snail *Anguispira alternata* in the field and laboratory. In the field, a mark-recapture study followed 35 snails in three plots for three months. Daily distances moved ranged from 0.0 cm to 160.2 cm (median 35.7 cm). This distance was not affected by maximum temperature, soil temperature, precipitation or snail size, but did differ significantly between the three plots. The distribution of recaptures among plots and within particular sub-areas of the plots was non-random. However, most snails in the field demonstrated random movement behavior. In the laboratory, 23 snails were followed in eight arenas, four with random food placement and four with non-random food placement. Daily distance moved ranged from 0.0 cm to 61.23 cm (median 12.02 cm). These distances were significantly less than the distances moved in the field. Moreover, the distance moved in one day was significantly greater in arenas where food was placed randomly than in those with non-random food placement. There was a non-random distribution of recaptures among arena sub-areas and eleven of 23 individuals indicated non-random movement behavior. Possible explanations of the observed movement patterns are discussed.

For Dad-

Your love of life and laughter will never be forgotten.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Dr. James Atkinson, the Chairman of my committee, for his help during all phases of this research. Thanks also to Dr. Catherine Lindell and Dr. Antonio Nunez for their assistance and guidance in producing this manuscript. Finally, I would like to thank Kristi Davis for her assistance in the collection of field data.

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Introduction

Recently, considerable research has focused on both short-term and long-term movement patterns of a variety of animal species (for summary, see Golledge 1999). Patterns of movement may reveal something about whether an organism utilizes some sort of "cognitive map" or other internal spatial representation to navigate through its environment (Golledge 1999). For example, it is known that many vertebrate species find their way to and around their "home range" using learned landmarks (Papi 1992, Golledge 1999). However, until recently animal movement pattern research has focused almost exclusively on radio tracking of mammals and birds. Short term and seasonal movement patterns of invertebrate species have remained largely unstudied (Tinbergen 1958, Papi 1992, With and Crist 1995).

Invertebrate spatial behavior research is important for several reasons. First, finding, maintaining and relocating particular shelters could be of vital importance to terrestrial invertebrates as many are vulnerable to desiccation and extreme temperatures due to their small size (Rollo and Wellington 1981). Second, though limited, there have been a few examples of invertebrate spatial navigation based on memorization and use of landmarks such as in wasps, ants, bees and octopuses (Mather 1991; Etienne et al. 1999). Such examples suggest that many invertebrate sensory systems are capable of complex processes such as learning and memory. Research examining invertebrate systems is then important, as relatively simple nervous systems may allow us to better understand the cellular and molecular basis of learning and memory which can then be applied to our understanding of more complex systems (Carew and Sahley 1986). Finally, movement patterns have important influences on the genetic and demographic structures of populations (Dobzhansky and Wright 1943).

Terrestrial gastropods (snails and slugs) are particularly useful organisms with which to examine invertebrate movement patterns. Snails are relatively easy to mark, move slowly, and do not travel great distances. Thus, it is relatively easy to monitor their movements over long periods of time (Hansson 1991). Because of their delicate membranes, terrestrial gastropods require adequate moisture and moderate temperatures. This suggests that the ability to locate and relocate known shelter areas with the appropriate microclimate may be especially important to this group (Rollo and Wellington 1981). Finally, several observations of terrestrial gastropod homing behavior have suggested the existence of spatial memory (Edalstam and Palmer 1950; Pollard 1975; Rollo and Wellington 1981; Lind 1989). Unfortunately, little research has examined this matter closely.

Both movement patterns and homing behavior have been examined in a small number of molluscan species. Several clear examples of gastropod homing behavior and reasonable mechanisms for the behavior have been identified and explained. Often times molluscs return to their home sites by using a return path that closely follows the initial outward path used by the animal (Ingram and Adolph 1943; Southwick and Southwick 1969; Chase et al. 1978;

Cook 1979). In such instances, the molluscs are likely using the mucous trail left behind on the outward trip in order to relocate the home site. This phenomenon is called trail following by contact chemoreception.

It is often the case, however, that molluscs return to particular sites using a different route than the original outgoing path (Gelperin 1974). Obviously, such examples cannot be explained by trail following. Such homing behavior may be accomplished by long-distance reception of distinct odors associated with the home site (called distance chemoreception). Thus far, most examples of homing in molluscs have been explained by trail following, distance chemoreception or a combination of these two mechanisms (Rollo and Wellington 1981; Lind 1989). In essence it is generally thought that homing in gastropod molluscs is dependent on some sort of "chemical beacon."

There are certain instances of homing in which are not fully explained by the aforementioned mechanisms. Work with *Helix pomatia* demonstrates that every winter these snails return to within a few centimeters of particular hibernation sites (Edelstam and Palmer 1950; Pollard 1975;Lind 1989). Because they are able to do this after long periods of time away from these sites and over relatively great distances, it is unlikely that this yearly return to the hibernaria is accomplished solely through trail following or distance chemoreception (Lind 1989). To Lind, the results of such studies suggest that *Helix pomatia* have long-term memory of the location of the hibernaria and that the snails navigate around their familiar areas using olfactory "maps" or other internal representations of their habitats.

Although homing behavior based on topographic memory has been largely dismissed, it appears that limpets are able to relocate home sites on substrates with topographic features that lack chemical cues, but cannot relocate home sites on uniformly flat substrates (Cook 1979; Jessee 1968). This work suggests memory and the use of topographic characteristics in homing behavior. Rollo and Wellington (1981) suggested that topographic memory has not yet been demonstrated because most experimental designs provide few topographic features, allowing little opportunity for learning. Thus, it seems inappropriately early to eliminate topographic memory or some sort of internal spatial representation of the snail's habitat as a wayfinding mechanism.

The land snail *Anguispira alternata* is a good candidate for behavioral studies. *A. alternata* is very common, has a large distribution, and withstands a wide variety of environmental conditions. It is distributed between Maine and Alabama, west to South Dakota and Texas. Within this distribution, *A. alternata* is found in leaf litter and around decaying logs in deciduous forests, on roadsides, in gardens and in vacant lots (Hubricht 1985; Burch and Jung 1988).

No previous work has examined *A. alternata's* movement patterns. Initial laboratory observations demonstrated that these snails will use artificial shelters and suggested that individuals may have a preference for particular shelters. Interestingly, shelter use was not demonstrated in *A. alternata* when placed in an arena with the carnivorous land snail *Haplotrema concavum* (Atkinson unpublished data). These observations raised questions as to whether or not *A. alternata* uses particular shelter sites under natural conditions, and what factors might influence whether these animals use and return to particular shelters. Thus, I was interested in exploring movement patterns of *Anguispira alternata* and the relation of these patterns to use of particular shelter sites (both natural and artificial). My study was exploratory and aimed to determine whether these snails exhibited homing behavior.

Therefore, the purpose of this study was:

1. To gather data on short term and seasonal movement patterns of the terrestrial gastropod *Anguispira alternata* and to examine the effects of various abiotic factors on these movement patterns.
2. To determine whether observed movement patterns indicated random or directed movement with respect to the surrounding habitat.
3. To compare patterns of movement of *A. alternata* in the field to the controlled conditions of the laboratory.

Materials and Methods

Field Observations

Field observations were conducted in Lott North Woodland, a wood lot (approximately 62,500 m^2 in size) located just south of Michigan State University campus in East Lansing, MI. This area is a beech-maple climax forest with abundant leaf litter, scattered vernal ponds, and a large number of fallen trees scattered throughout.

Within North Lott, three rectangular plots, each with an area of approximately 10 m^2, were established. Selection of the plots was based on topographic similarities between the three plots as well as similar initial densities of *A. alternata* within the three plots. Plots were marked in each corner by a stake and were surrounded by twine to clearly delineate the borders. After establishing the plots, all *A. alternata* with a shell diameter of 12 mm or greater within each plot were marked. All snails were marked with numbers written in nail polish. Measuring and marking occurred in the field and all snails were immediately released to their original positions after the marks had dried. Thirty-six snails were marked in total (sixteen in plot one, eleven in plot two and nine in plot three).

All plots were searched carefully for marked *A. alternata* approximately three to five times per week between June 4' 1998 and September 9, 1998. The position of each snail was recorded by measuring the distance of the snail from both the horizontal and vertical (X and Y) perimeters of the plot. Using the

Cartesian coordinates of the position of each individual snail, I calculated; (1) the distance between positions of subsequent recaptures, (2) the angle (direction) of each displacement, and (3) the angle between successive displacements (calculated by subtracting the previous angle of displacement from the subsequent angle of displacement). This method was consistent with that of Baur and Baur (1993) who determined that distances calculated in this manner are highly correlated with those distances measured directly.

Daily air temperature, soil temperature, and precipitation were obtained from Michigan State University's Horticulture Teaching and Research Center. This weather station is located about half a mile from Lott North Woodland and therefore should provide accurate data for the study site. During the study, the daily maximum temperature ranged from 63 degrees Fahrenheit to 88 degrees Fahrenheit. During the course of the study, precipitation occurred on 30 of 89 days.

Laboratory Observations

Laboratory observations were conducted in Tupperware "arenas" measuring 36 cm by 51cm wide by 15 cm high. Each container was filled with a layer of soil measuring approximately 1.5 cm high and was covered with a fitted, plastic lid. Within each arena, I provided several "shelter sites" including two terra cotta "half pots" in two of the corners and a piece of wood located between the center and top edge of the arena. In order to keep the arenas moist, a small amount of water was added one or two times per week. Each arena housed three, size-matched (14-16 mm) *A. alternata.* At the beginning of the observations, the snails were given identifying marks with nail polish and placed in the center of the arena.

The snails in each arena were fed with small slices of carrot placed in the arenas every two weeks and left for four days. In four of the arenas a feeding location was chosen randomly at the beginning of the study and all subsequent feedings occurred at this location (arenas one, four, five and eight). In the other four arenas a different location was chosen randomly for each feeding (arenas two, three, six and seven).

The laboratory observations occurred in two parts. Half of the arenas (two with random and two with non-random food placement) were observed between May 31, 1998-July 12, 1998. The other half (again, two with random and two with non-random food placement) were observed between September 24, 1998-February 24th, 1999.

Again, using the Cartesian coordinates of each individual within the arenas I calculated (1) the distance between subsequent sightings, (2) the angle of displacement, (3) the angle between successive displacements (calculated by subtracting the previous angle of displacement from the subsequent angle of displacement) and, (4) the distance of the snail from the current (or most recent) feeding location.

Results

Field Observations

A total of 207 daily distances moved by 36 *Anguispira alternata* in the field were recorded. The mean recovery rate of the 36 marked snails was approximately 13% per search day and decreased steadily throughout the study (Figure 1). Recaptures of marked individuals occurred most frequently within zero to three days of a prior recapture (Figure 2). The distribution of recaptures among each of the three plots was non-random, with the greatest number of recaptures occurring in plot three (Table 1). Moreover, the locations of recaptures among nine sub-areas within each of the three plots were scattered non-randomly (Table 2). Maps of the plots including the divisions of the plots into the nine sub-areas are illustrated in figures 3 through 5.

Minimum distances moved per one-day interval ranged from 0.0 cm to 160.20 cm (mean value: 40.85 cm, median value: 35.65 cm) and their frequency distribution fitted a function with logistic decay (Figure 6). In about 29% of the observations of one-day distances, *A. alternata* remained inactive or moved relatively short distances (less than twenty cm). Distance covered per two-day interval (not including data considered in the one-day interval analysis) ranged from 0.00 cm to 133.08 cm (mean value: 46.28 cm, median value: 37.63 cm) and their frequency distribution also fitted a function with logistic decay (Figure 7). In observations of distance traveled in two days, approximately 18% of the snails remained inactive or moved short distances.

The mean distance moved per one-day interval (by all snails) was not influenced by air temperature (One-way ANOVA, F=1.57, n=56, P≈0.22), soil temperature (One-way ANOVA, F=0.014, n=56, P>0.9), snail size (One-way ANOVA, F=0.707, n=56, P≈0.50), or amount of precipitation (One-way ANOVA, F=0.06, n=56, P=0.81). The distance moved per one-day interval did, however, vary significantly between plots (Figure 8). A means separation test indicated a significant difference between two of the three pairs tested in this ANOVA (pairs one-three and two-three)

Representative movement tracks of six, recaptured *A. alternata* (two from each plot) are illustrated in figures 9 through 14. Rayleigh and Rao tests (described in Batschelet 1981 and Russell and Levitin 1997) were used in order to determine whether movements between subsequent recapture locations of each individual snail appeared random or directed. Overall, the snails showed no preference in direction of movement (Table 3). Moreover, it appears that the direction of each movement was independent of the preceding direction of movement (Table 4).

Laboratory Observations

In the laboratory, a total of 988 daily distances moved by 23 *Anguispira alternata*, in eight different arenas, were recorded. Minimum distances moved per one-day interval ranged from 0.00 cm to 61.23 cm (mean 15.38 cm, median value: 12.02 cm). There was a significant difference between the distance moved per one-day interval in laboratory observations and in field observations

(Figure 15). In about 34% of the observations of one-day distances, *A. alternata* remained inactive. The mean number of observations in which individual snails were found inactive did not differ between arenas where food was placed randomly and arenas where food was placed non-randomly (one-way ANOVA, F=5.987, n=566, P=0.83).

The distance covered in one day was significantly greater in arenas where feeding location was random (arenas two, three, six and seven) than in those arenas where feeding location was uniform (arenas one, four, five and eight). (Figure 16). Moreover, the recapture locations of those snails that were fed in a uniform location remained closer to the feeding location than were recapture locations of snails fed in a random location (Figure 17).

There was a non-random distribution of recapture locations within seven of the eight arenas (Table 5). There was also indicated a non-random distribution of recapture locations for seven of the 23 individuals (Table 6). Rayleigh and Rao test were used in order to determine whether angles of movements or the angle between subsequent movements implied random or directed movement patterns. Overall, the snails showed no preference in direction of movement (Table 7). However, for eleven of twenty-three individuals in the laboratory, the direction of movement appears dependent on the preceding direction of movement (Table 8).

Discussion

This study monitored the movement patterns of *Anguispira alternata* in its natural habitat over a relatively long period of time. Few studies have examined the movement patterns of terrestrial snails, and even fewer have attempted to relate observed movements within a natural habitat over a specific amount of time with movement patterns observed in the laboratory. Studies such as the present one will continue and allow us to gain a greater understanding of factors acting as determinants of movement patterns.

The mean one-day distance traveled had a large range in both the field and the laboratory. Unlike Baur and Baur's (1988) study of the land snail *Punctum pygmaeum*, this high variability among individuals was not explained by snail size. Because I was only able to measure distances moved within my plots, however, it is difficult to assess whether size might have influenced dispersal, as large snails may have left the plots sooner than smaller snails. Because only 49 of my total measured displacements were of snails I considered large (compared with 152 of medium-sized snails), I have reason to believe that snail size may have affected the distance traveled in *Anguispira alternata*. Because the snails were size matched, I was unable to go back and do look at this with extant laboratory data.

The field results may be biased because the most and least active snails may have been recaptured less than other snails. Snails that travel furthest are least likely to be recovered in the study-area and snails that remain inactive are likely to bury themselves under the soil (Baur and Baur, 1993). Baur and Baur (1993) assert that these two sources of bias may balance each other out to some extent. Nonetheless, it seems as though the field data is biased toward moderately active snails.

Precipitation, air temperature and soil temperature had no effect on the mean distance traveled in the field. This could be due to several factors. First, it is possible that I do not have enough data to establish whether there is an effect. Because inactive snails may bury themselves making them impossible to recover, and because warm, dry weather conditions may lead to inactivity, it is possible that these factors did affect movement in a manner my data could not reflect. Secondly, it is likely that nighttime air temperature, soil temperature and precipitation may affect movement behavior. *A. alternata* is active at night and thus, a majority of their movements may have occurred nocturnally. Thus, there may be a correlation between nighttime activity in *A. alternata* and weather conditions. Further studies could easily ascertain whether this is the case. Finally, it could be that within the range investigated these abiotic factors had no effect.

It is interesting that the mean one-day distance traveled differed significantly amongst the three plots. On average, snails in both plots one and two traveled further than snails in plot three. Several factors may have contributed to this finding. Plot three was about 50 meters West from plots one and two (which were about eight meters apart) and thus may have differed qualitatively from plots one and two. However, plot three did not appear shadier or damper than the other plots. Dispersal in land snails is often affected by vegetation type (Cowie 1980). In plot three, many recaptures occurred in sub-areas that included a particular. Thus, it seems likely that the log located in the middle of plot three may have accounted for the observed differences in mean one-day distance traveled. *A. alternata* may have preferred particular logs for a number of reasons, such as: the time the log had been rotting, the species of the tree, the type of fungus growing on the log, etc. Perhaps the snails did not exhibit the same preference for the age, species, etc. of the logs in plots one or two. Unfortunately, I was unable to determine much about the rotting logs in any of the plots.

Unlike the field data, the laboratory data was not biased toward snails moving particular distances, as all snails remained within the arenas and were easily located. The lack of such bias in the laboratory may explain the difference in mean distance moved between the field and laboratory. If inactive snails did bury themselves in the field, a number of zero cm per day distances would have been ignored, thus increasing the mean. This seems highly likely considering the greater inactivity level found in laboratory snails. However, differences may also be due to the relatively small size of the laboratory arenas, thus limiting movement of snails.

A. alternata in the laboratory traveled shorter distances and had a slightly higher percentage of inactivity than did their field counterparts. This may be attributed to the fact that there is less area to explore within the arenas and perhaps there is also less environmental pressure to relocate suitable feeding or "shelter" sites. Rollo and Wellington suggested that homing behavior in terrestrial gastropods would only be observed when there was some sort of environmental pressure for the animal to do so (1981). In the laboratory, the animals were provided with adequate moisture and food. This might have eliminated the snails' "need" to search the arenas for particular food or shelter sites.

The patterns of distribution of recapture locations suggested that recaptures occurred in particular areas within the arenas and plots. This might imply that *A. alternata* prefers certain microhabitats within the plots or locations within the arenas. This is more strongly suggested by the seven individuals in the laboratory who preferred particular locations in the arenas. Unfortunately, this analysis was not possible for each of the individuals in the field, as there was inadequate data due to small numbers of recaptures of each snail.

The concentration of recaptures in the field data may be explained by sampling bias. It is possible that snails were easier to relocate in certain sub-areas of the plots. This interpretation cannot explain such findings in the laboratory, however, as snails were relocated with ease within all portions of the arenas. Thus, one cannot rule out the possibility that a large number of recaptures of particular individuals within certain locations may be due to some sort of preference by these individuals.

Not only were the recaptures scattered non-randomly, the data suggest that some snails in this study exhibited non-random movement behavior. In the field, snails from plot three showed directed movement. In the laboratory, ten different snails (split equally amongst arenas where the feeding location was random and non-random) showed directed movement. Non-random movement may indicate that snails return to particular remembered areas. This could explain a phenomenon such as the fidelity of the snails in plot three to the log, or the fidelity of snails in arenas where food placement was consistent to areas close to the feeding location. If the log in plot three was a favorable location, it might have been advantageous for the snail to relocate to the log after wandering away. Thus, there may be some sort of environmental pressure to remember particular areas.

Non-random movement may, however, indicate that particular snails may have been continually following the same set of slime trails. The fact that more snails in the laboratory exhibited directed movement behavior than their counterparts in the field may favor this interpretation. It seems that snails in small, confined, areas may have a higher likelihood of encountering their own or other snails' slime trails than do those in large, boundless areas. Thus, it possible that directed movement patterns are an artifact of the number of times a particular set of slime trails is relocated. Preliminary experiments have indicated that trail following of conspecifics is not a strong behavior in *A. alternata* (Atkinson, unpublished data) however, and thus, this may fail to explain the non-random patterns of movement that I observed.

One could distinguish between these two interpretations by performing experiments such as those of Pollard (1975) or Lind (1989). In these studies snail populations were followed over several years. Pollard found that *Helix* *pomatia* showed a tendency to repeat tracks of the previous year. Lind found that *Helix pomatia* showed a tendency to return to particular hibernaria on a yearly basis. One is hard pressed to attribute these findings to simple trail following, as slime trails cannot last for such long periods of time. Thus, non-random movement patterns in these studies may indicate memory of particular areas or routes. Though snails have the ability to follow slime trails to particular locations, it is possible that they may rely on other means of relocation when slime trails are not available.

I did attempt to recover marked snails during the late spring of 1999. Unfortunately, I was unable to relocate the marked snails. Thus, it is difficult to ascertain whether *Anguispira alternata* is similar to *Helix pomatia* in that they relocate important sites without the use of slime trails. Very little is known about *A. alternata*, including whether they rely on a particular set of "shelter sites" or hibernaria. Again, one could ascertain that *A. alternata* would "remember" or return to particular areas only if this species relies on these particular areas.

One interesting observation by Elwell and Ulmer (1971) of 23 *A. alternata* reported that tree climbing was common after long periods of heavy rainfall. Moreover, once conditions became dry the snails would aestivate on the tree and as weather conditions became favorable they would continue up the tree. During these observations, no snail moved downward once located on a tree. This observation is additional evidence for non-random movement behavior in this species and this non-random movement does not rely on following slime trails. Elwell and Ulmer (1971) suggest that *A. alternata* tend to remain in optimal habitats and will return to such habitats after excursions brought on by favorable environmental conditions. Elwell and Ulmer hypothesize that this is a function of their responses to wind, light, moisture and food, and do not explain this phenomenon by trail following. This provides support for the hypothesis that the ability to relocate certain optimal areas may be an important determinant of movement behavior in this species.

The fact that certain individuals did demonstrate directed movement indicates that further investigation of this topic may be useful. A similar field study with more marked individuals, more plots, and more careful analysis of characteristics of the plots themselves (such as the age or species of rotting logs within the plots, the amount of shade, soil moisture, etc.) could provide very interesting data. Such studies may help to ascertain what characteristics of the plots may affect movement behavior.

The searching procedure used in this study may have influenced the movement patterns of *A. alternata*. Repeated recoveries of marked individuals required repeated searching, which may have damaged vegetation or changed the microhabitat within the plots. Also, recaptures require repeated handling of the marked individuals. Thus, recovery may influence the snails' behavior (Cameron and Williamson 1977), but would not explain differences between the plots as all plots were searched using the same technique. Cameron and Williamson (1977) suggest restoring plots after searching them by watering the plots. Unfortunately, this practice would most likely affect the movement behavior of the snails and therefore would not work in this particular circumstance. At present, I am hard pressed to offer a less invasive searching technique apart from radio tracking of the animals.

It would also be informative to follow the snails for a longer period of time. Studies such as Lind's (1989) and Pollards (1975) where populations were followed between spring emergence and winter hibernation for several years in a row may reveal interesting information related to movement patterns in this snail. Perhaps the use of small radio transmitters would allow for a more descriptive analysis of snail movement patterns while not requiring extensive searching or handling of the snails.

In terms of further laboratory investigations, I think it may be interesting to pursue the differences in movement patterns of snails fed in random and non-random feeding locations. It may also be interesting to run a similar experiment where previous slime trials are eliminated, thus eliminating the likelihood that non-random patterns of movement were an artifact of repeated encounters with the same set of slime trails. Another way to assess the importance of slime trails would be to continually videotape snails in the arenas and determine whether they are always taking the same set of trails to move about the arenas.

Laboratory experiments could also be useful in determining what sorts of factors might influence movement patterns in the field. For instance, one could look at preferences for rotting log or leaf types, or particular fungi, or influences of other species of snail. Further laboratory investigations of this type may reveal previously unknown influences on terrestrial snail movement patterns. Few studies have correlated patterns of movement of snails in the laboratory and field. Studies of this sort could continue to provide information as to what characteristics of the environment or objects in the environment affect the movement patterns of these snails.

If further studies were to yield similar results, a next and important step would be to isolate the cause of directed movement patterns. Non-random patterns of movement may or may not indicate spatial learning ability. However, non-random patterns do indicate that the snail's surroundings are not homogeneous. In other words, cues in the environment may strongly affect the direction traveled. This is quite different from the view that snails move randomly with respect to their surroundings, save the influence of other slime trails. Whilst this study did not prove that *Anguispira alternata* exhibits homing behavior, it did indicate that some individuals move in non-random directions. If further studies yield similar findings, it would be interesting to examine whether the location of a reliable food source affects the movement patterns of these snails.

APPENDICES

APPENDIX A

TABLES

Table 1. χ^2 **results of the distribution of the total number of recaptures of marked *A. alternata* among plots one, two and three.**

	Number of snails recaptured
Plot 1	64
Plot 2	30
Plot 3	120
n	214
χ^2	57.93
P	**P<0.001**

Table 2. χ^2 results of the distribution of locations of marked *A. alternata* recaptures among nine sub-areas within plots one, two and three.

	Number of snails recaptured		
	Plot 1	**Plot 2**	**Plot 3**
Sub-area A	12	3	0
Sub-area B	4	1	0
Sub-area C	1	11	0
Sub-area D	1	11	18
Sub-area E	17	1	45
Sub-area F	3	0	5
Sub-area G	3	1	6
Sub-area H	10	2	42
Sub-area I	13	0	4
n	64	30	120
χ^2	39.78	47.45	195.3
P	**<0.001**	**<0.001**	**<0.001**

Table 3. Rayleigh and Rao results of the distribution of angles of displacement in field observations of *A. alternata*.

Snail	**Rayleigh**	**Rao**
101	r≈0.217, P≈0.70	U=118.25, P≈0.55
106	r≈0.296, P≈0.42	U=87.6, P>0.91
108	r≈0.204, P≈0.74	U=107.49, P≈0.70
109	r≈0.234, P≈0.78	U=78.97, P>0.76
110	r≈0.237, P≈0.34	U=133.8, P≈0.39
114	N/A	U=125.7, P≈0.39
302	r≈0.177, P≈0.50	U=123.06, P≈0.62
303	r≈0.025, P≈0.88	U=168.5, **P≈0.054**
304	r≈0.048, P≈0.16	U=167.17, P≈0.08
306	r≈0.279, P≈0.37	U=177.47, **P≈0.025**
307	r≈0.061, P≈0.88	U=119.56, P≈0.71
308	r≈0.236, P≈0.76	U=51.05, P≈0.76
309	r≈0.235, P≈0.45	U=161.19, P≈0.08

Table 4. Rayleigh and Rao results of the distribution of angles between successive displacements in field observations of *A. altemata*.

Snail	Rayleigh	Rao
101	r=0.060, P>0.88	U=95.43, P~0.79
106	r=0.239, P~0.61	U=70.11, P>0.89
108	r=0.302, P~0.55	U=127.22, P~0.43
109	N/A	U=99.69, P~0.60
110	r=0.396, P~0.054	U=146.88, P~0.22
302	r=0.278, P~0.21	U=152.02, P~0.12
303	r=0.336, P~0.26	U=107.00, P~0.78
304	r=0.425, P~0.30	U=181.56, **P<0.05**
306	r=0.332, P~0.28	U=140.99, P~0.28
307	R=0.198, P~0.40	U=165.48, **P~0.03**
308	N/A	U=89.26. P~0.69
309	r=0.29, P~0.368	U=129.72, P~0.44

Table 5. χ^2 results of the distribution of recapture locations of marked *A. alternata* among nine sub-areas of each arena. Recaptures in sub-areas where food was placed in non-random feeding arenas are bolded.

	Arena							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Sub-area 1	8	16	16	6	11	22	4	4
Sub-area 2	6	14	6	15	1	2	6	2
Sub-area 3	14	31	34	**57**	8	14	38	6
Sub-area 4	22	11	9	7	6	8	2	3
Sub-area 5	9	4	9	3	4	7	5	**9**
Sub-area 6	4	5	12	10	10	4	0	3
Sub-area 7	17	12	11	5	5	3	4	1
Sub-area 8	5	4	17	3	2	1	0	2
Sub-area 9	**16**	7	9	5	**18**	5	3	2
n	101	104	123	99	65	63	62	32
χ^2	27.94	50.37	41.13	154.9	30.68	49.66	162.74	14.09
P-value	**<0.05**	**<0.005**	**<0.005**	**<0.005**	**<0.005**	**<0.005**	**<0.001**	>0.05

Table 6. χ^2 results of the distribution of recapture locations of seven marked *Anguispira alternata* amongst nine sub-areas of their laboratory arenas. Recaptures in sub-areas where food was placed in non-random feeding arenas are bolded.

	Snail						
	3B	**4A**	**4B**	**4C**	**7A**	**7B**	**7C**
Sub-area 1	7	4	2	0	11	22	4
Sub-area 2	4	10	4	1	1	2	6
Sub-area 3	14	**21**	**17**	**18**	8	14	38
Sub-area 4	4	3	2	2	6	8	2
Sub-area 5	3	2	1	0	4	7	5
Sub-area 6	3	2	4	4	10	4	0
Sub-area 7	1	1	2	2	5	3	4
Sub-area 8	3	0	1	2	2	1	0
Sub-area 9	1	1	2	2	18	5	3
n	40	44	35	31	65	63	62
χ^2	28.92	73.66	52.05	72.7	58.42	43.06	74.26
P-value	**<0.005**	**<0.005**	**<0.005**	**<0.005**	**<0.005**	**<0.005**	**<0.001**

Table 7. Rayleigh and Rao results of the distribution of angles of displacement in laboratory observations of *A. alternata*.

Snail	Rayleigh	Rao
1a	r=0.09, P~0.83	U=127.7, P~0.68
1b	r=0.02, P>0.90	U=118.73, P~0.76
1c	r=0.07, P>0.90	U=125.58, P~0.58
2a	r=0.09, P~0.80	U=146.6, P~0.17
2b	r=0.132, P~0.78	U=131.16, P~0.47
2c	r=0.11, P~0.76	U=151.43, P~0.13
3a	r=0.311, **P~0.02**	U=167.52, **P~0.04**
3b	r=0.03, P>0.90	U=144.43, P~0.19
3c	r=0.10, P~0.68	U=165.96, **P~0.01**
4a	r=0.07, P~0.84	U=134.42, P~0.37
4b	r=0.20, P~0.56	U=129.33, P~0.45
4c	r=0.20, P~0.57	U=124.66, P~0.56
5a	r=0.09, P~0.87	U=102.09, P~0.94
5b	r=0.14, P~0.71	U=100.71, P~0.92
5c	r=0.14, P~0.74	U=159.58, P~0.08
6a	r=0.04, P>0.90	U=144.23, P~0.21
6b	r=0.17, P~0.61	U=108.11, P~0.87
6c	r=0.02, P>0.90	U=137.82, P~0.28
7a	r=0.01, P>0.90	U=113.42, P~0.72
7b	r=0.074, P>0.90	U=144.59, P~0.22
7c	r=0.11, P~0.89	U=127.28, P~0.58
8a	r=0.12, P~0.59	U=108.71, P~0.84
8b	N/A	N/A
8c	r=0.12, P=0.56	U=110.2, P~0.82

Table 8. Rayleigh and Rao results of distribution of angles between successive displacements in laboratory observations of *A. alternata*.

Snail	Rayleigh	Rao
1a	r=0.427, ***P*<0.003**	U=162.68, **P~0.003**
1b	r=0.32, P<0.45	U=128.46, P~0.64
1c	r=0.21, P~0.42	U=135.52, P~0.37
2a	r=3.37, **P~0.019**	U=124.91, P~0.63
2b	r=0.39, P.064	U=144.76, P~0.21
2c	r=0.23, P~0.32	U=140.77, P~0.28
3a	r=0.18, P~0.65	U=122.6, P~0.65
3b	r=0.646, **P<0.001**	U=185.71, **P<0.01**
3c	r=0.28, P~0.084	U=153.84, P~0.09
4a	r=0.44, **P<0.001**	U=141.28, P~0.25
4b	r=0.30. P~0.29	U=154.19, P~0.08
4c	r=0.41, P~0.056	U=166.56, **P<0.05**
5a	r=0.446, P~0.95	U=148.37, P~0.20
5b	r=0.698, **P<0.001**	U=177.82, **P<0.001**
5c	r=0.46, **P~.039**	U=156.81, P~0.12
6a	r=0.60, **P~0.002**	U=161.1, P~0.08
6b	r=0.36, P~0.08	U=162.6, P~0.07
6c	r=0.63, **P<0.002**	U=165.98, **P~0.03**
7a	r=0.57, **P~0.006**	U=152, P~0.13
7b	r=0.66, **P~0.002**	U=232.65, **P<0.01**
7c	r=0.10, P>0.859	U=95.41, P~0.87
8a	r=0.36, P~0.073	U=114.11, P~0.76
8b	N/A	N/A
8c	r=0.33, P~0.09	U=110.60, P~0.79

APPENDIX B

FIGURES

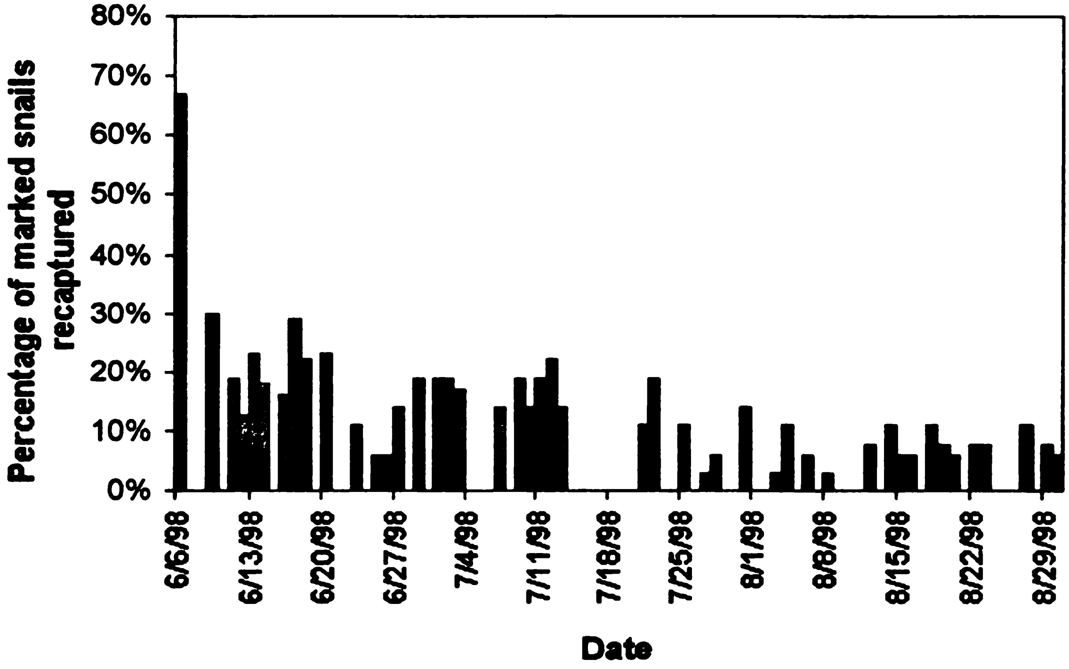

Figure 1. Frequency distribution of the percentage of *A. alternata* recaptured per search day (recovery rate). A linear function was fitted to the distribution: $y=-0.023x+81.606$, $r^2=0.3206$, t=, d.f.=45, $P<0.001$.

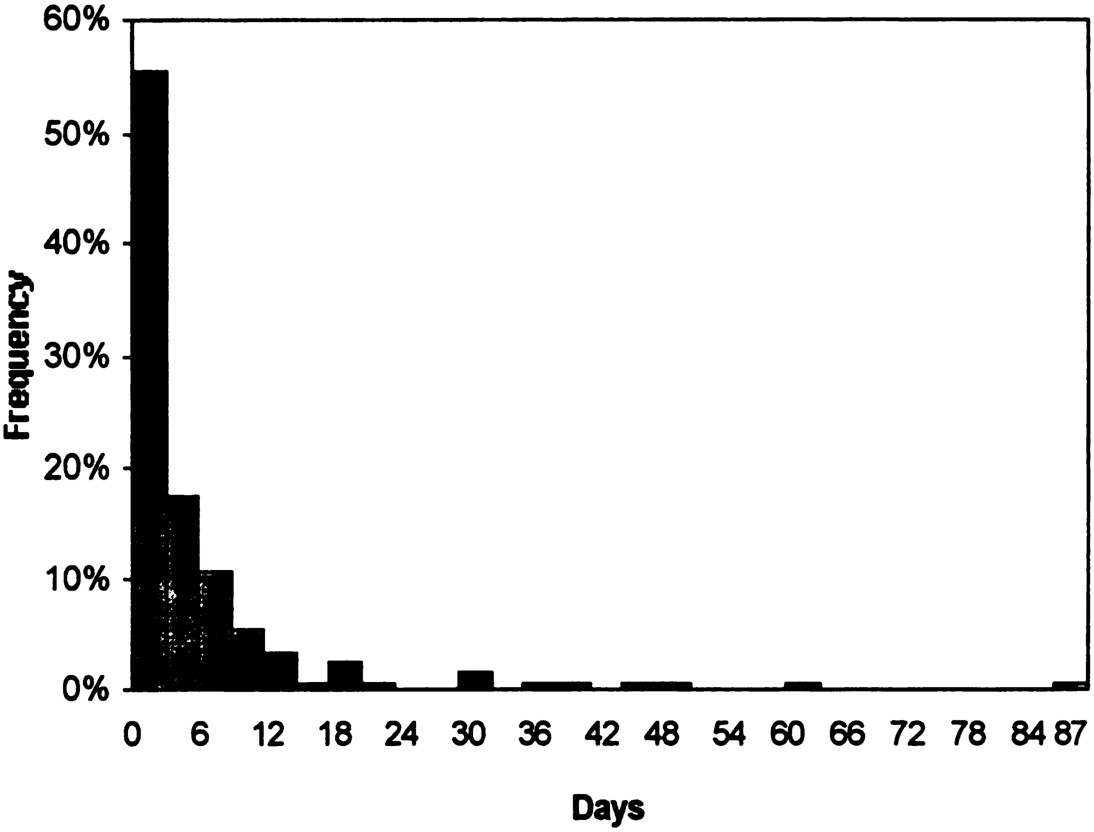

Figure 2. Frequency distribution of the number of days between field recaptures of *Anguispira alternata*. A logistic function was fitted to the distribution:$y=-0.0949\ln(x)+0.2676$, $r^2=0.5645$, d.f.=13, t=4.105, $P<0.001$.

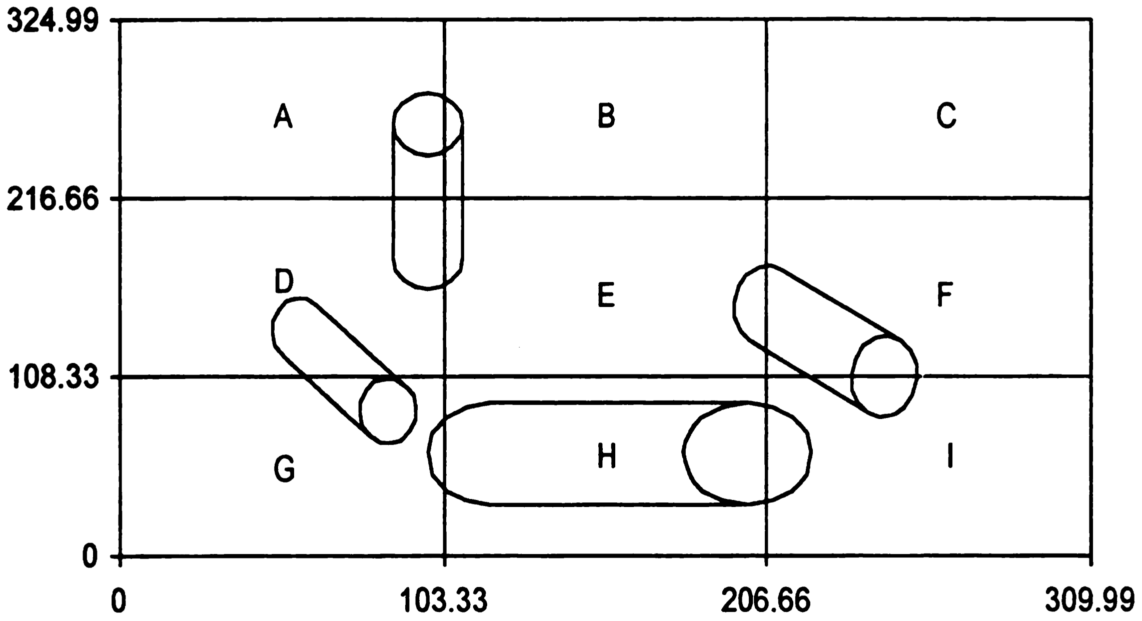

Figure 3. A map of plot one (310 cm by 325 cm) illustrating the location of rotting logs within the plot as well as the division of the plot into nine sub-areas (labeled A through I).

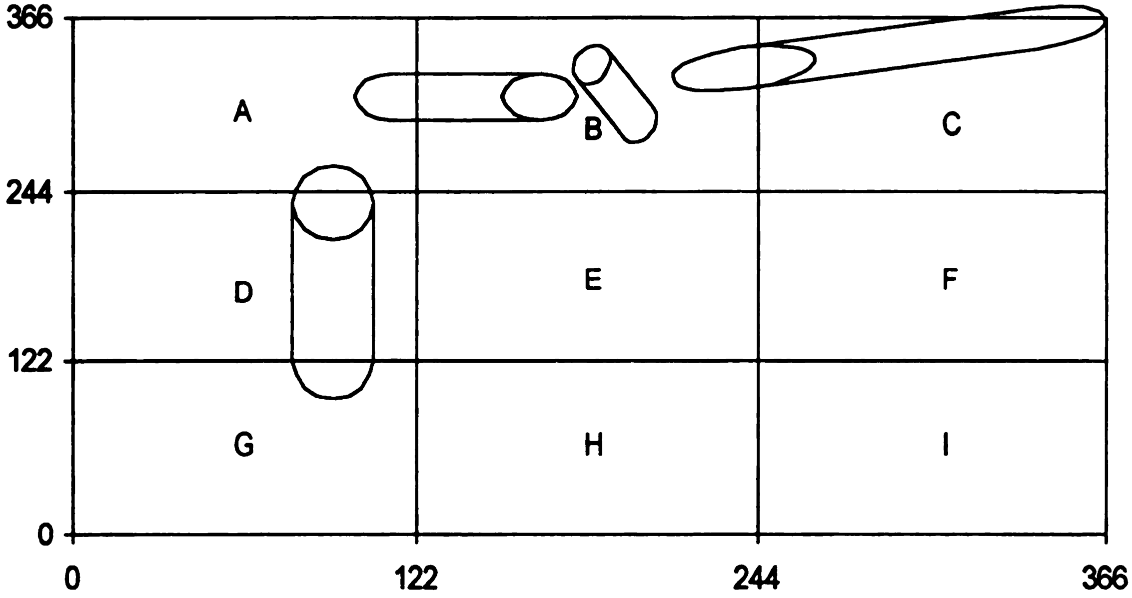

Figure 4. A map of plot two (366 cm by 366 cm) illustrating the location of rotting logs within the plot as well as the division of the plot into nine sub-areas (labeled A through I).

409

27

1

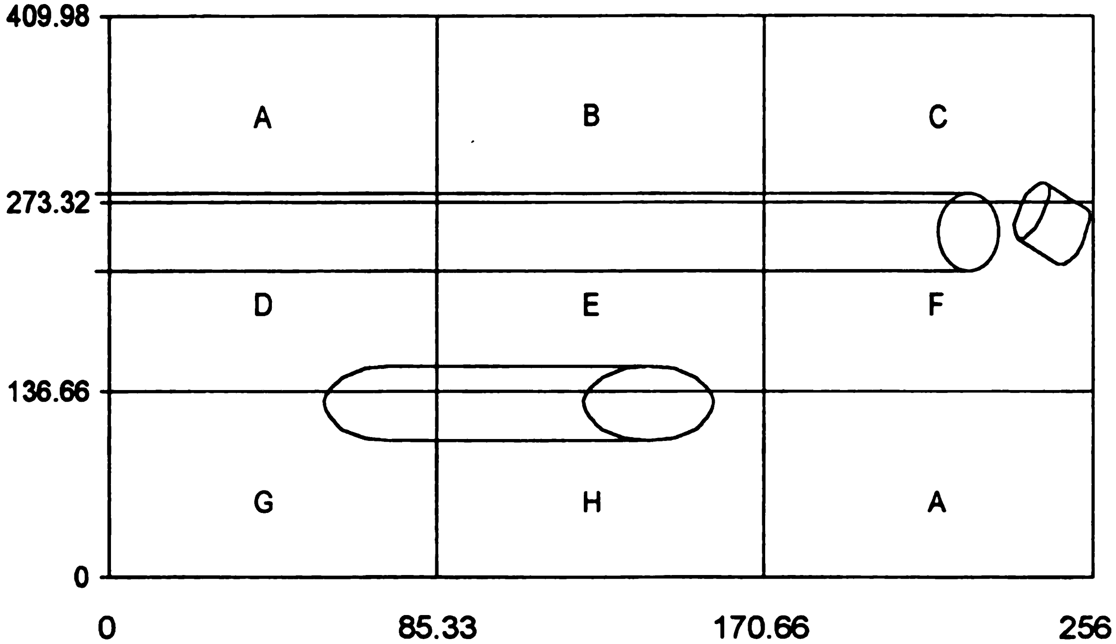

Figure 5. A map of plot three (256 cm by 410 cm) illustrating the location of rotting logs within the plot as well as the division of the plot into nine sub-areas (labeled A through I).

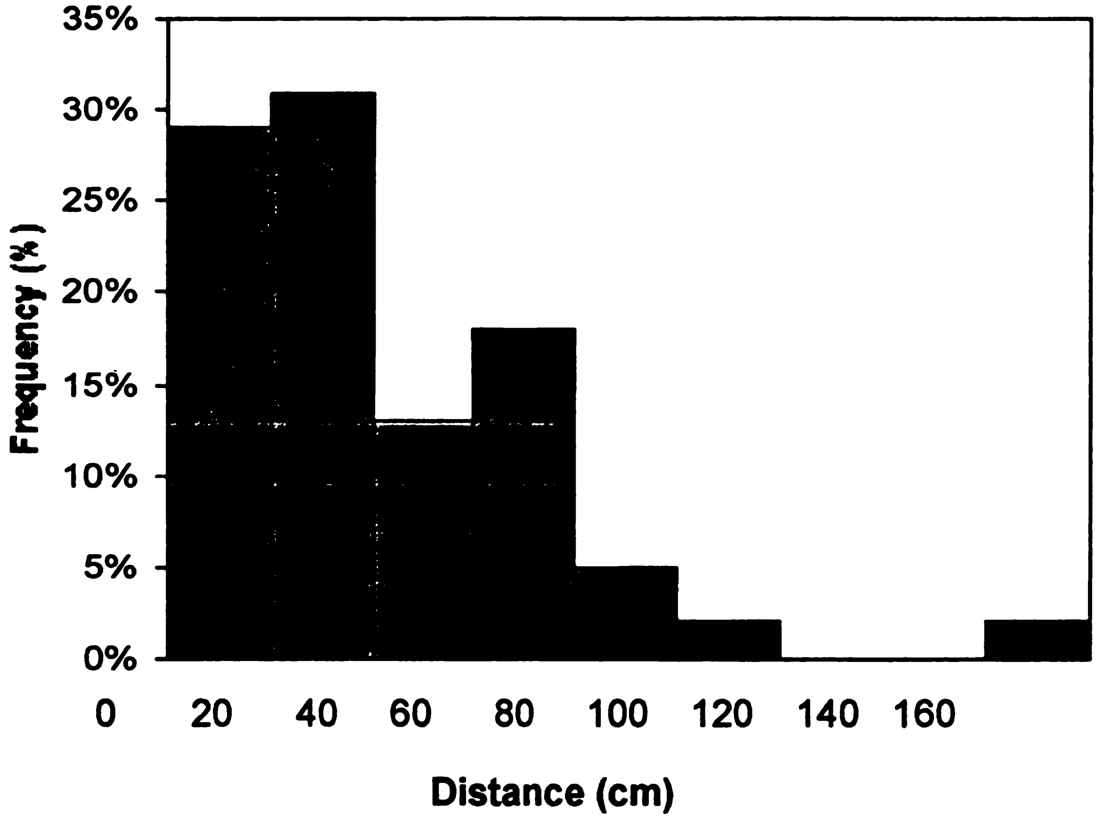

Figure 6. Frequency distribution of distances moved per one-day interval by *Anguispira alternata*. A logistic function was fitted to the distribution: $y=-0.1582\mathrm{Ln}(x)+.3362$, $r^2=5.36$, d.f.=5, $P<0.005$.

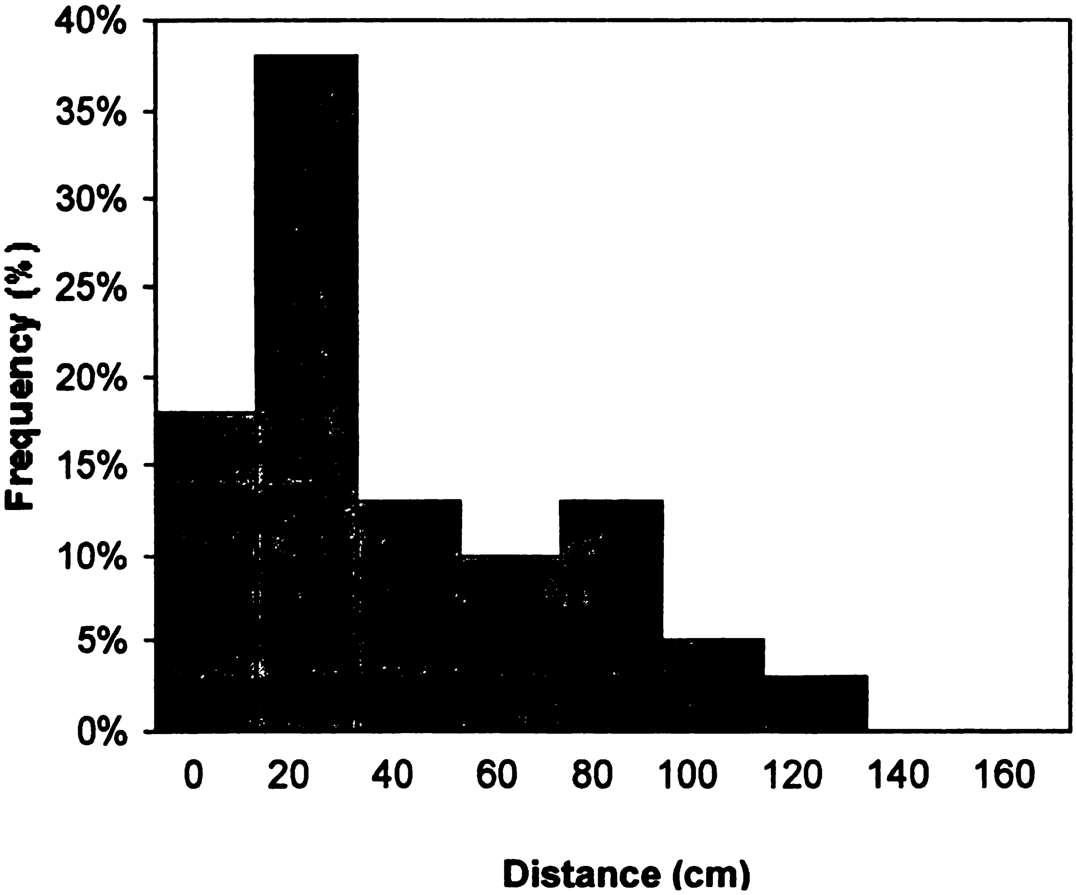

Figure 7. Frequency distribution of distances moved per two-day intervals by *Anguispira alternata*. A logistic function was fitted to the distribution: $y=-0.1257Ln(x)+0.29$, $r^2=0.5796$, d.f.=5, t=2.63, $P<0.025$.

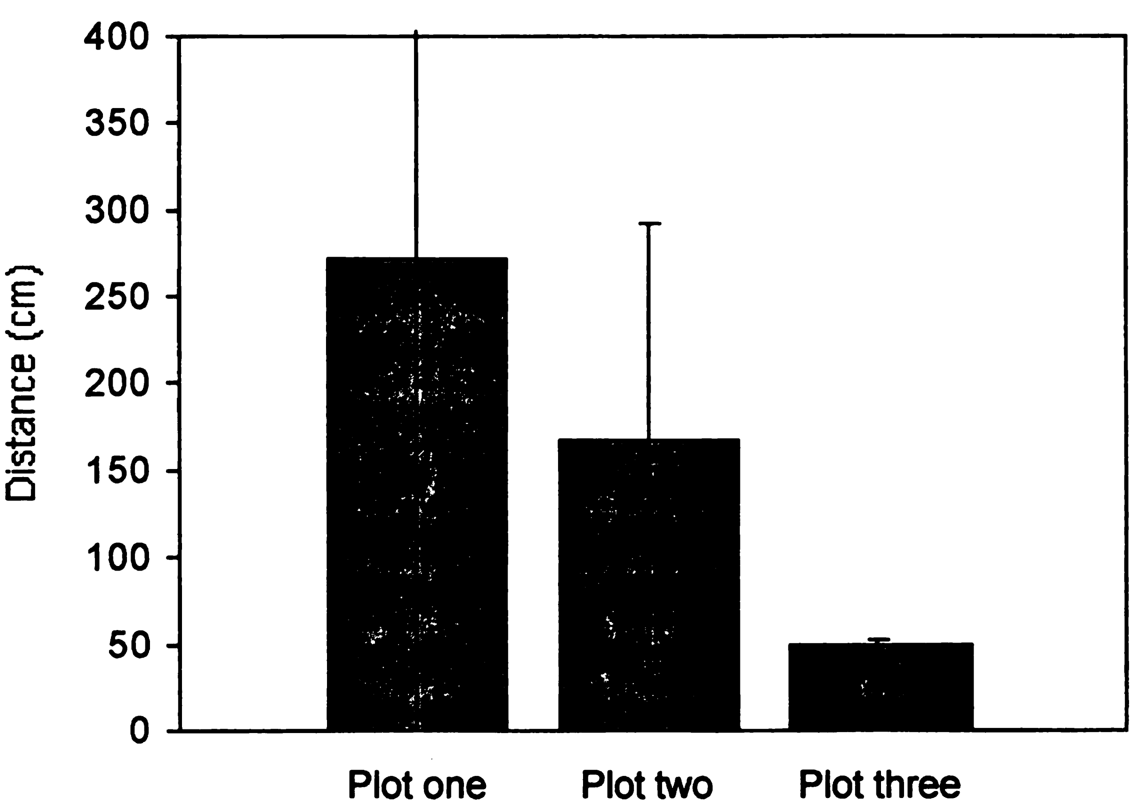

Figure 8. Mean one-day distance moved by *Anguispira alternata* in plots one, two and three (One-way ANOVA, n=56, F=3.736, P=0.0256).

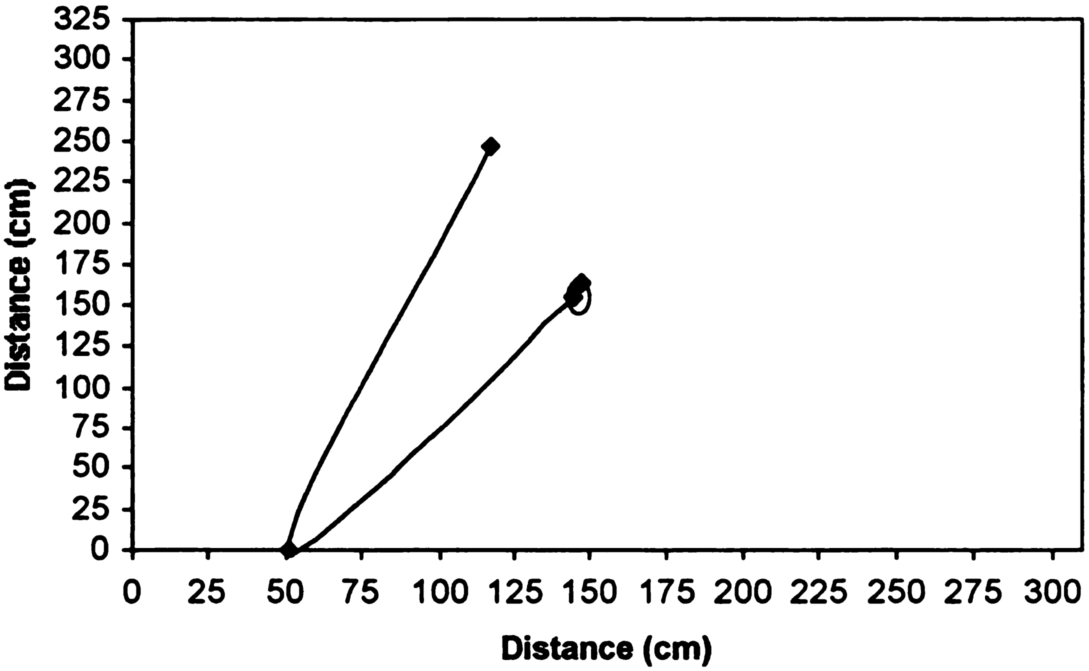

Figure 9. Representative movement tracks of snail #107 within plot one. All points indicate the actual location of recapture. The starting point is circled.

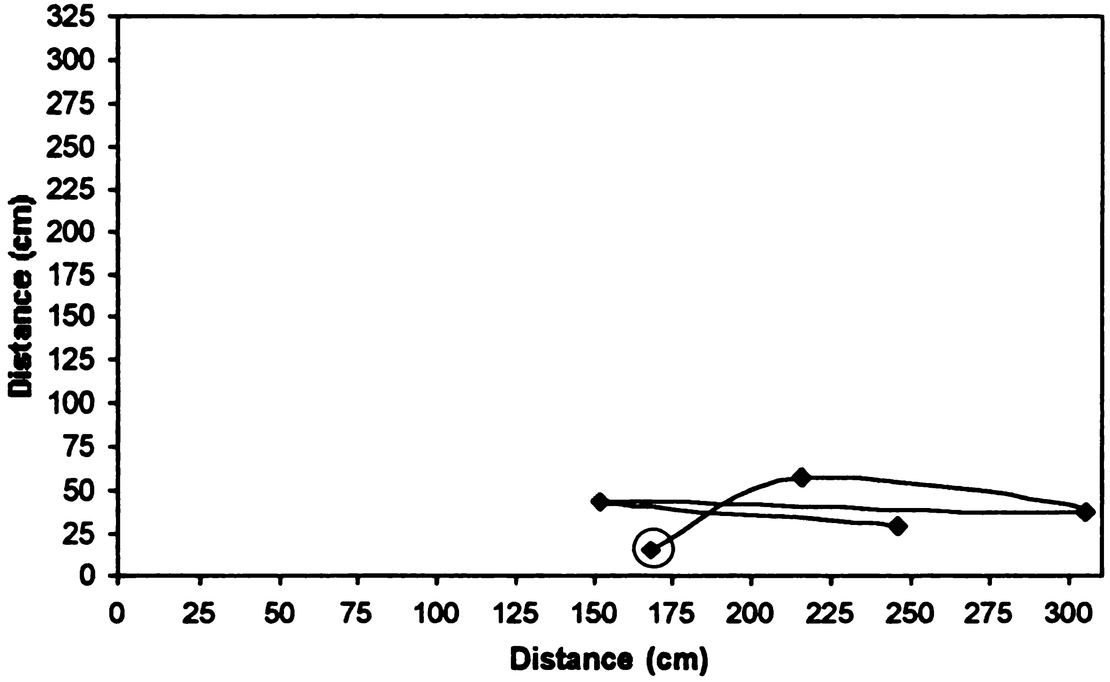

Figure 10. Representative movement tracks of snail #114 within plot one. All points indicate the actual location of recapture. The starting point is circled.

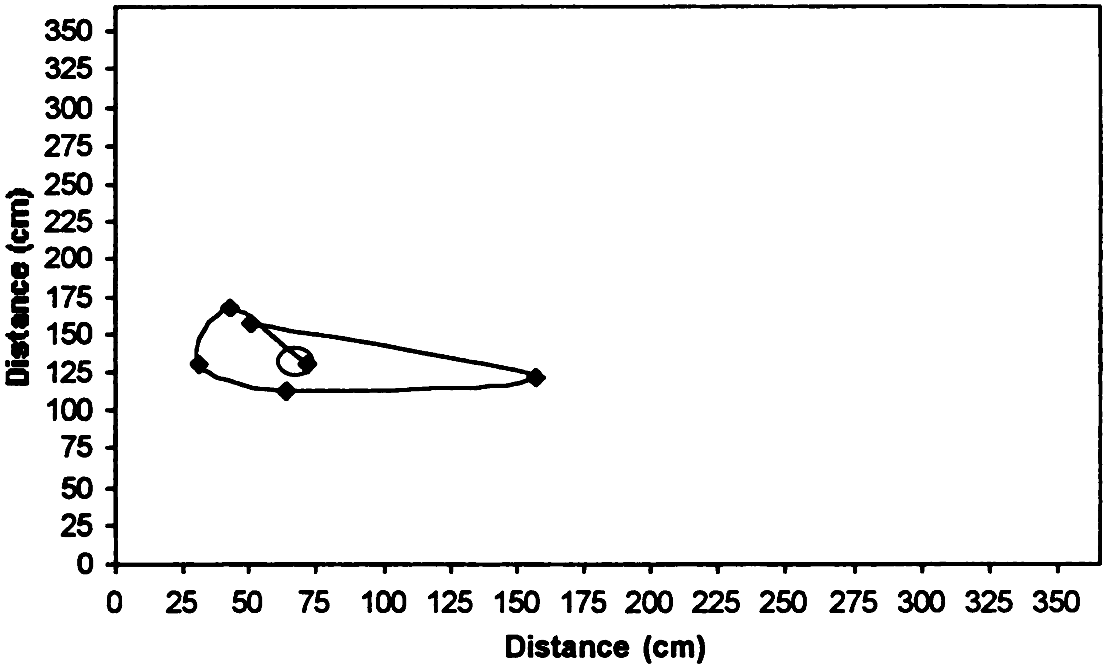

Figure 11. Representative movement tracks of snail #201 within plot two. All points indicate the actual location of recapture. The starting point is circled.

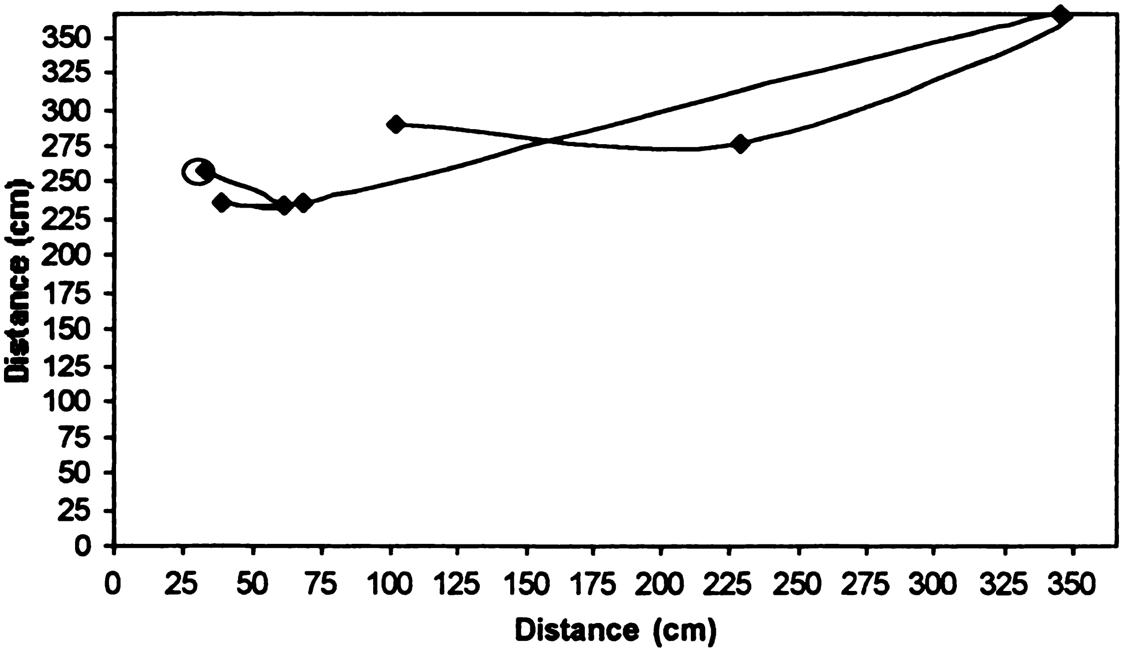

Figure 12. Representative movement tracks of snail #210 within plot two. All points indicate the actual location of recapture. The starting point is circled.

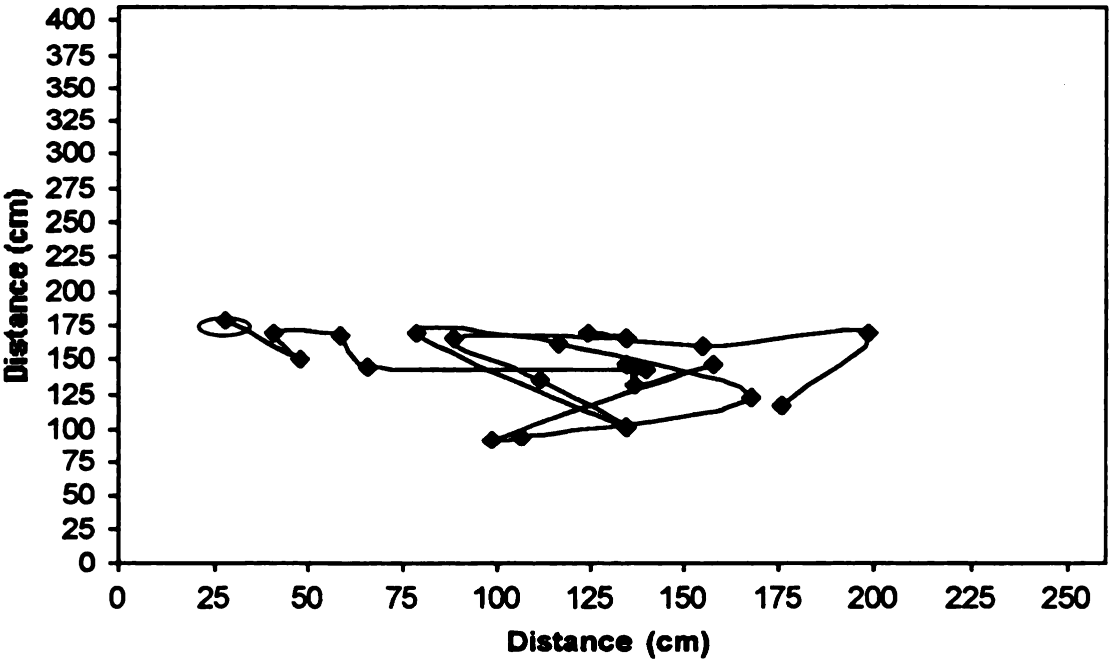

Figure 13. Representative movement tracks of snail #302 within plot three. All points indicate the actual location of recapture. The starting point is circled.

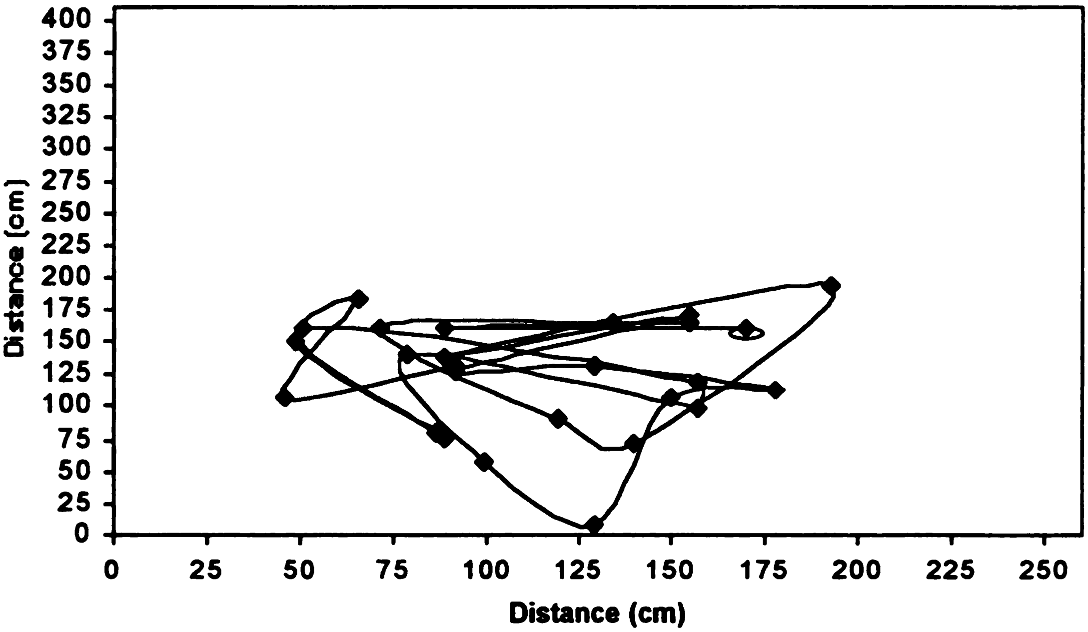

Figure 14. Representative movement tracks of snail #307 within plot three. All points indicate the actual location of recapture. The starting point is circled.

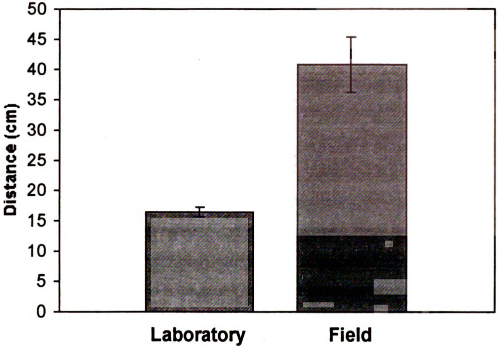

Figure 15. ANOVA comparison of mean one-day distance traveled of *Anguispira alternata* in the laboratory and field: n=622, F=8.374, P<0.001.

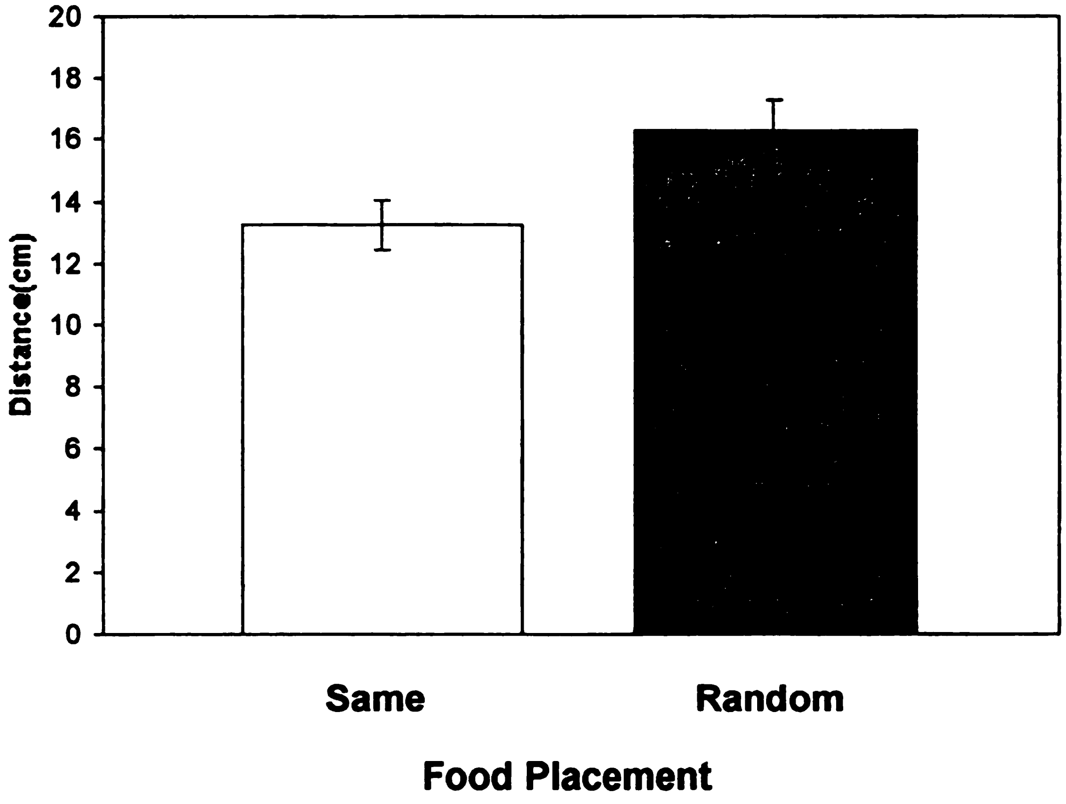

Figure 16. ANOVA comparison of food placement versus one-day distance traveled in the laboratory: n=566, F=5.697, P=0.017.

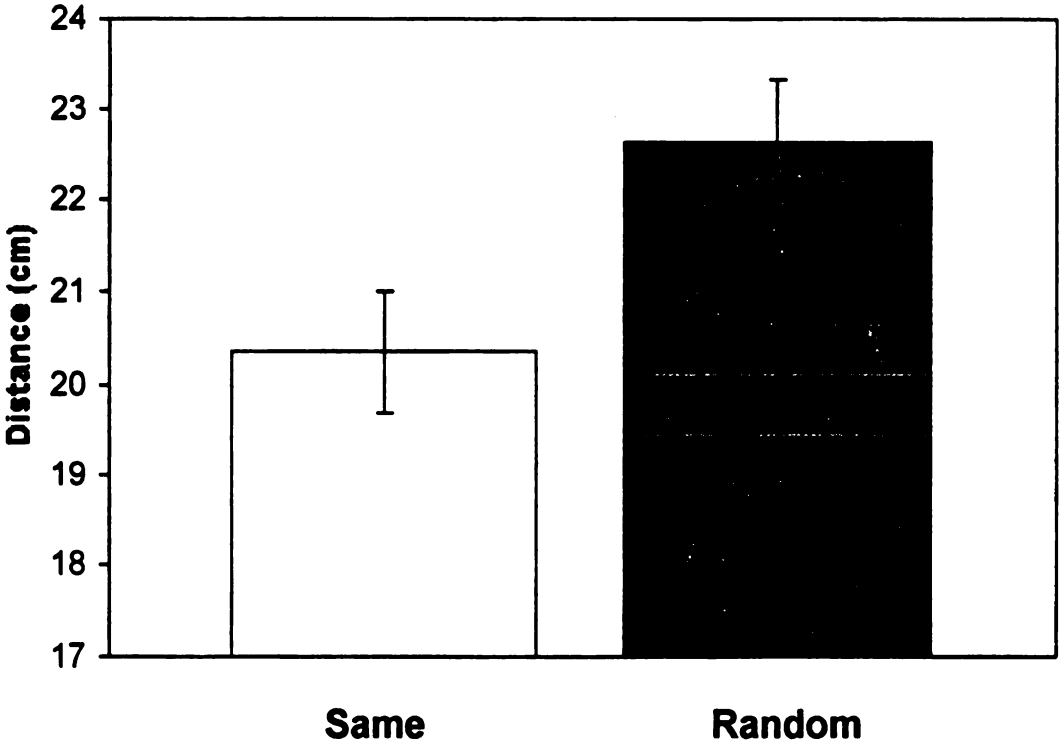

Figure 17. ANOVA comparison of feeding type versus mean distance from food in the laboratory: n=1010, F=5.711, P=0.017.

LITERATURE CITED

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Batschelet, E. 1981. *Circular Statistics in Biology*. Academic Press, London.

Baur, A. and Baur, B. 1988. Individual movement patterns of the minute land snail *Punctum pygmaeum* (Draparnaud) (Pulmonata:Endodontidae). The Veliger, 30:372-376.

Baur, A. and Baur, B. 1993. Daily movement patterns and dispersal in the land snail *Arianta arbustorum*. Malacologia, 35: 89-98.

Burch, J.B. and Jung, Y. 1988. Land snails of the University of Michigan biological station area. Walkerana, 3:1-177.

Cameron, R.A.D and Williamson, P. 1977. Estimating migration and the effects of disturbance in mark-recapture studies on the snail *Cepea nemoralis L.* Journal of Animal Ecology, 46:173-179.

Carew, T.J. and Sahley, C.L. 1986. Invertebrate learning and memory: from behavior to molecules. Annual Review of Neuroscience, 9:435-487.

Chase, R., Pryer, K., Baker, R. and Madison, D. 1978. Responses to conspecific chemical stimuli in the terrestrial snail *Achatina fulica* (Pulmonata: Sigmurethra). Behavioral Biology, 22:302-315.

Cook, A. 1979. Homing by the slug *Limax pseudoflavus*. Animal Behavior, 27:545-552.

Cowie, R.H. 1980. Observation on the dispersal of two species of British land snail. Journal of Conchology, 30:201-208.

Dobzhansky, T. and Wright, S. 1943. Genetics of Natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. Genetics, 28:304-340.

Edalstam, C. and Palmer, C. 1950. Homing behavior in gastropods. Oikos, 2:259-270.

Elwell, A.S. and Ulmner, M.J. 1971. Notes on the biology of *Anguispira alternata* (Stylommatophora:Endodontidae), Malacologia, 11:199-215.

Etienne, A.S., Maurer, R., Georgeakopoulos, J. and Griffin, A. 1999. Dead reckoning (path integration), landmarks and representation of space in a comparative perspective. In R.G. Golledge (ed.), *Wayfinding Behavior: Cognitive*

Mapping and Other Spatial Processes (pp197-228). The Johns Hopkins University Press, Baltimore.

Gelperin, A. 1974. Olfactory basis of homing behavior in the giant garden slug, *Limax maximus*. Proceedings of the National Academy of Sciences, 71:966-970.

Golledge, R.G. (ed). 1999. *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes*. The Johns Hopkins University Press, Baltimore.

Hansson, L. 1991. Dispersal in the edible land snail, *Helix pomatia*: a test case for present generalizations. Acta Ecologica, 12: 761-769.

Hubricht, L. 1985. The distributions of the native land mollusks of the eastern United States. Fieldiana, N.S. 24:1-191.

Ingram, W.M. and Adolph, H.M. 1943. Habitat observations *of Ariolimax columbianus*. The Nautilus, 56:96-97.

Jessee, W.F. 1968. Studies of homing behavior in the limpet *Acmaea scabra*. The Veliger (suppl.), 11:52-55.

Lind, H. 1989. Homing to hibernating sites in *Helix pomatia* involving detailed long-term memory. Ethology, 81: 221-234.

Mather, J.A. 1991. Navigation by spatial memory and use of visual landmarks in octopuses. Journal of Comparative Physiology (A), 168:491-497.

Papi, F (ed.). 1992. *Animal Homing*. Chapman and Hall, London and New York.

Pollard, E. 1975. Aspects of the ecology of Helix pomatia L. Journal of Animal Ecology, 44:305-329.

Rollo, C.D. and Wellington, W.G. 1981. Environmental orientation by terrestrial Mollusca with particular reference to homing behavior. Canadian Journal of Zoology, 59:225-239.

Russell, G.S. and Levitin, D.J. 1997. An expanded table of probability values for rao's spacing test. [online] Available http://cm.stanford.edu/~levitin/AnExpand.htm , May 8, 1999.

Southwick, C.H. and Southwick, H.M. 1969. Population density and preferential return in the giant African snail *Achatina fulica*. American Zoologist, 9:566.

Tinbergen, N. 1958. Curious Naturalists. Basic Books, Inc., New York.

With, K.A. and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology, 76:2446-2459.