1982

Band pattern in Helix Aspersa: Variation, selection and microgeographic distribution

John. Elliott

BAND PATTERN IN *HELIX ASPERSA*: VARIATION, SELECTION AND MICROGEOGRAPHIC DISTRIBUTION

A Thesis

Presented to the

Faculty of

California State

College, San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

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ABSTRACT

Band pattern of the Helicid land snail *Helix aspersa* was studied in a one hectare area in Sacramento, California. Variations in band number, fusion, color intensity and width are described. Analysis of pattern frequencies found at seven collecting sites in the area shows pattern frequencies are not independent of collection site. Selection does not appear to account for differences in pattern frequencies. Genetic drift and founder effects are postulated as the source of differences in pattern frequencies. Experiments with populations of *H. aspersa* in enclosures placed in the study area showed survival was related to density, microhabitat and vegetation. High temperatures appeared to be the cause of death in the experimental populations. Band patterns lacking bands suffered higher mortality. It is postulated the disadvantage of this pattern type in hot weather is compensated by advantage in the juvenile stage during cool weather.

ACKNOWLEDGEMENTS

I wish to thank Jerry Clark, Caltrans Landscape Supervisor, for his assistance at the field site and knowledge of its landscaping history. Earl Purdue assisted in construction of the experimental enclosures. I greatly appreciate the efforts of Drs. Harrington, Sokoloff and Wilson in critically reading the manuscript and for giving cogent advice.

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INTRODUCTION

Polymorphism in shell color and band pattern has been studied in several land snails (Cain and Sheppard 1950, Komai and Emura 1955, Owen 1963, Cook and King 1966). *Cepaea nemoralis* L. and *Cepaea hortensis* Muller, common in England and Europe, have received considerable attention and differences in morph frequencies have been attributed to predator selection (Cain and Sheppard 1954), genetic drift (Goodhart 1962, 1964), environment gradients (Day and Dowdeswell 1968), colony size (Brussard 1974) and climatic selection (Jones 1973, Richardson 1974).

The banding pattern of *Helix aspersa* Muller, a snail introduced in cultivated areas of the Western United States (Hanna 1966), has not been well studied and little is known of its ecological genetics. Pilsbry (1939) describes "band types" and shell size for several locations in the United States and California. He describes the "typical" shell found at a location but does not give other types present or frequencies. Gammon (1943) describes the "typical band pattern" of *H. aspersa* and states that many variations from typical banding occur. Yet he does not describe them except the fusion of all five bands.

Potts (1972, 1975) studied the selective impact of favorable and unfavorable environments on populations of *H. aspersa* near Santa Barbara, California. In his study he defined favorable environments as those under active cultivation and unfavorable environments as those previously cultivated, but neglected at the time of study, or those never under active cultivation. He determined that greater numbers of *H. aspersa* in unfavorable environments had darker bands than those in favorable environments and that shells of the same size were heavier when collected from unfavorable environments. He did not find a difference in frequency of band fusions or number of bands. Though he did not present statistical data he stated that *H. aspersa* from unfavorable environments show greater contrast between band pigment and shell color and tend to have broader bands than *H. aspersa* in favorable environments.

Breeding experiments reported by Stelfox (1915, 1918), Diver (1932) and Cook (1969) reveal the presence in *H. aspersa* of recessive genes for albino shell and pale bands and three dominant genes; one which delays banding until the shell is 10 mm in size, another which removes pigment from bands 2, 3 and 4, and one for white shell color. The importance of these genes in *H. aspersa* populations is left untouched by these authors.

The study being reported here was undertaken to describe the band patterns of *H. aspersa* shells found in a one hectare study area located in Sacramento, California. An attempt will be made to demonstrate that frequencies of band pattern types are not associated with changes in habitat in the study area and are best explained by the founder effect and genetic drift. Evidence will also be presented to show selection against certain morphs by climatic factors.

METHODS AND MATERIALS

The brown garden snail, *Helix aspersa* Muller, was first described from the Mediterranean area and has since spread throughout the world (Pilsbry 1939, Gammon 1943). Its introduction to new localities has either been deliberate by epicures or unintentional as a contaminant on nursery stock (Mead 1971). It was first reported in the United States in New Orleans, Louisiana and Charleston, South Carolina by Binney (1851). The first report in California was made by Sterns (1881).

The introduction into California was intentional and made by Mr. A. Delmas of San Jose who brought *H. aspersa* from France and released them in vineyards in the west bank of the Guadalupe River about 1858 (Sterns 1881, 1900). *H. aspersa* was subsequently reported in Pacific Grove by Keep (1899), Oakland and Los Angeles by Sterns (1900), La Jolla by Smith (1907), and Redlands by Berry (1909). It was not likely all of these populations were from the San Jose stock, but represented several introductions (Sterns 1900, Hanna 1931). By 1932 *H. aspersa* was so widespread that no attempt was made to eradicate the species by the State of California Department of Agriculture (Gammon 1943).

The northernmost collection of *H. aspersa* on the west coast is Seaview, Washington (Hanna 1966) and

H. aspersa is found in gardens in Utah (Knight 1952) and Arizona (Mead 1951). *H. aspersa* is usually associated with active cultivation, though it has been found in uncultivated habitats (Hanna 1966, Potts 1975).

Helix aspersa grows to 38 mm in shell diameter and 33 mm in shell height. The shell is obliquely globose and covered by a yellowish-brown periostracum. There are four and one-half whorls which are banded parallel to the whorls with five chestnut-brown to chocolate bands. Bands 2 and 3 are often fused. Band color is melanotic and chemically associated with the shell protein conchiolin (Comfort 1951). The bands are often interrupted by lightly colored flecks or streaks. The embryonic one and one-half whorls are smooth and the rest striate. The last whorl is coarsely wrinkled and descends in front. The lip is reflexed in mature snails. The shell thickens with age (Diver 1932). Shell thickness is related to calcium supply in the soil and rate of growth (Hunter 1941, Wagge 1952). Body color is light to dark gray.

The principal study area is located at the junction of highways 90, 99 and 50 near Broadway and 19th Street in Sacramento, California. A freeway loop interchange provides several vegetated areas relatively isolated from surrounding neighborhood gardens. The area selected is roughly triangular in shape and about one hectare in size (Figure 1).

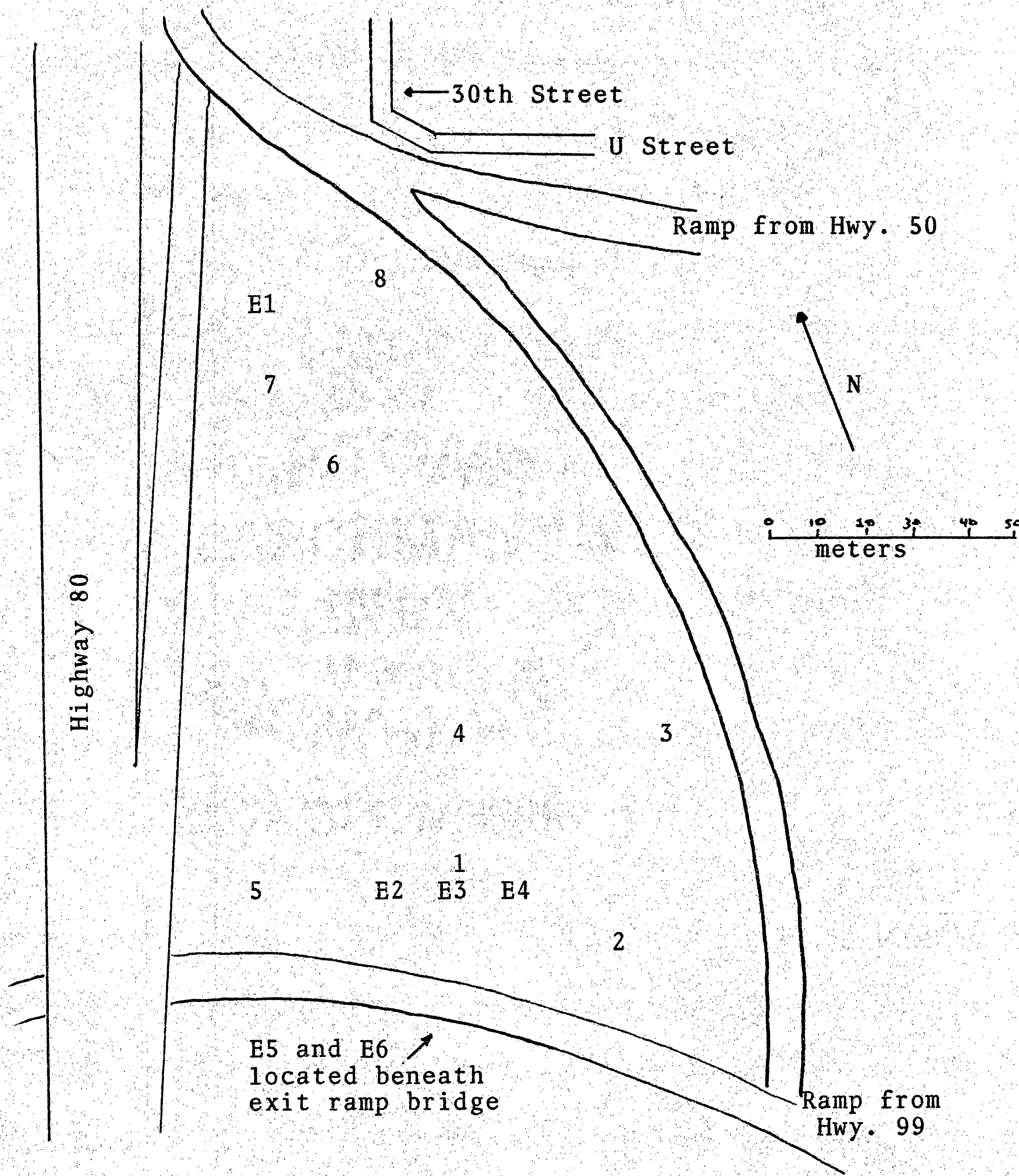

FIGURE 1. Location of study area, collection sites and enclosures at the junction of highways 80, 99 and 50, Sacramento, California. Numbers preceded by a capital E are enclosures.

An encroachment permit was obtained from the Department of Transportation, State of California and work was carried out during the spring and summer of 1978. Access to the site was made from the corner of "U" and 30th Street.

Vegetation is primarily *Carpobrotus edulis* (L.) N.E.Br., commonly known as Hottentot-fig or ice plant. Originally planted in 1970, it suffered from a severe frost during the winter of 1972-1973. Its cover is variable --at some spots thick and lush, while at others sparse and low growing.

Also present as ground covers are *Vinca major* L. and *Hypericum calycinum* L. Trees present are *Prunus serrulata* Lindl., *Sequoia sempervirens* Endl., *Betula pendula* Roth., and *Liquidambar styraciflua* var. *macrophylla* Ndz.

Helix aspersa has been noted in the area by Caltrans personnel since 1975. It may have been present but unnoticed before that date. In 1978 damage to the vegetation was extensive enough to cause concern to Caltrans personnel. No attempt has been made at any time to control the snail population in the study area with poisonous baits (Jerry Clark, Caltrans, pers. com.).

Climate in the area is generally mild (NOAA report 1978b). Precipitation occurs mostly from November to March with an annual mean of 43.3 cm. Mean maximum temperatures during July and August, the two warmest months, are 33.8°C and 33°C, respectively. Even when daytime temperatures occasionally exceed 39°C the nights cool to below 20°C. Extermely low relative humidity accompanies high temperatures. Minimum temperatures are reached in December and January with means of 3.4°C and 2.9°C, respectively. The study area receives daily watering by Caltrans personnel during the summer months.

In April, 1978, *H. aspersa* were collected at seven sites within the study area (Figure 1). Sites were selected for differences in vegetation and distance from each other. Notes on the vegetation were made, recording species present, height and estimation of percent cover.

At each site 100 snails were collected without preference to size or maturity. They were transported to the lab in plastic bags, frozen for two days, thawed and the bodies removed with forceps. The density of *H. aspersa* at each site was recorded at time of collection.

In addition, a collection was made at the Jefferson Avenue off-ramp and Highway 80 in West Sacramento, 5.6 kilometers from the main study site. This collection will be referred to as WS.

In the lab, banding patterns were determined. Patterns of snails under 1 cm were not classified because their shells are fragile, often being destroyed when the body is removed, and band pattern is often delayed in young snails under 1 cm (Cook 1969). For collections numbered 5, 6, 7 and WS, 75 snails from each group were randomly selected for classification. Within each group shells were segregated into two size classes; 10 mm to 19 mm, and 20 mm and larger. Adults were noted by placing a capital L after the measurement.

Bands were assigned consecutive numbers with band number 1, the first formed, at the top of the shell whorl (Figure 2). If bands were fused they were bracketed together and if a band was missing a zero was put in place of the band number. The configuration 1(23)05 would indicate fusion of bands two and three and a missing band four.

Banding pattern was determined while looking down on the body whorl of the shell. Fusions at the adult lip were ignored. It was sometimes easier to determine absence or fusion of a band by tracing it from the beginning whorl.

Bands were marked absent if they were not apparent. This included bands without pigmentation but with a textural difference in shell when held to light. The overall band color intensity of each shell was rated as standard, pale or dark by comparing each shell to a set of *H. aspersa* shells selected for varying band color intensity.

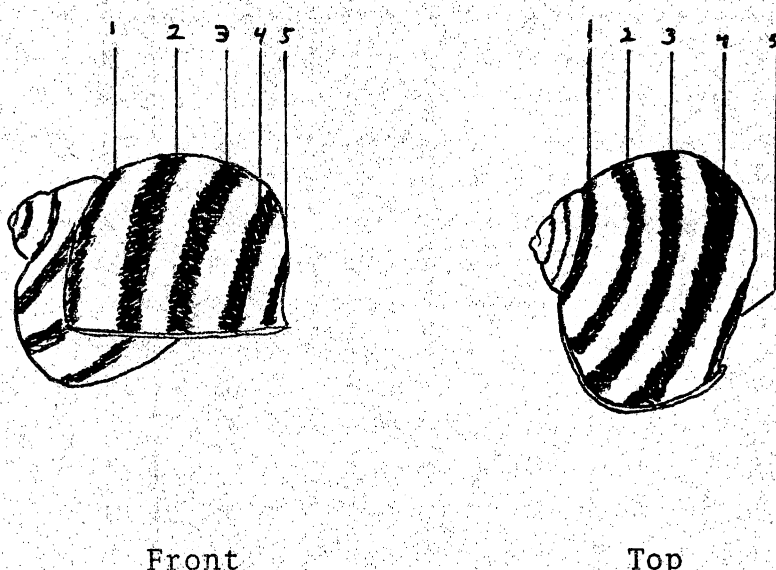

Figure 2. Method of numbering bands on *Helix aspersa* shell.

Band width and space between bands were measured with vernier calipers 1 cm behind the lip. Though not an absolute measurement of band width, ratios of band to interband measurements provide a comparison of shell types and an indication of shell appearance which could not be gained merely by listing presence or absence of bands.

Band width measurements were made on 36 shells from collection 8 (Figure 1) gathered for this purpose. Shell diameters range from 21 mm to 28 mm. Most are near 25 mm. The area between the 5th band and shell lip is rarely visible when viewing a shell from the top (Figure 2). For this reason the ratio of band to interband has been calculated twice -- both including and excluding the measurement from the 5th band to the lip.

Band pattern data were analyzed to determine significant differences in morph frequencies between collections. An RxC test of independence using the G-test as outlined by Sokal and Rohlf (1969a) was utilized. The G-test is similar to a chi-square test and is referred to as a likelihood ratio test. It provides a less tedious evaluation of a large number of rows and columns and is more exact than the chi-square test. The computation of the G-statistic is as follows:

G = 2 (sum of f ln f of frequencies in each cell of the table - sum of f ln f of column sums of frequencies - sum of f ln f of rows sums of frequencies + f ln f of total number of items in the table)

The transformations can be found in a table provided by Sokal and Rohlf (1969b). Degrees of freedom are calculated as:

df = (a-1) x (b-1)

where a is the number of rows and b the number of columns. The G-statistic is compared to a chi-square distribution to determine significance.

A computer program for the RxC test of independence is provided by Sokal and Rohlf (1969a). This program was utilized to test subsets of the data for homogeneity between collections. Subsets produced by the program are termed maximum homogeneous subsets. Addition of one more row (band type) or column (collection site) to each subset produces a significant heterogeneous set. The maximum homogeneous subsets can be analyzed to determine if one, two or several collections contribute to heterogeneity. A maximum homogeneous subset is to be considered as insufficient evidence of heterogeneity -- not as proof of homogeneity.

Two computer runs of this program were made by McDonnell Douglas Automation Company, Saint Louis, Missouri, on an IBM 370 Computer with MVS system. The first run was with data from both size classes. The second run was with data from the 20 mm+ size class. All collections, including WS, were included in these runs and significance level was set at 0.05.

Additional computer runs of this program were made at Washington University, Saint Louis, Missouri on an IBM 4341 computer. The WS data were not included and significance level was set at 0.01. Other computer runs discussed in this report were made on computer facilities at Washington University, Saint Louis, Missouri.

A partition of the data was made to test the independence of morph frequencies at collection sites with similar habitat. Collections 1, 2, 7 and WS were collected in habitats of *C. edulis*, 100% cover, height 30 to 32 cm and level ground. Using data from these collections, computer runs of the RxC test of independence were made for both size classes combined at significance level 0.01 and for the 20 mm+ size class at significance levels 0.05 and 0.01.

Selander and Kaufman (1975) indicate a minimum distance of 25 meters between breeding demes of *H. aspersa*. Data from collections within 25 meters of each other were pooled and an R x C test performed on the resulting set.

Collections were arrayed in order of decreasing frequency of the most common type, 1(23)45, the second most common type, 12345, decreasing frequency of fusions and decreasing frequency of rare types. These arrays were then compared with changes in height of vegetation, percent cover and diversity of habitat. Diversity of habitat was ranked by considering number of plant species present, cover, and amount of leaf vegetation as opposed to stem vegetation.

To determine the possible relationship of banding pattern to survivorship, enclosures were constructed and individual snails observed from April to September 1978.

The enclosures were circular, with an area of 0.5 m^2. They were constructed of an aluminum base 20 cm high with copper wire mesh cloth 16 cm high attached at the top. Pop rivets were used to attach the copper cloth to the aluminum base and secure the enclosure as a circle. The aluminum base was flashing obtained at a hardware store. The copper mesh cloth was obtained from Flynn and Enslow, Inc., San Francisco, California. Except for the first cage the copper mesh cloth was folded inward twice to form an overhanging lip. The enclosures were buried at least 5 cm in the ground when installed.

Potts (1972), following procedures developed first by Moen et al (1967), used a copper mesh fence to enclose a large area (20 m^2) without loss of the enclosed snails. Recognizing that my enclosures were considerably smaller, I tested snails against the copper mesh in the lab. Most snails showed distress in less than a minute after climbing upward 2 to 3 cm on the mesh cloth. They then turned downward and away from the copper cloth.

Six enclosures were placed in the study area (Figure 1). Enclosure 1 was installed in early April, 1978, in a thick growth of *C. edulis*. All snails found inside the enclosure were removed, their shell diameters measured and returned to the cage. The snails were again removed and measured on May 5, May 24, June 23, and September 22, 1978.

Enclosures 2, 3 and 4 were placed in thick growths of *C. edulis* in late April, 1978. One hundred fifty *H. aspersa* were placed in enclosure 2, fifty in enclosure 3, and 20 in enclosure 4.

Enclosures 5 and 6 were located in full shade under an overpass. The height from ground level to the bottom of the overpass is 1.6 meters. Enclosure 5 was in *H. calycinum* and enclosure 6 was in sparse, low growing *C. edulis*. Enclosures 5 and 6 were started with 15 snails each on April 24, 1978. Enclosures 5 and 6 did not receive moisture until a rainbird was installed by Caltrans personnel in late May, 1978.

Twenty snails in enclosure 1, twenty in enclosure 2, ten in enclosure 3 and fifteen in enclosure 4 were tagged with numbered wire code markers overpainted with dekophane technical cement in the manner described by Potts (1972).

All snails were removed, measured and returned in enclosures 2, 3, 4, 5 and 6 on May 5, May 24, June 23, August 28 and September 22, 1978. Whenever the enclosures were searched empty shells were removed, measured and dated. On September 22 the surviving snails were collected, transported to the lab, killed and the shells prepared as previously described.

Measurement of shell diameter was made with a vernier caliper. The instrument has precision to 0.05 mm. Due to the difficulty of measuring a large number of live snails in the field, sometimes under adverse conditions, great accuracy was not expected. Measurements in the field were recorded in size classes varied by 0.5 mm.

Searching the enclosures presented some problems. I wanted to disturb the habitat as little as possible. This prevented finding every snail during each search. On three occasions I crushed small snails by movement of the vegetation. These snails were not counted in mortality statistics.

Band patterns and color intensity of bands for all snails within the six enclosures were determined at the end of the experiment. R x C tests of independence were performed by computer to demonstrate the relationship of mortality to band pattern type, band color intensity, density in enclosures, and size class. The association of band color intensity with band pattern and size class was also tested. In a 2 x 2 test, such as in a mortality/size class test of independence, Yates correction for continuity was applied.

Density sampling was made in the area on a monthly basis from February 1978 to September 1978. A hoop with an area of .25 m^2 was constructed from 9 gauge wire joined with a copper tube coupling filled with solder. This was tossed into vegetation at the sampling location and all *H. aspersa* within the hoop were removed and counted. Three samples were taken at a time and averaged.

Four samples of *H. aspersa* were taken outside the enclosures late in the summer. Both live snails and empty shells were collected. These samples were analyzed to determine if differential mortality of band types occurred outside the enclosures.

RESULTS

Scoring of band pattern morphs presented some difficulties. The yellowish periostracum may obscure extremely faint pigmentation in the band area. Alternately, textural differences may create the appearance of a band where pigmentation is lacking. Scoring of fusion is also made difficult by mottling, which sometimes gives the appearance of separating bands which otherwise are fused. These difficulties are not unique to *H. aspersa* but are a factor in scoring band patterns of other Helicid snails (Cook and King, 1966).

The bands of *H. aspersa* shells were found to vary in number and fusion of bands, band width, intensity of band color and continuity or degree of fusion.

When fusions are not complete pigmentation is paler near the join. Pigmentation intensity along a band sometimes varies and intensity may be related to growth rate. Where growth appears to have been interrupted pigmentation may be darker, giving a blotched appearance. Resumed growth may have darker or paler bands. In juveniles pigmentation of bands 4 and 5 may be less intense than bands 1, 2 and 3. This is rarely seen in adults. The band pattern is interrupted by shell damage and repair.

Background color is usually white and is not developed well in juveniles which tend to a transparent background. The background may be tinged with cinnamon or pinkish colors. It is nearly always covered by the yellow-brown periostracum and for this reason background color is not easily determined in juvenile and young adult snails.

Ratios of band and interband widths are presented in Table 1. Measurements are presented in Appendices 1 and 2. Band width, as would be expected, generally increases with increases in shell diameter. In 14% of the shells examined a narrow (0.5 mm - 1 mm) strip of background color is visible between the body whorl (being scored) and the previous whorl, but usually band 1 adjoins the preceding whorl. Band 1's ratio to total band color is .208 in type 12345. This ratio decreases as fusions increase.

Bands 2, 3 and 5 are slightly narrower than band 1 and band 4 is broader. I have distinguished two types of band pattern 1(23)45 based on the width of band 4 and the distance between bands (23) and 4. The first type, 1(23)45A, has a narrow band 4 (about 22% of band total) and a distance roughly equal to band 4 between bands (23) and 4. The second type, 1(23)45B, has a wider band 4 (33% of total) and a narrow (1 mm) distance between bands (23) and 4. These differences make them easily distinguishable as 1(23)45A appears striped and 1(23)45B appears more solidly colored. In type 1(23)45B band 4 is nearly as broad as fused bands (23). These and other band types are illustrated in Figure 3.

TABLE 1. Ratios of individual band width to total band width and total band width to body whorl in 8 band patterns of *H. aspersa*. The ratio of total band width to the visible body whorl when viewed dorsally is also given.

Pattern 12345

Band	1	2	3	4	5
Band/Total Band	.208	.192	.167	.258	.175
Total Band/Whorl		.408			
Total Band/Visible Whorl		.571			

Pattern 1(23)45A

Band	1	(23)		4	5
Band/Total Band	.187	.438		.219	.156
Total Band/Whorl		.451			
Total Band/Visible Whorl		.627			

Pattern 1(23)45B

Band	1	(23)		4	5
Band/Total Band	.156	.347		.329	.168
Total Band/Whorl		.568			
Total Band/Visible Whorl		.773			

Pattern (123)45

Band	(123)			4	5
Band/Total Band	.641			.205	.154
Total Band/Whorl		.544			
Total Band/Visible Whorl		.761			

Pattern (1234)5

Band	(1234)				5
Band/Total Band	.805				.195
Total Band/Whorl		.694			
Total Band/Visisble Whorl		.924			

Pattern 1(23)(45)

Band	1	(23)		(45)	
Band/Total Band	.142	.344		.514	
Total Band/Whorl		.698			
Total Band/Visisble Whorl		.910			

Pattern (123)(45)

Band	(123)			(45)	
Band/Total Band	.481			.519	
Total Band/Whorl		.750			
Total Band/Visible Whorl		.986			

Pattern (12345)

Band	(12345)				
Band/Total Band	1.00				
Total Band/Whorl		.747			
Total Band/Visible Whorl		1.000			

The ratio of band to shell whorl increases as the number of band fusions increase, giving the shell a more solidly dark appearance. The bands of type 12345 cover about 41% of the shell whorl; of type 1(23)45B 57%; and of type (12345) 75%. The effect is increased when viewing from the top of the shell because only in a few shells (16%) can any of the ground color be seen after band 5. Even when seen very little is visible. If band cover is compared with the ground color visible between bands 1 to 5, 57% is band cover in type 12345, 77% is band cover in type 1(23)45B, and 100% is band cover in type (12345). In band types 12345 and 1(23)45A what catches the eye is the striping caused by alternating band and ground color. In other five banded and fused types the solid dark coloring of the bands catch the eye. In the field, striping or solid color are the most noticeable characteristics of *H. aspersa* shells.

Eighteen variations in band number and fusions were identified for *H. apsersa* collected at the seven collection sites in the study area and WS. Eleven of these types are found in shells 20 mm or larger. Band patterns absent in the larger size class have unfused bands and lack one or more bands. The band types and their frequencies in each collection are listed in Table 2 for both size classes and Table 3 for the 20 mm+ class. The most common type is 1(23)45. Frequency of this type for all shells ranges from

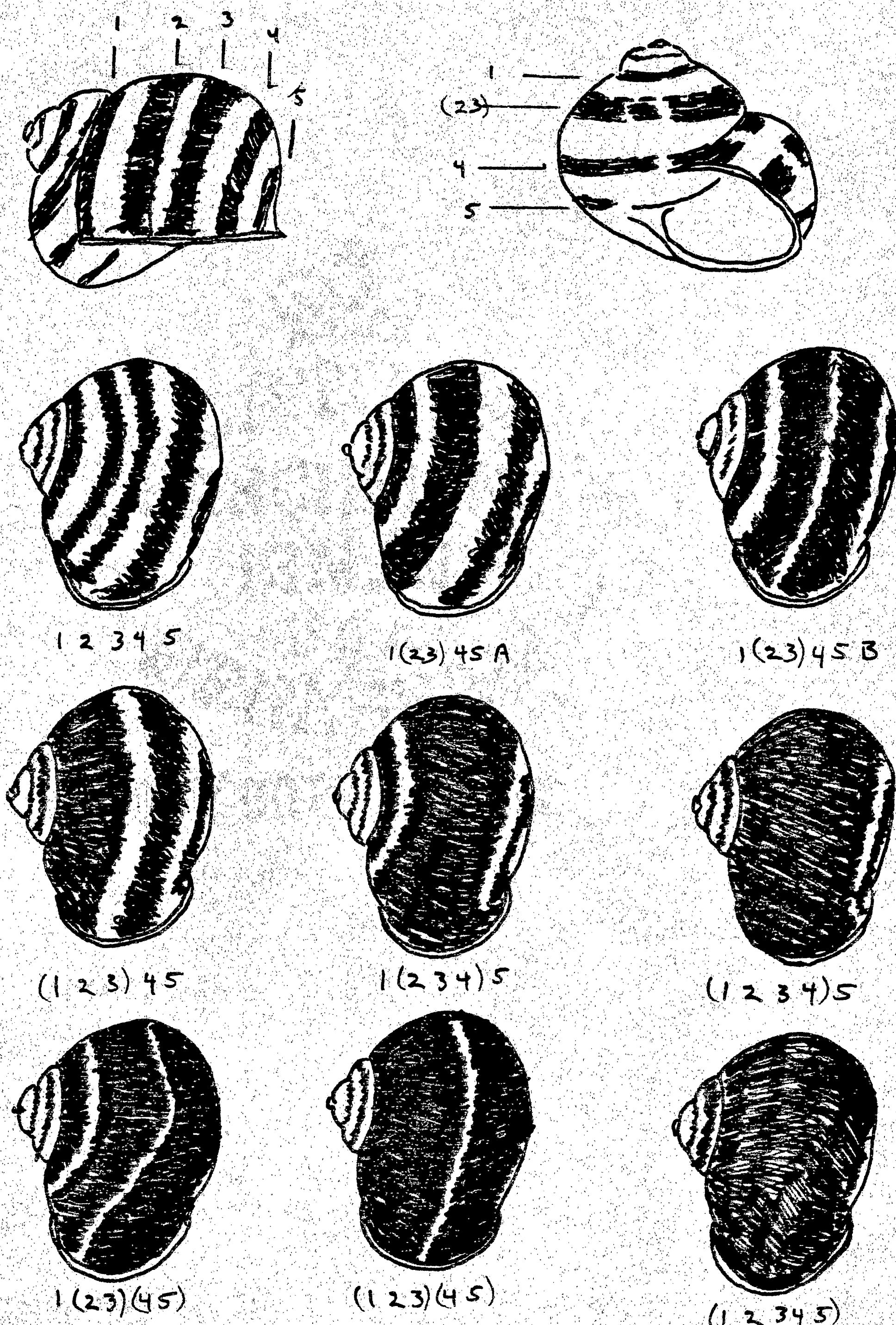

FIGURE 3. Method of numbering bands on the body whorl and nine band patterns of *Helix aspersa*.

.53 in collection 2 to .89 in collection WS.

Five distinct bands, type 12345, is second highest frequency. The type is absent from collections 5 and 6 in the 20 mm+ size class. Frequencies range from .05 to .37 in the combined size classes. Fusion of three bands, type (123)45 and type 1(234)5, occurs in most collections with frequencies ranging between .01 and .12.

Other types occurring include those with fusion of four bands, type (1234)5 and fusion of all bands, type (12345). On some shells bands are fused into two distinct groups, type (123)(45). A sixth band is present in three individuals, one of these in the 20 mm+ size class.

Four to ten percent of the shells in each collection lack one or more bands. Of the eight types described, types 12340, 12000, 10000, and 00000, occur in more than half the collections. Type 12045 and type 00000 occur in the 20 mm+ size class. There were no shells lacking a band in collection WS.

The G-test analysis of the entire collection of shells shows that frequencies of shell type are not independent of collection site. For the set 1 through 7, $G = 174.0577$ ($P < .001$) and for set 1 through 7 plus WS, $G = 202.6369$ ($P < .001$).

Similar results are obtained for the 20 mm+ size class. For set 1 through 7, $G = 131.5323$ ($P < .001$) and set 1 through 7 plus WS, $G = 146.1691$ ($P < .001$).

TABLE 2. *Helix aspersa* shell band patterns and frequency in the study area and West Sacramento (WS) collection. The table includes data from both size classes.

		Collection							
		1	2	3	4	5	6	7	WS
Type	Sample Size	95	90	78	81	75	75	75	75
12345		.368	.289	.141	.123	.067	.067	.053	.093
1(23)45		.547	.533	.718	.691	.680	.720	.773	.893
1(234)5		.010			.037	.067	.027	.067	.013
(123)45			.078	.051	.049	.027	.120	.067	
1(23)(45)		.010		.013					
(1234)5						.013			
(123)(45)					.025				
(12345)						.040			
123456		.010							
1(23)456					.025				
12340		.021	.044	.013		.013	.013		
12045					.012		.013		
12300		.010		.013				.013	
12040							.013		
12000			.022	.013	.012		.013	.013	
10300				.013					
10000		.010	.011		.025	.067	.013	.013	
00000		.010	.022	.027		.027			

TABLE 3. *Helix aspersa* shell band patterns and frequency in the study area and West Sacramento (WS) collection, size class 20 mm+.

		Collection							
		1	2	3	4	5	6	7	WS
Type	Sample Size	36	72	55	50	44	50	50	51
12345		.250	.319	.127	.080			.020	.137
1(23)45		.694	.569	.800	.720	.841	.780	.800	.863
1(234)5		.028	.083		.040	.091	.040	.100	
(123)45				.036	.080		.160	.080	
1(23)(45)		.028							
(1234)5						.023			
(123)(45)					.040				
(12345)						.045			
1(23)456					.020				
12045					.020		.020		
00000			.028	.036					

Contingency tables for both size classes together and the 20 mm+ size class are given in Appendices 3 and 4. Critical values and degrees of freedom are given in Table 4.

That the 20 mm+ class with fewer rare types is significantly heterogeneous indicates heterogeneity is largely due to variations in the frequencies of common types. In the 20 mm+ class the subset of the 4 most common types, types 12345, 1(23)45, 1(234)5 and (123)45 is heterogeneous at the 0.025 signficance level (Table 4).

The maximum homogeneous subsets computed by the R x C test of independence on data from all collections are presented in Table 5. At signficance level $P < 0.05$, 30 subsets are listed for size classes combined and 30 for the 20 mm+ class. For size classes combined 16 of the subsets contain 5 collections and 14 contain 6 collections. For the 20 mm+ size class 3 of the subsets contain 4 collections, 22 subsets contain 5 collections, and 5 contain 6 collections. The addition of any collection to these subsets would produce a heterogeneous set. Clearly, a large number of heterogeneous sets could be compiled from the data and heterogeneity is not due to a particular collection.

Collections 1, 2, 5 and 6 are frequent in the smaller maximum homogeneous subsets. Combinations of these collections contribute towards a high G-statistic.

TABLE 4. G-statistics generated by R x C tests of independence and appropriate chi-square values. Under test is the independence of *Helix aspersa* band pattern frequencies and collection sites.

Collections	Size Class	G-statistic	Chi-value	df	P<
1234567WS	Both	202.6369	172.418	119	.001
1234567WS	20 mm+	146.1691	112.317	70	.001
1234567	Both	174.0577	151.884	102	.001
1234567	20 mm+	131.5323	99.607	60	.001
127WS	Both	93.4773	59.703	30	.001
127WS	20 mm+	51.2520	37.697	15	.001
(124)3567WS*	Both	144.93	131.041	85	.001
1234567WS**	20 mm+	100.02	95.023	70	.025

* 124 data pooled

** 4 common types

TABLE 5. Maximum homogeneous subsets computed by an R x C test of independence on band frequency data from collections of *Helix aspersa* in the study area and West Sacramento (WS). The critical chi values, $P < 0.05$, are 145.181 for the entire collection and 90.531 for the 20 mm+ class.

Entire Collection		20 mm+ Class	
Subset of Collections	G-statistic	Subset of Collections	G-statistic
123467	132.4798	12347WS	83.7327
12346WS	136.2968	13457WS	84.9024
12347WS	136.8131	13467WS	77.3208
12367WS	133.2985	14567WS	89.9400
12467WS	143.8892	34567WS	86.3279
134567	144.4455	12345	84.5136
13467WS	131.2327	12346	82.4613
234567	124.6899	12357	80.3980
23456WS	134.6693	1235WS	69.2517
23457WS	133.5623	12367	81.9265
23467WS	114.5154	1236WS	78.2298
23567WS	127.9163	12457	90.2498
24567WS	129.9029	1245WS	85.1274
34567WS	108.1817	12467	86.3886
12345	121.9504	1246WS	86.7341
12356	120.9832	1257WS	81.0118
12357	119.2001	1267WS	86.1993
1235WS	121.5891	13456	80.4547
12456	129.5189	13567	76.2923
12457	129.6224	1356WS	79.8129
1245WS	133.8423	23457	90.1651
12567	128.8040	2345WS	86.7026
1256WS	135.4266	23467	83.9722
1257WS	131.6132	2346WS	84.5813
1345WS	123.2713	2357WS	81.9388
1356WS	126.2107	2367WS	83.4789
1357WS	117.9940	2467WS	88.9017
1456WS	130.9421	1256	88.0945
1457WS	124.4909	2356	86.9822
1567WS	127.2408	2567	81.3337

Collections 1 and 2 differ from collections 5 and 6 in having a higher proportion of type 12345 and lower proportion of type 1(23)45 (Table 2). The vegetation at collection sites 1 and 2 are similar and differ from the vegetation at sites 5 and 6 (Table 6). This could indicate selection of shell type by environmental variables.

The results of arranging the collections in arrays of decreasing frequency of types and comparing these arrays with changes in habitat are presented in Table 7. There does not appear to be a firm relationship between frequency of types and changes in the habitat. Collections 1, 2, 7 and WS were collected in similar habitats yet 1 and 2 are very different in type frequencies from collections 7 and WS. The only tendency apparent is that collections from the similar habitats found at 1, 2, 7 and WS have low frequencies of rare types. Collection 5, with the greatest frequency of rare types, is from a habitat ranked as most diverse. This possible trend is not supported by collections 3, 4 and 6.

The results of partitioning the data into collection sites of uniform habitat show that even in the most similar habitats, sites 1, 2, 7 and WS, band type frequencies are not independent of collection sites ($P < .001$). G-statistics are presented in Table 4 and maximum homogeneous subsets are presented in Table 8. For both size classes combined every combination of 2 sites is

TABLE 6. Vegetation characteristics at collecting sites and West Sacramento (WS).

Site	Species Present	Height cm	Percent Cover	Comments
1	*Carpobrotus edulis*	30	100	Luxurious
2	*Carpobrotus edulis*	30	100	Luxurious
3	*Carpobrotus edulis*	13	50	35% slope, yellowish
4	*Carpobrotus edulis*	25	95	Edged by bare ground
5	*Carpobrotus edulis*	22	60	Small bank near freeway
	Hypericum calycinum	20	40	
6	*Carpobrotus edulis*	20	90	Cover mostly old stems, leaves sparse
7	*Carpobrotus edulis*	32	100	Luxurious
WS	*Carpobrotus edulis*	30	100	Luxurious

TABLE 7. Variables of band type frequencies and vegetative cover arrayed by collection site number.

Variable	Rank by Collection Site Numbers							
Decreasing frequency of type 1(23)45	WS	7	6	3	4	5	1	2
Decreasing frequency of type 12345	1	2	3	4	WS	5	6	7
Decreasing frequency of fusions	WS	7	6	4	5	3	2	1
Decreasing frequency of rare types	5	4	3	2	1	6	7	WS
Decreasing plant height	7	2	1	WS	4	5	6	3
Decreasing cover	1	2	7	WS	4	5	6	3
Decreasing diversity of habitat	5	3	6	4	7	WS	2	1

a maximum homogeneous subset. Any combination of 3 produces a heterogeneous set.

When data of collection sites within 25 meters of each other are pooled, the resulting collections remain significantly heterogeneous for shell type ($P < .001$, Table 4).

The results of sorting band pigment intensity into three groups is presented in Appendices 5 and 6. The majority of shells in both size classes are judged standard. The two size classes differ in that the 20 mm+ class has more standard and dark shells. In the smaller size class dark shells are rare and pale pigmentation fairly common. Color intensity difference between size classes are statistically significant for shells from collections, enclosures, and collections and enclosures combined ($P < .001$, Table 9). Color intensity is also associated with the presence of all five bands. Shells lacking bands are more frequently classed as pale (86%) compared to those with 5 bands (11.8%). Those with 5 bands are more frequently classed as dark (31.4%) than shells lacking bands (3.5%). These differences are significant ($P < .001$, Table 9).

The number of empty shells of *H. aspersa* found during searches of the enclosures are given in Appendix 7. The highest mortality occurred between searches on May 24 and June 23, 1978. During the June 23 search 41 empty

TABLE 8. Maximum homogeneous subsets of data from collections 1, 2, 7 and WS located in similar habitats. The subsets were determined by an R x C test of independence testing the independence of *Helix aspersa* band type frequencies and collection sites. A significance level of 0.01 was used in computing this data.

Maximum homgeneous subset	G-statistic	Chi-value	df	Size Class
12	20.3988	50.892	30	Combined
13	44.4017	50.892	30	Combined
14	29.6187	50.892	30	Combined
23	34.9179	50.892	30	Combined
24	36.9970	50.892	30	Combined
34	15.4786	50.892	30	Combined
124	20.8978	30.578	15	20 mm+
134	29.2187	30.578	15	20 mm+
23	29.3894	30.578	15	20 mm+

TABLE 9. G-statistics from R x C tests of independence testing *Helix aspersa* band color intensity and size class, presence of 5 bands and mortality in enclosures.

R x C Test	G-statistic	Chi-value	df	P <
Color intensity/ size class (Collections)	76.4611	13.816	2	.001
Color intensity/ size class (Enclosures)	70.6331	13.816	2	.001
Color intensity/ size class (Combined)	147.4551	13.816	2	.001
Color intensity/ 5 bands (Enclosures)	106.2975	13.816	2	.001
Color intensity/ mortality (Enclosures)	10.0209	9.210	2	.01
Color intensity/ mortality (Enclosures, 10-19 mm class)	6.2601	5.991	2	.05
Color intensity/ mortality (Enclosures, 20 mm+ class)	3.216	2.706	2	.10 ns

shells were found in enclosure 1, 20 in enclosure 2, 30 in enclosure 3 and 7 in enclosure 4. This represents 32%, 13%, 60% and 46%, respectively, of the starting densities in these enclosures. Increasing mortality values correspond with an increase of maximum ambient temperatures. Maximum daily temperatures from April, 1978, through September, 1978, at the NOAA Office, 1416 Ninth Street, Sacramento, California, are given in Appendix 8 (NOAA 1978a). This station is 2.9 kilometers from the study area. A series of 5 high temperature days occurred from June 4 to June 8 with a maximum of 39.4°C on June 6, 1978. Three days of high temperature occurred before the May 24 search on May 18, 19 and May 20 with a maximum of 33.3°C on May 19, 1978.

Highest mortality of *H. aspersa* occurred in enclosures with low densities. Enclosure 4 with a starting density of 20 had 17 empty shells recovered by the end of the experiment. Enclosure 3, starting with 50 had 43 empty shells and enclosure 2, starting with 150, had 45 empty shells.

The association of mortality and density is statistically significant ($P < .001$, Table 10) for all enclosures and for the subset E1, E2, E3, and E4. These four enclosures were placed in similar environments. E6 does not follow the trend of low density/high mortality found in the other enclosure. Only 1 *H. aspersa* died in E6

TABLE 10. G-statistics from R x C tests of independence for mortality of *Helix aspersa* and variables of density, size class, band pattern, and presence of bands.

Test	G-statistic	Chi-value	df	P <
Mortality/Density (All enclosures)	58.2209	20.515	5	.001
Mortality/Density (E1, E2, E3, E4)	37.626	16.266	3	.001
Mortality/Size Class	2.1848	1.323	1	.25 ns
Mortality/Band Pattern	43.2981	37.697	15	.001
Mortality/# of Bands (Combined)	22.7851	10.828	1	.001
Mortality/# of Bands (10 mm - 19 mm)	11.3325	10.828	1	.001
Mortality/# of Bands (20 mm+)	14.976	10.828	1	.001
Mortality/# of Bands (outside enclosures, combined size classes)	8.954	7.879	1	.005
Mortality/# of Bands (outside enclosures, 10 mm - 19 mm class)	2.688	1.323	1	.25 ns

during the experiment. This individual and the 9 empty shells in E5 were found on August 28, 1978, two months after the majority of empty shells were collected from enclosures placed in full exposure to sunlight.

Density of live *H. aspersa* sampled outside the enclosures was highest on April 7, 1978, and decreased during the summer months (Appendix 9). This corresponds with the decrease of live *H. aspersa* in the enclosures.

Within the enclosures mortality was independent of size class. Of 100 20 mm+ shells at the end of the experiment 50% had been collected empty. Of 194 10-19 mm shells at the end of the experiment 59.8% had been collected empty. This tendency toward higher mortality of the 10-19 mm class is not statistically significant (Table 10).

Band patterns of empty shells and survivors within the enclosures are given in Appendix 10. A G-test shows that mortality is not independent of band pattern ($P < .001$, Table 10). Examination of Appendix 10 shows that a higher mortality occurred in individuals lacking one or more bands, in particular types 12300, 12000, 10000 and 00000. Of all shells lacking one or more bands at the end of the experiment 80% had been collected empty. Of all 5 banded shells at the end of the experiment 48.4% had been collected empty. The difference is statistically significant ($P < .001$, Table 10). G-tests show the association of high mortality and lack of bands significant for both size classes tested separately and combined (Table 10).

Of shells collected outside the enclosures in late summer, 15% of empty shells lacked one or more bands and 4% of live *H. aspersa* had shells lacking one or more bands. All shells lacking bands were in the 10-19 mm size class. The difference in mortality is significant for both size classes combined ($N = 190$, $P < .005$) but is not significant for the smaller size class, possibly because of the sample size ($N = 46$, Table 10).

As it has been shown, both pale band pigmentation and higher mortality are associated with lack of bands. It is expected that mortality would not be independent of band pigment intensity. This is the case. Higher mortality occurs in pale banded shells (Appendix 11). A G-test shows mortality is not independent of band pigmentation ($P < .01$, Table 9) for both size classes combined and the 10-19 mm class. Higher mortality of pale banded shells is not statistically significant in the 20 mm+ class.

Shell diameter growth of tagged snails in each enclosure is given in Appendix 12. Increase was greatest in E6. Most of this increase occurred after May 24, 1978 and averages 1.0 mm for each 30 day period. E2 and E5 had extremely low increases in shell diameter, averaging .08 mm and .005 mm, respectively, per 30 day period. Shell growth rate is variable between individuals. Some individuals did not grow in shell diameter during the time of the experiment.

At the end of the experiment the vegetation in E1 and E2 had been degraded and the litter below the stems of *C. edulis* was moist, deeper, and covered with snail mucus. A fungus, *Pestalotia* species was found growing on the stems of *C. edulis* in E2. The lower leaves of *C. edulis* were decaying in both enclosures. The vegetation in E3, E4, E5 and E6 remained much the same as at the beginning of the experiment.

DISCUSSION

Essential to the study of ecological genetics is the relationship of an organism's variability to the environment in which it lives. In this study significant differences in the frequencies of *H. aspersa* shell type were found in collections from a one hectare area. This area presents no physical barriers to gene flow and the distances involved are not beyond the dispersal ability of the organism (Ingram 1946). The flora habitat is dominated by one species, *C. edulis*. Differences in cover, height and diversity of habitat did not correlate with changing frequencies of band pattern types. Four collections from collecting sites of very similar habitat are significantly heterogeneous for band pattern. These results do not preclude the influence of selection on band pattern. They do indicate other causes are more important at this location.

Founder effects and genetic drift best explain differences in the band pattern frequencies at the collecting sites. Founder populations would have been introduced when the area was landscaped in 1970 and during replacement plantings. Isolated populations could also have been created during the severe winter of 1972-1973 when much of the plant cover died.

Differences in band pattern frequencies may also be due to genetic drift. *H. aspersa* has strong homing tendencies (Ingram 1946, Potts 1972) which would restrict gene flow between panmictic units. Panmictic units of *H. aspersa* are small and may comprise as few as 15 adults (Selander and Kaufman 1975). Many panmictic units would be possible in the study area. In the absence of strong environmental selection, genetic drift could account for the differences in band pattern frequencies found in the study area.

It is probable that both founder effects and genetic drift account for the differences described. This conclusion is supported by the work of Selander and Kaufman (1975), who found significant heterogeneity of allele frequencies at five enzyme loci of *H. aspersa* collected from two city blocks in Bryan, Texas.

The cause of mortality was not determined. Predation is not likely as predators such as birds and small mammals often remove the prey or damage the shell (pers. obs., Potts 1972) and empty shells found in the enclosures were not damaged. Mortality may be associated with high temperatures, as the majority of deaths occurred after hot weather. Ionic disturbances of the sodium/potassium ratio are thought to be the cause of heat related death in *H. aspersa* (Grainger 1975).

H. aspersa are not truly poikilotherms as they regulate their internal temperatures below the environmental temperature by water loss (Hogben and Kirk 1944). *H. aspersa* remain active at 35°C and become inactive at higher temperatures (Hogben and Kirk 1944). Inactive *H. aspersa* reduce evaporative loss of water (Machin 1966). This, in turn, prevents cooling by evaporation and internal temperature reaches that of the external environment (Hunter, 1966). In an environment of high temperature and low humidity, such as the study area in summer, *H. aspersa* could survive for short periods of time by regulating its body temperature through water loss. This would not enable it to survive extended periods of high temperature without dehydration. If it estivated under conditions of high temperature internal body temperature would be close to the surrounding environment and heat death likely.

It is interesting to note that within the enclosures survival rate increased at higher densities. In enclosures with high snail densities there appeared to be an increase of litter and moisture, a more humid microhabitat which might favor survival at higher temperatures.

If higher density in enclosures favored survival it did not favor growth. Few individuals grew at all in enclosures of high density. Similar results were obtained by Herzberg (1965), who found crowding of *H. aspersa* in laboratory containers resulted in slow or no growth and inactivity.

Shell diameter growth was greatest for snails in E6, the enclosure in *C. edulis* located under a bridge. Temperature readings taken under the bridge on days when enclosures were searched averaged 4°C lower than outside the bridge. Increase of growth in this enclosure occurred after the area began to receive water in late May, 1978. The snails in the enclosure located in *H. calycinum* under the bridge 2 meters from E6 did not grow and many died during the experiment. Evidently *H. calycinum* does not provide a suitable environment for *H. aspersa*.

Higher mortality among band pattern types lacking 1 or more bands may at first seem contradictory to the hypothesis of heat kill. Banded and dark shells would absorb more radiation. For *C. nemoralis*, Richardson (1974) found yellow unbanded shells heat tolerant compared to pink 5-banded shells and Jones (1973) found dark colored individuals placed in direct sunlight reached a higher equilibrium temperature than faint banded individuals of the same size.

Differences in size class may explain the apparent contradiction. The majority of shell types lacking bands were found in the smaller size class. In the 10-19 mm class background shell color is often faint and the shell translucent. Light energy would be absorbed directly by the body and would increase with the absence of band pigmentation. I believe that in *H. aspersa* juveniles, lighter pigmented shell types absorb more energy than darker shell types.

The following observations support this idea. Body and mantle color greatly affect the snails' appearance. I have often removed a body from what I thought was a dark banded shell to find the shell bands light or narrow. What I believed was band pigmentation was actually body color. Additionally, the shells of faint or narrow banded snails often are thin and fragile. A thinner shell would increase energy absorption and water loss. In the laboratory Wagge (1952) found that individual *H. aspersa* with high growth rates had thin and fragile shells. These animals died after short exposure to sunlight.

Selection against shell patterns lacking bands or faint in pigmentation was most intense under experimental conditions, yet was evident in *H. aspersa* collected outside the enclosures in late summer. A possible advantage and reason for the persistence of these band types in the population might be their ability to absorb light energy in cool temperature situations, such as during the winter and early spring. Juveniles are diurnally active in the study area during these months. Absorption of light energy would increase activity and feeding time and subsequently increase growth and survivorship. Shells lacking bands or with faint pigmentation would be beneficial to *H. aspersa* during the early juvenile stage of development. This advantage could offset the disadvantage found for these shells types during high temperature weather.

BIBLIOGRAPHY

Berry, S. S. 1909. The known Mollusca of San Bernardino County, California. Nautilus 23:73-79.

Binney, A. 1851. Terrestrial mollusks. 2:116.

Brussard, P. F. 1974. Population size and natural selection in the land snail *Cepaea nemoralis*. Nature 251:713-715.

Cain, A. J. and P. M. Sheppard. 1950. Selection in the polymorphic land snail *Cepaea nemoralis*. Heredity 4:275-294.

Cain, A. J. and P. M. Sheppard. 1954. Natural selection in *Cepaea*. Genetics 39:89-116.

Comfort, A. 1951. The pigmentation of molluscan shells. Biol. Revs. Cambridge Philosophical Society 26(3):285-301.

Cook, L. M. 1969. Results of breeding experiments of Diver and Stelfox on *Helix aspersa*. Proc. Malac. Soc. Lond. 38:351-358.

Cook, L. M. and J. M. B. King. 1966. Some data on the genetics of shell-character polymorphism in the snail *Arianta arbustorum*. Genetics 53:415-425.

Day, J. C. L. and W. H. Dowdeswell. 1968. Natural selection in *Cepaea* on Portland Bill. Heredity 23(2):169-188.

Diver, C. 1932. Mollusca genetics. Proceedings of the 6th International Congress of Genetics 2:236-237.

Gammon, E. T. 1943. Helicid snails in California. Bull. Dept. Agriculture, State of California. 32(3):173-187.

Goodhart, C. B. 1962. Variation in a colony of the snail *Cepaea nemoralis* (L.).J. Animal Ecology 31:107-237.

Goodhart, C. B. 1964. "Area Effects" and non-adaptive variation between populations of *Cepaea* (Mollusca). Heredity 18(4):459-465.

Grainger, J. N. R. 1975. Mechanism of death at high temperatures in *Helix* and *Patella*. J. Thermal Biol. 1(1):11-13.

Hanna, G. D. 1931. Exotic Mollusca in California. Bull. Dept. Agriculture, State of California. 28(5):298-321.

Hanna, G. D. 1966. Introduced mollusks of western North America. Occ. Papers, Calif. Academy of Sciences. 48:1-108.

Herzberg, Fred. 1965. Crowding as a factor in growth and reproduction of *Helix aspersa*. Am. Zoologist 5:254.

Hogben, L. and R. L. Kirk. 1944. Studies on temperature regulation. I. The *Pulmonata* and *Oligochaeta*. Proc. Roy. Soc. B132:239-252.

Hunter, W. R. 1966. Physiological aspects of ecology in nonmarine molluscs. Pages 83-126 in K. M. Wilbur and C. M. Yonge, Eds. Physiology of Mollusca. Academic Press, New York.

Ingram, W. M. 1946. The European brown snail in Oakland, California. Bull., So. Calif. Academy of Sciences. 45(3):152-159.

Jones, J. S. 1973. Ecological genetics and natural selection in molluscs. Science 182:546-552.

Keep. 1899. Nautilus 13:60.

Knight, H. 1952. A new record of *Helix aspersa* Muller. Nautilus 65:75-77.

Komai, T. and S. Emura. 1955. A study of population genetics on the polymorphic land snail *Bradybaena similaris*. Evolution. 9:400-418.

Machin, J. 1966. The evaporation of water from *Helix aspersa* IV. Loss from the mantle of the inactive snail. J. Exp. Biology 45:269-278.

Mead, A. R. 1951. Recent invasion of Arizona by the European brown snail. Amer. Malacol. Union Ann. Rept. 17:21-22.

Mead, A. R. 1971. Helicid land mollusks introduced into North America. The Biologist 53(3):104-111.

Moens, R., E. Francois, A. Riga and W. E. van den Bruel. 1967. A mechanical barrier against terrestrial gasteropods. Parasitica 23:22-27.

National Oceanic and Atmospheric Administration (NOAA). 1978a. Local Climatological Data, Monthly Summary, Sacramento, California. U. S. Department of Commerce, Asheville, North Carolina.

National Oceanic and Atmospheric Administration (NOAA). 1978b. Local Climatological Data, Annual Summary with Comparative Data, 1978, Sacramento, California. U. S. Department of Commerce, Asheville, North Carolina.

Owen, D. F. 1963. Polymorphism and population density in the African land snail, *Limicolaria martensiana*. Science 140:666-667.

Pilsbry, Henry A. 1939. Land Mollusca of North America (North of Mexico). Academy of Natural Sciences of Philadelphia, Monograph No. 3, Vol. 1. 573 pp.

Pollard, E. 1975. Aspects of the ecology of *Helix pomatia* L. J. Animal Ecology 44(1):305-330.

Potts, D. C. 1972. Population ecology of *Helix aspersa*, and the nature of selection in favorable and unfavorable environments. Ph.D. Thesis (Unpublished). University of California, Santa Barbara, Santa Barbara, California.

Potts, D. C. 1975. Persistence and extinction of local populations of the garden snail *Helix aspersa* in unfavorable environments. Oecologia (Berl.) 21:313-334.

Richardson, A. M. M. 1974. Differential climatic selection in natural populations of land snail *Cepaea nemoralis*. Nature 247:572-573.

Robertson, J. D. 1941. The function and metabolism of calcium in the Invertebrata. Biol. Revs. Cambridge Philosophical Society 16:106-133.

Selander, R. K. and D. W. Kaufman. 1975. Genetic structure of populations of the brown snail *(Helix aspersa)*. I. Microgeographic variation. Evolution 29:385-401.

Smith, M. 1907. Nautilus 21:57.

Sokal, R. R. and F. J. Rohlf. 1969a. *Biometry*. Freeman, San Francisco. 776 pp.

Sokal, R. R. and F. J. Rohlf. 1969b. *Statistical Tables*. Freeman, San Francisco. 253 pp.

Stelfox, A. W. 1915. A cross between typical *Helix aspersa* and var. Exalbida: Its results and lessons. J. Conch. 14:293-295.

Stelfox, A. W. 1918. Researches into the hereditary characters of some of our British Mollusca. J. Conch. 15:268-275.

Sterns, R. E. C. 1881. On *Helix aspersa* in California, and the geographical distribution of certain West American land-snails, and previous errors relating thereto, etc. Annals, New York Academy of Sciences 2:129-139.

Sterns, R. E. C. 1900. Exotic Mollusca in California. Science 11:655-659.

Wagge, L. E. 1952. Quantitative studies of calcium metabolism in *Helix aspersa*. J. Experimental Zoology 120:311-342.

APPENDIX 1. Measurements of band width for eight *Helix aspersa* band patterns. Measurements are in millimeters and were made 1 centimeter from lip on the body whorl. Shells selected for measurement are from Collection 8 and are in order of increasing diameter within pattern type.

Pattern 12345

Band	1	2	3	4	5
	1.2	1.4	1.2	2.4	1.8
	2.0	2.2	1.8	2.2	2.0
	2.8	1.4	1.8	2.3	2.0
	3.2	2.7	3.0	3.4	2.2
	3.3	3.5	2.2	5.3	2.7

Pattern 1(23)45A

Band	1	(23)	4	5
	2.1	6.0	3.6	2.2
	2.5	5.5	3.2	3.2
	2.8	5.9	2.9	1.8
	2.6	6.0	3.0	1.7
	2.4	5.3	2.1	1.8
	2.2			
	2.2			
	2.5			
	2.6			

Pattern 1(23)45B

Band	1	(23)	4	5
	2.1	5.0	5.0	2.7
	2.2	4.9	5.1	1.6
	2.2	5.4	4.4	2.0
	2.9	5.7	4.9	2.5
	3.1	6.4	5.3	2.6
	2.5	5.6	6.4	3.1
	2.6	5.7	5.7	2.6
	2.7	6.2	6.3	4.5
	2.1	7.1	5.8	3.0
	3.4	6.3	5.7	3.9

Pattern (123)45

Band	(123)	4	5
	10.2	3.2	2.4
	11.2	3.4	2.7
	8.7	3.6	2.2

Pattern (1234)5

Band	(1234)	5
	16.3	3.9
	15.1	3.7

Pattern 1(23)(45)

Band	1	(23)	(45)
	2.5	5.4	10.2
	2.7	7.2	8.7

Pattern (123)(45)

Band	(123)	(45)
	10.4	11.2

Pattern (12345)

Band	(12345)
	20.6
	22.7
	26.7

APPENDIX 2. Measurements of interband width for eight *Helix aspersa* band patterns. Measurements are in millimeters and were made 1 centimeter from lip. Shells selected for measurement are from Collection 8 and are in order of increasing diameter within pattern type.

Pattern 12345

Band	1-2	2-3	3-4	4-5	5-Lip
	2.0	1.7	2.4	3.0	7.7
	1.8	1.6	3.0	3.3	8.8
	2.2	1.1	3.8	2.9	8.7
	2.3	1.8	4.1	2.7	9.5
	1.2	0.7	1.1	2.1	7.6

Pattern 1(23)45A

Interband	1-(23)	(23)-4	4-5	5-Lip
	2.0	3.5	2.7	7.4
	2.7	2.6	2.7	7.6
	1.6	1.8	2.0	8.0
	1.7	3.2	1.3	7.7
	2.4	3.2	3.6	8.2
	1.6	2.7	1.8	8.2
	2.2	2.9	3.4	7.6
	2.1	3.3	3.5	8.9
	2.5	2.5	3.6	8.7
	2.2	1.9	2.8	8.1

Pattern 1(23)45B

Interband	1-(23)	(23)-4	4-5	5-Lip
	1.9	0.7	2.7	7.5
	1.6	0.8	2.6	7.9
	1.6	0.6	2.5	7.0
	1.5	0.7	2.6	8.9
	1.4	1.1	1.8	7.6
	1.6	0.7	2.1	7.4
	1.9	1.0	2.1	7.5
	1.6	0.8	2.1	7.0
	1.8	1.5	2.3	9.6
	1.7	1.1	2.2	7.6

Pattern (123)45

Interband	(123)-4	4-5	5-Lip
	2.1	3.2	9.1
	2.2	2.6	7.8
	2.0	2.7	7.7

Pattern (1234)5

Interband	(1234)-5	5-Lip
	2.0	7.2
	1.2	6.7

Pattern 1(23)(45)

Interband	1-(23)	(23)-(45)	(45)-Lip
	1.6	0.5	4.5
	1.2	0.4	7.7

Pattern (123)(45)

Interband	(123)-(45)	(45)-Lip
	0.3	6.9

Pattern (12345)

Interband	(12345)-Lip
	8.4
	7.8
	7.6

APPENDIX 3. Number of *Helix aspersa* shells of each band pattern type in the study area and West Sacramento (WS) collections.

	Collection							
Band Type	1	2	3	4	5	6	7	WS
12345	35	26	11	10	5	5	4	7
1(23)45	52	48	56	56	51	54	58	67
1(234)5	1			3	5	2	5	1
(123)45		7	4	4	2	9	5	
1(23)(45)	1		1					
(1234)5					1			
(123)(45)				2				
(12345)					3			
123456	1							
1(23)456				2				
12340	2	4	1		1	1		
12045				1		1		
12300	1		1				1	
12040						1		
12000		2	1	1		1	1	
10300			1					
10000	1	1		2	5	1	1	
00000	1	2	2		2			

APPENDIX 4. Number of *Helix aspersa* shells of each band pattern type in the study area and West Sacramento (WS) collections, 20 mm+ size class.

	Collection							
	1	2	3	4	5	6	7	WS
Band Type								
12345	9	23	7	4			1	7
1(23)45	25	41	44	36	37	39	40	44
1(234)5	1	6		2	4	2	5	
(123)45			2	4		8	4	
1(23)(45)	1							
(1234)5					1			
(123)(45)				2				
(12345)					2			
1(23)456				1				
12045				1		1		
00000		2	2					

APPENDIX 5. Color intensity of *Helix aspersa* shell bands in the study area and West Sacramento (WS) collection. The number of shells segregated into each group is shown for both size classes and size classes combined.

	Size Class									
	10 mm to 19 mm			20 mm+			Combined			
Collection	Pale	Standard	Dark	Pale	Standard	Dark	Pale	Standard	Dark	Sample Size
1	6	51		4	30	4	10	81	4	95
2	11	7		4	68		15	75		90
3	10	12	1	4	51		14	63	1	78
4	12	15	4	5	31	14	17	46	18	81
5	13	12	5	3	31	11	16	43	16	75
6	11	14		3	37	10	14	51	10	75
7	11	14		4	29	17	15	43	17	75
Total	74	125	10	27	277	56	101	402	66	569
Frequency	.35	.60	.05	.08	.77	.15	.18	.70	.12	
WS							7	66	2	75
Frequency							.09	.88	.03	

APPENDIX 6. Band color intensity of *Helix aspersa* in enclosures by size class and size classes combined. 5 banded shells and shells lacking one or more bands are grouped separately under combined.

Enclosure	10 mm to 19 mm			20 mm +			Combined		
	Pale	Standard	Dark	Pale	Standard	Dark	Pale	Standard	Dark
2	31	24	6	2	25	21	33	49	27
3	20	13	1	2	9	13	22	22	14
4	8	6	0	1	1	1	9	7	1
5	2	5	0	0	3	1	2	8	1
6	0	3	2	1	4	5	1	7	7
Total	61	51	9	6	42	41	67	93	50
Percentage	50.4	42.2	7.4	6.7	47.2	46.1	31.9	44.3	23.8
Total 5 Banded							18	87	48
Total Lacking Bands							49	6	2

APPENDIX 7. Empty shells of *Helix aspersa* collected from enclosures and dates collected.

Date (1978)	10 mm - 19 mm Class						20 mm+ Class						Totals
	Enclosure						Enclosure						
	1	2	3	4	5	6	1	2	3	4	5	6	
April 24	7												7
May 5		4		2									6
May 24	3	6	2	7				3	6	1			28
June 23	35	5	21	5			6	15	9	2			98
August 28		4	5		7	1		4			2		23
September 22		2						2					4
Totals	45	21	28	14	7	1	6	24	15	3	2		166

APPENDIX 8. Maximum and minimum daily temperatures from April, 1978 to September, 1978 recorded at the NOAA Office, 1416 Ninth Street, Sacramento, California.

Date (1978)	April		May		June	
Temperature °C	Max.	Min.	Max.	Min.	Max.	Min.
Day 1	15.6	8.9	25.6	10.0	26.7	11.7
Day 2	17.8	3.9	28.9	10.0	28.3	11.1
Day 3	15.6	7.2	28.9	11.1	28.9	11.1
Day 4	16.7	6.7	25.0	12.8	36.7	11.1
Day 5	14.4	5.0	21.1	10.6	38.9	14.4
Day 6	12.8	5.0	25.0	10.0	39.4	16.1
Day 7	15.6	4.4	28.3	10.0	36.1	13.9
Day 8	21.7	4.4	30.6	10.0	38.9	12.8
Day 9	27.2	8.3	28.3	11.1	30.6	13.3
Day 10	25.0	8.3	23.3	10.0	26.7	13.3
Day 11	24.4	10.6	25.0	7.8	31.1	11.7
Day 12	23.3	10.0	29.4	9.4	27.2	13.3
Day 13	19.4	8.9	32.3	12.2	28.9	12.2
Day 14	15.6	6.1	24.4	12.8	26.7	10.0
Day 15	13.3	6.7	21.7	8.9	28.9	11.1
Day 16	16.1	5.6	25.0	8.9	28.9	11.7
Day 17	17.8	3.9	29.4	11.7	31.7	12.2
Day 18	19.4	6.7	31.1	10.0	26.7	12.2
Day 19	18.9	7.2	33.3	11.7	30.0	10.6
Day 20	17.2	5.6	32.8	11.7	27.8	11.7
Day 21	18.3	3.3	23.9	11.1	30.0	11.7
Day 22	21.1	3.9	23.9	10.0	27.8	11.7
Day 23	22.8	6.1	21.7	7.2	26.7	11.7
Day 24	17.2	11.7	21.1	6.7	27.2	12.2
Day 25	17.2	10.6	22.2	6.7	29.4	11.1
Day 26	21.1	9.4	25.6	8.3	29.4	11.7
Day 27	23.9	8.9	32.2	10.0	24.4	15.6
Day 28	22.8	8.9	33.9	14.4	25.0	14.4
Day 29	25.0	8.9	34.4	14.4	27.8	12.8
Day 30	18.9	10.0	32.8	18.9	27.2	12.8
Day 31			32.2	13.9		

APPENDIX 8. (Cont.) Maximum and minimum daily temperatures from April, 1978 to September, 1978 recorded at the NOAA Office, 1416 Ninth Street, Sacramento, California.

Date (1978)	July		August		September	
Temperature °C	Max.	Min.	Max.	Min.	Max.	Min.
Day 1	26.1	12.2	35.0	17.2	34.4	15.0
Day 2	26.1	11.7	34.4	15.0	35.6	16.7
Day 3	28.3	11.7	35.0	13.9	31.7	13.9
Day 4	32.3	12.8	36.1	16.7	27.8	15.6
Day 5	33.9	13.9	40.6	18.3	20.6	16.7
Day 6	34.4	14.4	41.1	20.0	26.1	12.2
Day 7	31.1	13.3	39.4	19.4	25.0	10.0
Day 8	36.7	15.0	42.2	18.9	27.8	10.0
Day 9	37.8	16.1	41.1	18.3	17.2	13.9
Day 10	27.8	12.2	35.6	16.7	24.4	13.9
Day 11	26.1	11.7	32.2	15.0	27.2	12.8
Day 12	30.0	11.7	28.9	14.4	31.1	12.8
Day 13	34.4	15.6	28.3	13.3	30.6	10.0
Day 14	37.2	16.7	33.3	12.2	29.4	13.9
Day 15	31.7	15.0	33.3	15.6	31.1	13.3
Day 16	35.0	12.8	27.8	14.4	31.1	13.9
Day 17	36.1	15.6	30.6	11.7	25.0	12.8
Day 18	37.2	17.2	33.9	14.4	23.9	9.4
Day 19	37.8	15.6	34.4	12.8	26.7	9.4
Day 20	35.0	15.0	32.8	14.4	27.8	6.1
Day 21	37.8	14.4	29.4	12.8	28.3	9.4
Day 22	36.1	17.2	26.7	9.4	30.6	10.0
Day 23	35.6	15.6	27.2	11.7	33.9	11.1
Day 24	38.9	17.8	27.8	11.1	34.4	13.9
Day 25	31.7	16.1	28.3	13.3	35.6	14.4
Day 26	32.2	15.6	28.3	13.9	30.6	13.3
Day 27	33.3	14.4	31.1	11.7	29.4	11.7
Day 28	33.3	12.8	35.6	13.9	32.2	10.6
Day 29	33.9	11.1	34.4	15.6	33.9	12.2
Day 30	35.6	11.7	30.0	14.4	35.6	15.0
Day 31	38.3	15.6	31.7	12.2		

APPENDIX 9. Density of *Helix aspersa* in study area from February 1978 to September 1978. The number given is adult and juvenile snails per square meter.

Date	Samples			Average
	1	2	3	
February 24	82	156	116	118
March 7	288	124	192	201
April 7	68	250		159
May 24	112	98	72	94
June 22	95	20	8	41
August 28	16	20	11	16
September 16	25	12	8	15

APPENDIX 10. The number of empty shells and surviving *Helix aspersa* of each band pattern type from the enclosures.

Band Pattern	Empty	Surviving	Total
12345	11	18	29
1(23)45	77	74	151
1(234)5	7	7	14
(123)45	7	8	15
(123)(45)	1	4	5
(12345)	3	2	5
12340	2	2	4
12045	2	1	3
12300	9	1	10
12040	1	3	4
12000	4	0	4
10000	23	4	27
00000	9	0	9
1(23)40	5	2	7
(123)40	2	1	3
1(23)00	3	1	4
	166	128	294

APPENDIX 11. Empty shells and surviving *Helix aspersa* from enclosures grouped by band color intensity ratings.

		10 mm to 19 mm			20 mm +			Combined		
Enclosure		Pale	Standard	Dark	Pale	Standard	Dark	Pale	Standard	Dark
2	Empty	15	4	2	2	13	9	17	17	11
	Survivor	16	20	4	0	12	12	16	32	16
3	Empty	17	10	1	2	5	8	19	15	9
	Survivor	3	3	0	0	4	5	3	7	5
4	Empty	8	6	0	1	1	1	9	7	1
	Survivor	0	0	0	0	0	0	0	0	0
5	Empty	2	5	0	0	1	1	2	6	1
	Survivor	0	0	0	0	2	0	0	2	0
6	Empty	0	1	0	0	0	0	0	1	0
	Survivor	0	2	2	1	4	5	1	6	7
Totals	Empty	42	26	3	5	20	19	47	46	22
	Survivor	19	25	6	1	22	22	20	47	28

APPENDIX 12. Shell diameter measurements of tagged *Helix aspersa* in enclosures. Measurements are in millimeters.

Enclosure 1

	April 7	May 24	Increase
	12.2	11.9	0.0
	12.4	13.0	0.6
	9.2	9.5*	0.3
	16.6	17.1	0.4
	10.8	11.5	0.7
	16.5	17.0	0.5
	23.5	23.8	0.3
	10.6	12.0	1.4
	14.2	14.4	0.2
	18.3	19.3	1.0
	10.8	10.6	0.0
	16.9	17.4	0.5
	18.8	18.7	0.0
	21.9	22.3	0.4
	12.1	13.0	0.9
Average			0.48

*Found emtpy

Enclosure 2

	April 25	June 23	Increase
	18.0	17.3	0.0
	12.6	12.0	0.0
	15.2	16.4	1.2
	15.1	15.4	0.3
	15.0	15.1	0.0
	19.3	19.1	0.0
	14.4	14.4	0.0
	27.5	27.6	0.0
	15.1	14.8	0.0
	21.5	21.6	0.1
	24.7	24.7	0.0
	11.1	11.4	0.3
Average			0.16

Enclosure 3

	April 23	May 24	Increase
	10.8	11.3	0.5
	19.4	20.1	0.7
	14.9	15.5	0.6
	20.2	20.2	0.0
	13.2	13.2	0.0
	12.6	12.3	0.0
	20.0	20.8	0.8
	14.7	14.1	0.0
Average			0.33

APPENDIX 12. (Cont.) Shell diameter measurements of tagged *Helix aspersa* in enclosures. Measurements are in millimeters.

Enclosure 4

	April 23	May 24	Increase
	12.2	12.6	0.4
	12.8	13.0	0.2
	14.5	14.3	0.0
	15.1	15.3	0.2
	20.8	21.0	0.2
	20.3	20.9	0.6
	26.6	27.4	0.8
Average			0.34

Enclosure 5

	April 23	June 23	Increase
	10.2	10.1	0.0
	13.6	13.5	0.0
	15.2	15.2	0.0
	18.5	18.5	0.0
	19.2	18.9	0.0
	20.0	20.1	0.1
	20.1	19.9	0.0
	25.6	25.6	0.0
	27.5	27.4	0.0
Average			0.01

Enclosure 6

	April 24	September 22	Increase
	12.1	17.5	5.4
	12.7	18.8	6.1
	14.8	19.2	4.4
	15.9	19.5	3.6
	16.8	19.6	2.8
	17.0	22.7	5.7
	17.2	19.9*	2.7
	18.6	23.4	4.8
	20.8	23.4	2.6
	20.8	24.0	3.2
	22.0	26.1	4.1
	24.4	28.7	4.3
	11.0	15.0	4.0
Average			4.1

*Found empty