

AN ABSTRACT OF THE THESIS OF

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Title: The Maintenance and Stability of the Shell Color Polymorphism
in the Rocky Intertidal Gastropod *Thais* (*Nucella*) *emarginata*.

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Thais (Nucella) emarginata is a common predatory gastropod of the rocky intertidal system of western North America. It is usually found at low tide on top of its sedentary prey, barnacles and mussels. Thais is also highly polymorphic for shell color, and breeding of isolated females has shown that the polymorphism has a genetic basis.

This study of the Thais polymorphism is divided into two parts. In the first part, I describe the variation, its genetic basis, consider patterns of variation and change for ten Oregon populations, and assess micro- and macrohabitat relationships of the different morph types. The second part is a study of snail movement and its relationship to morph frequencies at one of the sites.

Of the eight shell color categories examined at the Oregon sites, a solid colored Black morph and a striped Grey-Black morph are clearly the most common types. There were no consistent patterns of shell color frequency change associated with any environmental variable recorded. These included latitude, wave action, subtidal type (sand, gravel, or solid rock), relative abundance of any prey type, direction of facing (N, S, or W), Thais density, or Thais distribution.

One pattern did emerge from this investigation. Six of the ten sites had significant shell color frequency change between 1978 and 1979, and three others had marginally significant change, indicating

the polymorphism is a very dynamic one..

There was a significant association between shell color and micro-habitat type. However, Black and Grey-Black snails did not show such an association, and the causes of this relationship in the minor categories remains obscure.

There were also a significant association between shell color and macrohabitat (reef versus cobble type habitats). A comparison of the frequencies of Black and Grey-Black snails at seven of the sites (those having both habitat types) exhibited a slight, but very consistent relationship between shell color and macrohabitat. I postulate that this relationship is due to a differential response to wave action in the two macrohabitat types.

The study of movement was carried out at Cascade Head on the north central Oregon coast. Preliminary experiments with a marking method designed to minimally disturb the animals suggested that movement was responsible for the high losses of tagged animals reported in the literature.

Snails on a particular boulder at Cascade Head were painted with nail polish and their shell color frequencies were recorded. When a painted snail moved off that rock, it was given a numbered tag. Comparisons of the frequencies of painted snails, tagged snails, and overall frequencies of Black and Grey-Black snails in the population show a close concordance indicating that movement plays a role in the dynamics of shell color frequency change in the population.

There was no association between probability of movement and shell color frequencies of those that moved and were tagged. Black and Grey-Black tagged snails were not different in size, nor was there any

difference in mean distances moved.

There was, however, a significant difference in the directions the two morphs moved, which when taken within the context of the geography of Cascade Head, predicts a net loss of Black snails from the population. There was, in fact, a significant negative regression of the frequencies of Black snails over time, consistent with the idea that movement is very important in the dynamics of the polymorphism.

In the discussion of these results, voluntary versus involuntary movement is contrasted, and I note that Thais has the ability to find suitable habitat after a move. Differential directions of movement by the two morphs is postulated to be a response, as with the macrohabitat correlations, to wave action. I suggest that shell color, or genes closely linked to shell color loci, are causing the response in both cases.

This movement study suggests that delineation of a population of Thais is a formidable task, and the question of what a biological population of Thais emarginata is remains obscure.

The Maintenance and Stability of the Shell Color
Polymorphism in the Rocky Intertidal Gastropod

Thais (Nucella) emarginata

by

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THE MAINTENANCE AND STABILITY OF THE SHELL COLOR POLYMORPHISM IN
THE ROCKY INTERTIDAL GASTROPOD THAIS (NUCELLA) EMARGINATA

I. INTRODUCTION

This thesis is divided into two parts, as each of the following chapters were prepared as separate manuscripts. The first part describes the polymorphism in Thais, establishes a genetic basis for the polymorphism, and examines geographic variation and micro- and macrohabitat relationships of the different shell color types. Change in shell color frequencies over time are documented, and a slight, but very consistent relationship between shell color of the pre-dominant morph types, Black and Grey-Black, and macrohabitat type is shown. This relationship is postulated to be due to a differential response to wave action in the two macrohabitat types.

The second part is an examination of the relationship between movement and the dynamics of morph frequency change for Black and Grey-Black snails. Close concordance between the frequencies of moving snails and shell color frequency change in the overall population suggests movement is important in the dynamics of the polymorphism. Differential directions of movement by the two morph types also suggests that the direction of overall shell color frequency change in the population is related to movement. This pattern is also postulated to be a response to wave action. These results suggest that shell color, or genes closely linked to shell color loci, are important to both the ecological and genetical dynamics of Thais emarginata.

Geographic Variation and Habitat Relationships
in the Polymorphic Intertidal Gastropod
Thais emarginata

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Introduction

Investigations of the existence, maintenance, and dynamics of genetic and phenotypic polymorphisms in natural populations of plants and animals have proven to be extremely fruitful and challenging areas of study in population biology (Lewontin, 1974; Wright, 1978). In particular, studies of the evolutionary mechanisms by which populations maintain polymorphic variation have a long history of both theoretical and field investigations.

The most effective procedure for studying a polymorphism is to establish that evolution (i.e. genetic change) is occurring and can be readily detected in the populations under study, followed by an attempt to discern the evolutionary force or forces driving the changes. Most often this is done via correlation of phenotype or phenotypic changes with some environmental variable(s).

One common explanation for the maintenance of a polymorphism is the correlation of different morphological types to different habitat types or climatic regimes (e.g. Giesel, 1970; Jackson, et al. 1976; Nevo, 1973; Schoener and Schoener, 1976). Such relationships may have a variety of causes such as industrial smoke (Kettlewell, 1956), Pleistocene glaciation and other climatic conditions (Arnold, 1969; Williams, et al. 1968), or selective predation (Giesel, 1970; Nevo, 1973; Camin and Erlich, 1958). Levene (1953), Levins and MacArthur (1966), and May, et al. (1975) have provided theoretical support for some of these observations.

When no obvious correlation between phenotype and habitat or climate can be found (Anderson, et al. 1975), genetic mechanisms, such as

selection for modifier genes (Emlen, 1973), or selection acting on groups of closely linked genes (Dobzhansky, 1943), have been implicated as maintaining the polymorphisms (Clarke, 1966; Lewontin, 1974). Additionally, many polymorphisms without habitat correlations have been explained as being neutral with respect to fitness, and that genetic drift is responsible for the changes. Inferences of neutrality began with Darwin (1872); this argument has more recently been synthesized by Kimura and Ohta (1971), and the relative roles of natural selection and genetic drift in maintaining genetic variation in populations is one of the most controversial topics in evolutionary biology.

Little work has been done on polymorphic animals in the rocky intertidal system (the notable exception is Giesel's 1970 study of Acmaea limpets, in which correlations between habitat type and morphology were found). This ecosystem has many advantages, as much of the ecology and natural history of the organisms inhabiting the system are known (Bertness, 1977; Connell, 1961, 1970; Dayton, 1971; Emlen, 1966; Frank, 1965; Menge, 1972, 1978; Paine, 1969; Spight, 1972, 1976). The rocky intertidal system also has discrete micro- and macrohabitat types, which can facilitate an understanding of morphology - habitat relationships, critical to the study of a polymorphism.

Predatory gastropods of the rocky intertidal system have been the subject of extensive ecological study (Bertness, 1977; Connell, 1961; Emlen, 1966; Menge, 1978a, 1978b; Spight, 1972). Thais (Nucella) emarginata is one such intertidal snail commonly found on rocky shores of the western United States and Canada in the mid to high intertidal regions (Smith and Carlton, 1975). The animal feeds primarily on barnacles (Balanus spp) and mussels (Mytilus), and is usually found at low

tide in crevices or on top of its sedentary food. It is also highly polymorphic for shell color.

In this paper I will present part of the results of a study of the Thais shell color polymorphism. I will establish that evolution is occurring in many of the Thais populations I studied, in the form of morph frequency changes over time, and will examine the habitat relationships of different colored Thais in detail, as these are fundamental observations for an assessment of the evolutionary forces acting on a polymorphism in a natural population.

Description of the Polymorphism

The Thais emarginata polymorphism is a type of "conspicuous" polymorphism (Wright, 1978). Thais shells are either solid colored or striped, and these two basic types can be divided further on the basis of color. At the beginning of this study, I was able to distinguish 32 different shell color types. At any one time, all of these morph types could be found on a single boulder in the intertidal region. It is easy to group similar shell color types based on visual likeness of morphology. Eight groups, or shell color categories, emerged from this grouping:

Solid Colored Shells

Black (B)
 Grey (G)
 White (W)
 Green (Gr)
 Orange (O)

Striped Shells

Grey-Black (GB)
 Grey-Green (GGr)
 Green-Black (GrB)

The genetic basis of this shell color polymorphism has only been partially determined. Female Thais reproduce via the production of egg capsules laid directly onto their rocky habitat. Each capsule contains several fertilized eggs and many unfertilized nurse cells for the developing embryos (LeBoeuf, 1971; Houston, 1971). Development takes place within the egg capsules and the young emerge as colorless juvenile snails about 1.2 mm. long (Spight, 1971; pers. obs.). These young snails begin developing color at about two weeks post-hatching. Females will reproduce in the laboratory, and the offspring of isolated females, when hatched in a common environment, are polymorphic and distinct from the offspring of other such isolated females. Although this does not rule out a maternal effect for shell color, the lack of color at hatching, combined with no evidence of a permanent maternal effect on color formation in any other organism, mitigates against this explanation. I conclude the polymorphism has a genetic basis. Female Thais commonly store sperm (Houston, 1971; pers. commun.), and developmental time is approximately two years (Emlen, 1966), so the exact hereditary mechanism obtainable via crosses of known virgins is not yet known.

Study Sites and Methods

Ten rocky intertidal sites were surveyed for Thais shell color frequencies during this study (see Figure 1). The ten sites, from south to north, along with their physiographic characteristics, are presented below. Characteristics of each site include direction of facing (N, S, or W), exposure to wave action (estimated from several

clues such as presence of offshore islands, exposure to prevailing wind and wave directions, slope of the beach), subtidal type (rock or sand), presence or absence of prey species (barnacles and mussels), whether snails are found commonly or rarely, and whether their distribution is even or patchy. Distribution of Thais in the intertidal zone is not random. Rather, Thais is restricted to several habitat types, difficult to define, easy to recognize when in the field (a complex of indicators including tidal height, the size of a boulder or height of a ledge, exposure to wave action, presence of food and other variables enter into defining a habitat type). When snails occur at high frequency in these suitable habitats, I term their distribution even, if not, patchy.

1. Winchuck River (WR). A southwest facing site located approximately one km north of the Winchuck River in extreme southwest Oregon. The intertidal area that contains Thais is a long, wide stretch of sandy beach with boulders of varying sizes lying on the sand. Only the larger boulders (greater than one meter in diameter) have snails on them. The density of barnacles is high, mussels are rare. Exposure is intermediate to high. Thais occur rarely and are patchily distributed.

2. Mill Beach (MB). A south facing crescent shaped area consisting of large boulders and one very large (25 - 30 meters long) reef in the center of the crescent. The highest density of snails is on the boulders, with greatly reduced numbers on the reef. The subtidal is rock. Barnacle density is high, mussels are very rare. Exposure to wave action is low, with snails occurring in the least exposed areas. The density of snails is low to medium, and the distribution is patchy.

3. Lone Ranch (LR). Another crescent shaped cove similar to MB, facing northwest, consisting of large (five meters or larger in diam-

eter) boulders lying on a gravel subtidal. Barnacle density is high, and mussels are rare. Exposure to wave action is low due to the protection of large offshore islands. The density of snails is medium, and they are evenly distributed, not patchy.

4. North Humbug (NH). A west-southwest facing long cobble beach just south of a rocky head. The areas with snails are large boulders (one meter or larger) and one reef at the north end of the beach. Subtidal is sand and gravel. Both barnacles and mussels are present and common, but there are no extensive mussel beds. Exposure to waves is medium to high, as the only protection is the headland to the north. Density of snails is medium, but they are patchily distributed.

5. Cape Blanco (CB). The westernmost point of land in the Pacific Northwest, CB is a north facing beach with many large reefs and boulders lying on a sandy beach. Thais is found only in the most protected areas, and most commonly on cobble, not the reefs. Barnacles are common, and mussels are again rare. Exposure to northerly wave action is high. Snail density is low and distribution is very patchy.

6. Cape Arago (CA). A crescent shaped southwest facing boulder field with a very large island at the center of the crescent. The subtidal is rock. Both barnacles and mussels are present and common. Thais are found regularly on the larger boulders. Exposure to wave action is medium to light. Thais density is low but the snails are evenly spread.

7. Strawberry Hill (SH). A west-northwest facing sandy beach with very large (ten meters or larger) boulders lying on it. Both barnacles and mussels are common, and extensive mussel beds are found. Thais are found throughout on the boulders. Exposure to wave action is

high. Snail density is high and they are evenly spread.

8. Cascade Head (CH1 and CH11). There are two study sites at Cascade Head. CH1 is located at the mouth of the Salmon River and is a southwest facing boulder field lying on a sandy beach. Thais are found both on the boulders (2 - 4 meters in diameter) and on the small ledge area behind the boulders. Both barnacle and mussel beds are abundant. Exposure to wave action is medium. The density of snails is very high and even. CH1 is the primary study site for this research.

9. CH11 is located approximately 0.5 km upriver from CH1. CH11 is a south facing beach with very large rocks (10 - 15 meters in diameter) and a sand subtidal. Barnacles are abundant but no mussels are present. Exposure to wave action is very low, the lowest of the ten sites. Thais density medium and distribution is patchy.

10. Cape Kiwanda (CK). Cape Kiwanda is a northeast facing sandstone bluff surrounded by sandy beach, typical of the north Oregon coast. The intertidal area consists of boulders (1 - 3 meters) that have fallen off the bluff and a small wall (20 meters long), part of the head itself. The subtidal type is sand and gravel. Both barnacles and mussels are present, but there are no large mussel beds. Exposure to wave action is medium to low. Thais density is medium and distribution is even.

The methods used for obtaining data in this study were relatively simple. To assess changes in morph frequencies, I censused each of the ten sites during September of 1978 and 1979. During a census, the shell color of each snail seen is recorded, starting from a predetermined spot, and continuing for a fixed period of time. Immediately repeated

censuses show very little variation in shell color frequencies.

The first low tide series in September is somewhat unique in Oregon in that two daylight negative low tides can be worked per day. The timing of the censuses was arranged so that I was examining each population at the same time of day at the same point in the annual tidal cycle one year apart. Censuses were also taken at CH1 and CK on a monthly and seasonal basis. Observations of habitat affinities of the different morph categories were taken as either direct observations of morphology-habitat associations, or incidental information originally recorded for other purposes.

Results

Geographic Variation

Variation between populations can be examined as both variation over time and variation over space. The results of the annual censuses at the ten Oregon study sites are presented in figure 2. In each case, the solid colored Black morph and striped Grey-Black morph are clearly the most common shell color categories. At six of the sites (WR, MB, NH, SH, CH11, and CK) Black snails were the most frequent. At three others (LR, CA, and CH1) Grey-Black snails were more frequent. At one site, CB, the predominant category switched from Black to Grey-Black between censuses. The most common categories after Black and Grey-Black were Grey-Green, Green, and Grey. At none of the areas did any of these minor categories exceed 18%.

The changes in frequency from 1978 to 1979 appear small at first glance. However, a test of independence of the frequencies of each

shell color category over the two years shows that six of the ten areas did change significantly ($P < 0.05$) between 1978 and 1979 (WR, LR, CB, CA, CH1, and CH11; see figure 2). Three of the remaining sites showed marginally ($P < 0.1$) significant change (MB, SH, and CK). It is evident that a considerable amount of change is occurring in Thais shell color frequencies along the Oregon coast.

Further examination of these data shows that the changes between years significantly involved the two predominant categories (B and GB) at only three of the sites (WR, CB, and CA). At the other areas, the changes that occurred were primarily associated with the minor categories. This pattern presents a picture somewhat more stable, in that it appears that the two predominant color types may be relatively unchanging in frequency from year to year. Yet this is not so, as can be seen from the following observations of within year variation at two of the sites.

The monthly and seasonal changes of Black and Grey-Black snails at two areas, Cascade Head 1 and Cape Kiwanda, are shown in figure 3. Recall that between 1978 and 1979, CH1 changed significantly, but the changes were primarily due to minor category fluctuation; and that Cape Kiwanda showed only marginally significant change. The September censuses (the yearly censuses reported in figure 2) are indicated with arrows on each graph. Both sites are significantly heterogeneous ($P < 0.05$) over time. Moreover, the frequencies of the predominant morphs clearly changed over time at both areas. The dominant shell color category switched at both areas also, similar to the pattern seen at Cape Blanco in the yearly censuses. It appears that the shell color polymorphism in Thais emarginata, including the common morph types, is

rapidly changing at most of the sites examined.

There appears to be no consistent relationship between shell color frequencies and the environmental variables of each area including exposure to wave action, subtidal type, relative abundance of prey, direction of facing, latitude, or Thais density or distribution.

Intrapopulation Variation

Variation within a population can also be examined over time and space. Patchiness of phenotypic frequencies can be detected through descriptive analyses of micro- and macrohabitat correlations of different color morphs. The patterns seen in these types of observations can be misinterpreted due to the static nature of the observations in a possibly very dynamic system, so the observations were repeated at varying intervals throughout the study.

The observations of habitat affinities were made by recording the microhabitat (what substrate type the animal was on; Mytilus, Balanus cariosus, B. glandula, bare rock, algae, or in a crevice) and macrohabitat (whether a snail was on a boulder or a large reef) of different colored animals.

Microhabitat variation: Two types of microhabitat records were available for analysis. Over the course of the study, over 700 microhabitat records were taken at three of the sites (CH1, CK, and SH) for animals individually marked for other experimental purposes. Marking occurred at random with respect to microhabitat, so these observations represent a large independent sample of Thais microhabitat associations. Additionally, during the summers of 1978 and 1979, direct observations

were made of snails occupying particular mussel beds and barnacle beds at CH1, noting the relative frequencies of each shell color in each microhabitat. These observations resulted in 3192 individual records.

Analyses of this data set are presented in Table 1. In all cases there is a significant association between shell color and microhabitat type. However, when Black and Grey-Black snails are considered separately, they show no such association (Table 1). Some of the minor categories (approximately 16% of the combined group) seem to have strong associations between shell color and the particular substrate types they occupy. The predominant phenotypes (B and GB), when considered separately, are randomly distributed with respect to microhabitat.

Separate analyses of the sequential samples of CH1 are given in Table 2. These results are similar to those seen in Table 1 in that a three factor heterogeneity test shows a significant interaction between shell color and microhabitat. When Black and Grey-Black snails are analyzed separately, no such association is seen. Again it is the minor categories that appear to be substrate dependent. An examination of the three way interaction between shell color, microhabitat, and time is not significant, indicating that the relationship between shell color and microhabitat does not change through time.

Macrohabitat variation: In Oregon, T. emarginata is found in two common, distinct rocky intertidal macrohabitats; cobble and reef areas. I define cobble habitats as consisting of boulders up to 4 or 5 meters in diameter. A typical cobble habitat is a boulder field with rocks of varying size strewn along a beach. Reef habitats are areas where bedrock is exposed to the tides. Cobble areas support a greater density of snails than reefs, particularly where a large number of

boulders are packed together.

As these macrohabitats are easily distinguishable, in areas where both macrohabitats occurred, I simply noted the macrohabitat type in which I was working when taking a census. This allows: 1) comparisons of shell color frequencies within each macrohabitat type at a site on the same date, 2) comparisons of these frequencies between sites. At Cascade Head, these data were taken monthly over a five month period in 1978. This allows a third analysis; comparison of the relative frequencies over time.

The results of the third comparison, that of frequencies of all shell colors at CH1 over time within each macrohabitat type, are presented in Table 3. As with the microhabitat analyses, there is a significant interaction between shell color and habitat type ($P < 0.025$). The three way interaction between shell color, time, and macrohabitat was not significant. When Black and Grey-Black snails are considered separately, the frequencies of these two morphs are independent of time ($P < 0.95$) during the period of these observations, but there is marginal association ($P < 0.10$), between shell color and macrohabitat.

This same comparison between Black and Grey-Black snails can be made at seven sites, including CH1. Where multiple samples at a site were taken over time within a year, the samples were combined. This analysis provides observations of the macrohabitat correlations for about 28,000 snails from ten samples (Table 4). For nine out of the ten estimates, Black snails had a relatively higher frequency on cobble versus reef habitats. These independent samples can be analyzed using a binomial probability test. The probability of obtaining these results given an a priori probability that Black and Grey-Black snails

have an equal chance of having a higher frequency in both macrohabitat was 0.00977. There was a consistent association between shell color and macrohabitat for the two dominant phenotypes.

Discussion

Comparisons of morph frequency differences between populations of Thais emarginata show a lack of pattern similar to some other molluscan polymorphisms. No synchronous morph frequency relationships were found across populations associated with environmental variables such as latitude, exposure to wave action, subtidal type (sand or rock), prey species abundance, Thais density or distribution, or facing (N,S, or W). There was no indication of similarity of morph frequencies between closely adjacent areas (for example, CH1 and CH11 are only 0.5 km apart, but have different morph frequencies; see figure 2). Many times, studies of morphological variation attempt to document relatively small differences between populations and assess what forces might be causing the differences (e.g. Nussbaum, 1976). In Thais, I detected so little similarity between populations that patterns of variation become difficult to detect. These results suggest that there are no overriding external environmental variables driving morph frequencies or frequency changes, and imply that the changes are brought about by forces particular to each population.

One evolutionarily important pattern does emerge when considering the population frequencies as a whole. This pattern is change. Of the ten sites investigated, six had significant ($P < 0.05$) changes in morph frequency between 1978 and 1979. Three additional sites had marginally significant change. These changes were not all in the same direction

nor could any consistent relationship be found between the changes and the environmental variables discussed above. Presuming that changes in morph frequency reflect underlying changes in gene frequency, there appears to be a great deal of evolution occurring in the Thais populations examined.

At seven of the ten sites, changes did not significantly involve the dominant phenotypes Black and Grey-Black. However, the monthly and seasonal changes at CH1 and CK (figure 3) show that frequencies of these morphs are significantly heterogeneous and are evolving as well.

As mentioned in the introduction, once change has been established, it is very profitable to examine habitat relationships when studying a polymorphism, as these relationships could provide some insight into the evolutionary forces acting on the populations. I found significant associations between shell color and microhabitat (Table 1) considering all shell color categories. When Black and Grey-Black are considered separately, the relationship disappears, indicating it is the minor categories that are associated with substrate type.

There are two common explanations for such a relationship: organisms are choosing their habitat for some reason such as escape from predation, or protection from an environmental extreme such as sunlight (desiccation), wave action, etc.; or distribution is correlated with a habitat type due to a differential ability to survive in the various habitats. The second cause is not necessarily a matter of selection (Wiens, 1976).

The deviations from expected frequencies for the minor shell color categories are shown in Table 5. The lighter colored morphs (GGr and W) have higher frequencies on Mytilus, a dark colored microhabitat

type, and lower frequencies on the lighter colored barnacles. Green and Green-Black snails have higher frequencies on bare rock and lower frequencies on Mytilus. This pattern does not suggest that the snails are selecting cryptic habitats or are being differentially removed from other, non-cryptic microhabitat types. Additionally, there is little reason to suspect that differential susceptibility to an environmental force has produced the microhabitat associations. The explanation for the microhabitat associations in the minor categories remains obscure.

At CH1, there was a significant association between shell color and macrohabitat type. When Black and Grey-Black snails are considered separately, there is a marginal association between shell color and macrohabitat, expressed as a higher frequency of Black snails on cobble and Grey-Black snails on walls. When all macrohabitat observations are considered, only two sites showed significant frequency differences (CH1 77 and WR) between macrohabitats, but nine out of ten comparisons showed the same pattern of a higher frequency of Blacks on cobble and Grey-Black snails on reef. There is a slight, though very consistent pattern of association between shell color and macrohabitat for the pre-dominant phenotypes.

As mentioned previously, macrohabitat type along the Oregon coast can easily be divided into reef or wall type habitats and boulder or cobble areas. There is at least one environmental variable that is very different between these two macrohabitats. That is the force of wave action. The pressure of waves hitting a rock wall is very different than that of waves hitting cobble, where the energy of the wave can be dissipated. The same reasoning applies even more to the shear force of waves. Because the waves would be broken up, cobble

would experience considerably less shear force.

It has previously been shown that wave action is important in the rocky intertidal by others (Dayton, 1971; Connell, 1961, 1970; Menge, 1978). Emlen, 1966, suggested that wave shock is the most important source of mortality for Thais emarginata. Miller, 1974, gives further evidence for the importance of wave shock in Thais. These observations suggest that wave action is an important environmental variable to the snails. I suggest that the predominant morph types, Black and Grey-Black, are responding differentially to this force.

Though these results do not lead to an adaptive explanation for shell color per se, the correlation between shell color and response to an important environmental variable does suggest that shell color, or a product determined by genes closely linked to shell color loci, plays an important role in the ecological dynamics of this organism, and provide evidence for a tie between this "conspicuous" polymorphism and the population dynamics of T. emarginata.

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Summary

An examination of the shell color polymorphism in the rocky intertidal gastropod Thais (Nucella) emarginata revealed several patterns. Geographic variation over ten Oregon populations, in terms of shell color frequencies and frequency changes, showed no consistent pattern in terms of any environmental variable recorded for the sites. A solid colored Black morph, and a striped Grey-Black morph were the predominant phenotypes in all populations examined. There was a significant association between shell color frequencies and microhabitat type found for the minor shell color categories. The nature of the association did not seem to be cryptic and this pattern remains unexplained.

There was also an association found between shell color and macrohabitat type, this time involving Black and Grey-Black snails. An examination of macrohabitat associations over seven Oregon populations show a slight, but very consistent, association between Black and Grey-Black snails and macrohabitat type. I postulated that this association is due to a differential response by the two shell color types to wave action in these two macrohabitat types.

TABLE 1. Analyses of microhabitat correlations in Thais. Five microhabitats were sampled in two different ways for each of the eight shell color categories. These results represent tests of association conducted on each data set plus the combined data for all shell color categories and Black and Grey-Black snails separately.

Observations of Marked Animals

All Color Categories

N = 784

$\chi^2 = 53.9$

28 d.f.

P < 0.005

Black and Grey-Black Only

N = 563

$\chi^2 = 6.84$

4 d.f.

P < 0.25

CH1 Microhabitat Observations

All Color Categories

N = 2408

$\chi^2 = 47.82$

28 d.f.

P < 0.025

Black and Grey-Black Only

N = 2100

$\chi^2 = 5.30$

4 d.f.

P < 0.30

Combined Samples

All Color Categories

N = 3192

$\chi^2 = 99.32$

28 d.f.

P < 0.001

Black and Grey-Black Only

N = 2663

$\chi^2 = 5.06$

4 d.f.

P < 0.30

TABLE 2. Three way tests of independence of microhabitat observations at Cascade Head 1, 1978.

<u>All Color Categories</u>	<u>Black and Grey-Black Only</u>
N = 2434	N = 2089
$\chi^2 = 331.8$	$\chi^2 = 135.96$
129 d.f.	27 d.f.
P < 0.001	P < 0.001
Microhabitat X Date	Microhabitat X Date
$\chi^2 = 140.02$	$\chi^2 = 122.02$
8 d.f.	8 d.f.
P < 0.001	P < 0.001
Shell Color X Date	Shell Color X Date
$\chi^2 = 86.14$	$\chi^2 = 2.78$
36 d.f.	4 d.f.
P < 0.005	P < 0.75
Microhabitat X Shell Color	Microhabitat X Shell Color
$\chi^2 = 42.64$	$\chi^2 = 1.36$
1 d.f.	1 d.f.
P < 0.001	P < 0.25
Three Way Interaction	Three Way Interaction
$\chi^2 = 63$	$\chi^2 = 9.8$
70 d.f.	8 d.f.
P < 0.9	P < 0.5

TABLE 3. Three way tests of association of macrohabitat correlations of Thais over time at CH1.

<u>All Shell Color Categories</u>	<u>Black and Grey-Black Only</u>
N = 1717	N = 1501
$\chi^2 = 228.38$	$\chi^2 = 487.4$
52 d.f.	10 d.f.
P < 0.001	P < 0.001
Macrohabitat X Date	Macrohabitat X Date
$\chi^2 = 151.76$	$\chi^2 = 479.46$
3 d.f.	3 d.f.
P < 0.001	P < 0.001
Shell Color X Date	Shell Color X Date
$\chi^2 = 51.76$	$\chi^2 = 0.52$
21 d.f.	3 d.f.
P < 0.001	P < 0.95
Macrohabitat X Shell Color	Macrohabitat X Shell Color
$\chi^2 = 6.02$	$\chi^2 = 3.34$
1 d.f.	1 d.f.
P < 0.025	P < 0.10
Three Way Interaction	Three Way Interaction
$\chi^2 = 9.42$	$\chi^2 = 4.08$
21 d.f.	3 d.f.
P < 0.99	P < 0.30

TABLE 4. Binomial analysis of macrohabitat affinities in *Thais*. Seven different sites are represented, as well as samples from different years at CH1 and CK. A "*" represents a higher frequency of Black snails in the given macrohabitat type.

Observation	Shell Color	Macrohabitat	
		Reef-Wall	Cobble
CH1 1977 Census	Black	1994	1516*
	Grey-Black	1653	1136
CH1 1978 Habitat and Census	Black	2424	2678*
	Grey-Black	3647	3947
CH1 1979 Census	Black	241*	173
	Grey-Black	444	321
CK 1977 Census	Black	501	775*
	Grey-Black	435	612
CK 1978 Census	Black	645	1303*
	Grey-Black	714	1415
WR 1978 Census	Black	33	112*
	Grey-Black	6	4
LR 1978 Census	Black	54	100*
	Grey-Black	86	106
CB 1978 Census	Black	88	97*
	Grey-Black	78	75
MB 1978 Census	Black	122	33*
	Grey-Black	105	23
NH 1978 Census	Black	101	54*
	Grey-Black	34	14

The binomial probability of Black snails having a higher frequency on Cobble 9 out of 10 times is less than 0.01.

TABLE 5. Deviations from expected frequencies in the microhabitat observations in Thais minor shell color categories. A "+" signifies greater than expected numbers, a "-" means fewer than expected, and a "0" means observed and expected numbers were not significantly different.

		<u>Microhabitat Type</u>				
		<u>Mytilus</u>	<u>Balanus cariosus</u>	<u>B. glandula</u>	<u>Bare Rock</u>	<u>Crevice</u>
<u>Shell Color</u> <u>Category</u>	G-Gr	+	-	-	0	+
	Gr	-	0	0	+	+
	G	0	0	0	+	0
	0	0	0	0	0	0
	W	+	-	-	0	0
	Gr-B	-	0	0	+	0

Figure 1. Location of the ten Oregon study sites.

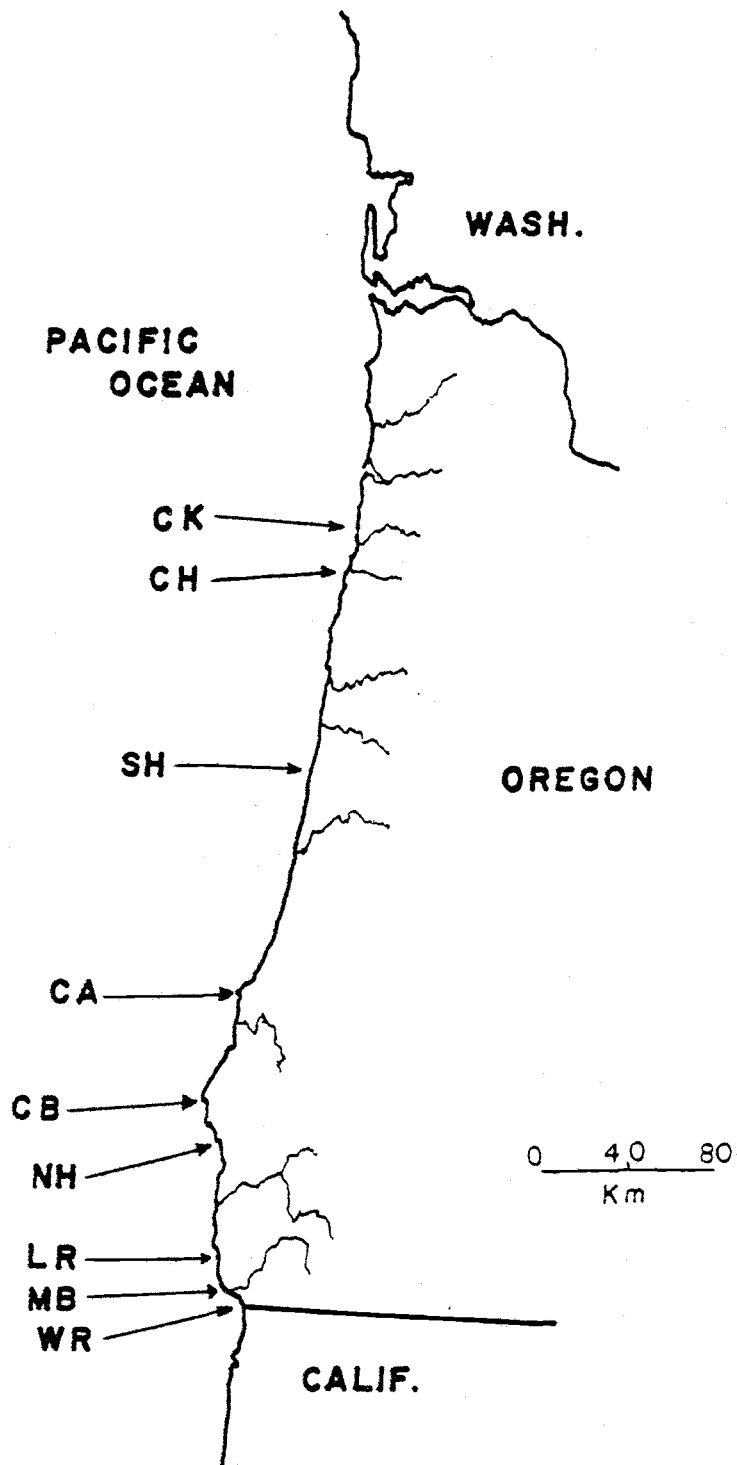
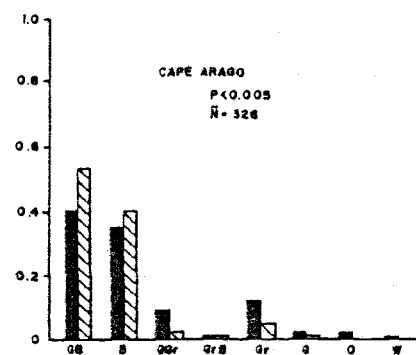
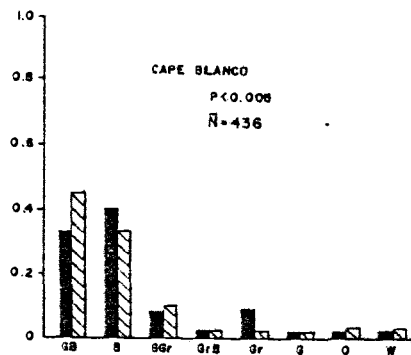
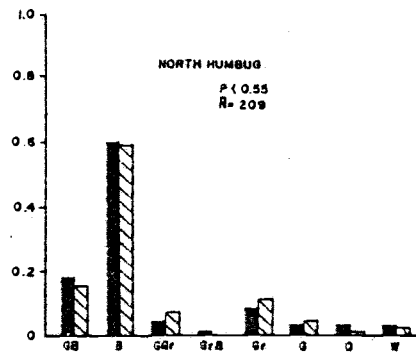
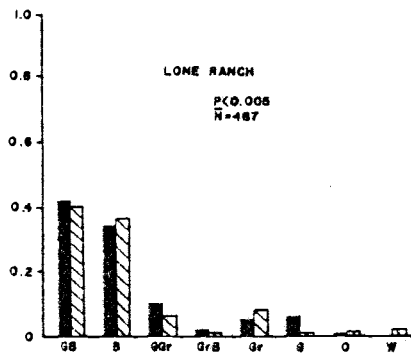
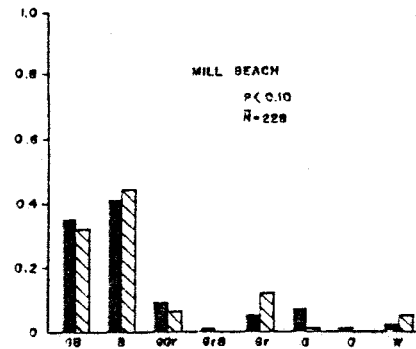
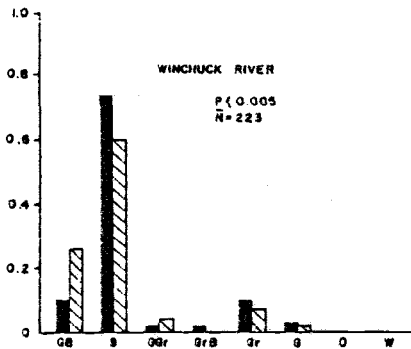


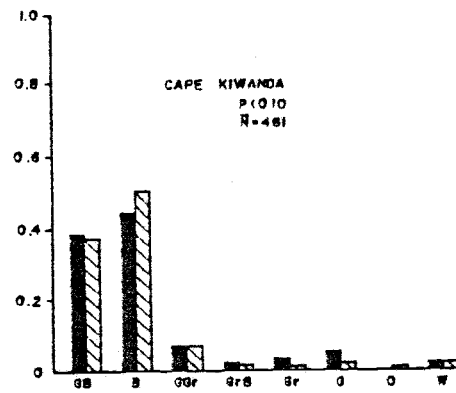
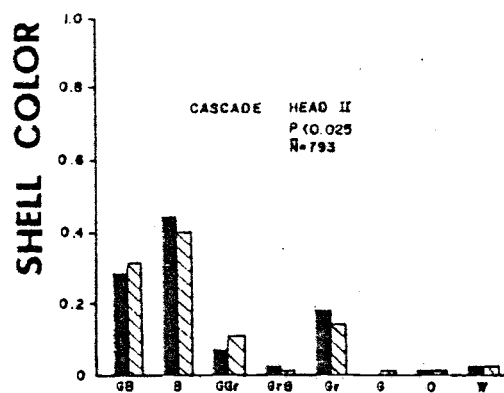
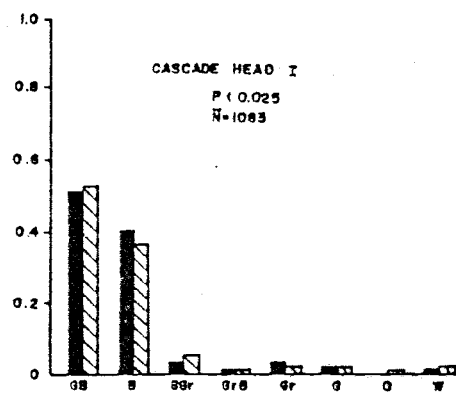
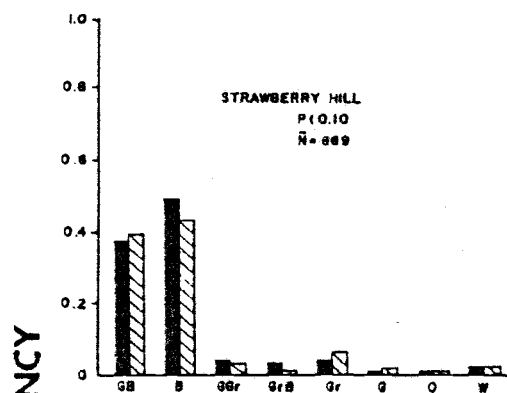
Figure 2. Results of the annual censuses at the Oregon study sites, 1978 - 1979. Below the name of each site is the probability associated with change between years, and the average sample size for each census.

SHELL COLOR · FREQUENCY



SHELL COLOR CATEGORY

Figure 2. (Con't)



SHELL COLOR CATEGORY

Figure 3. Monthly and seasonal changes in the frequency of Black and Grey-Black snails from CH1 and CK. The arrows in the figure refer to the September censuses reported in Figure 2.

X = Grey-Black; O = Black Snails

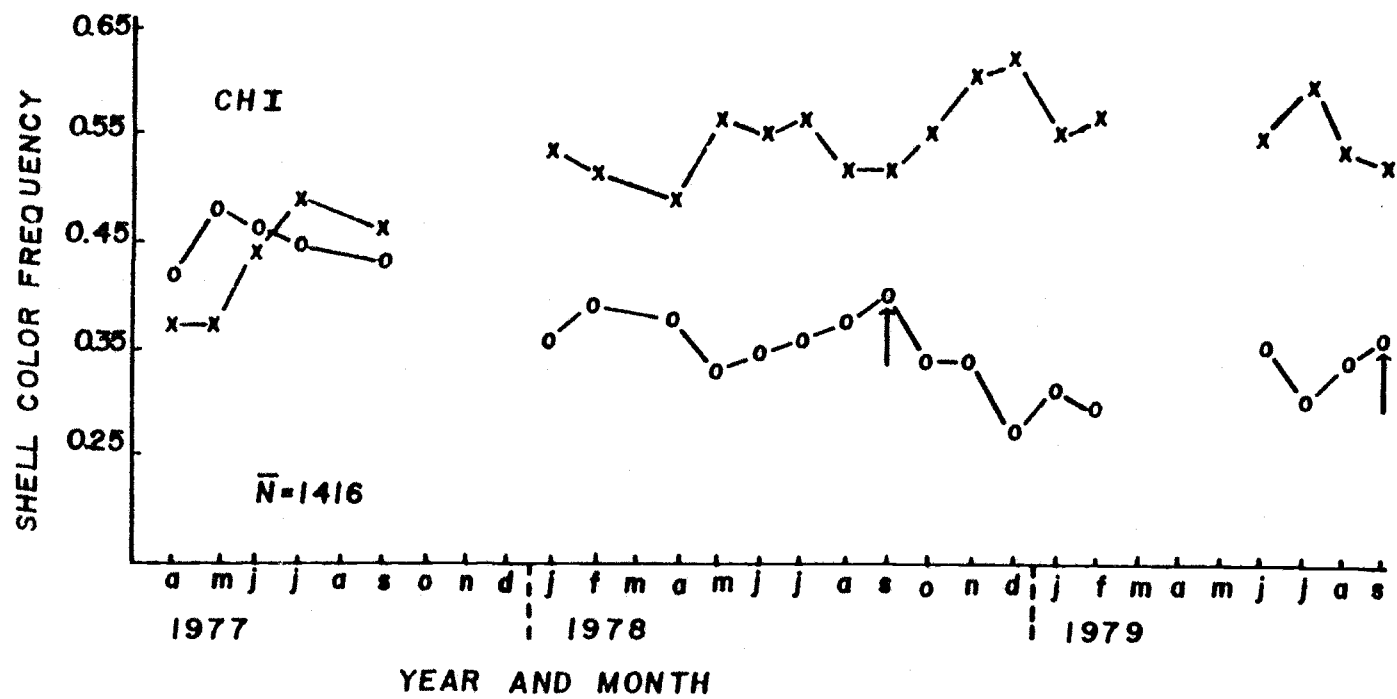
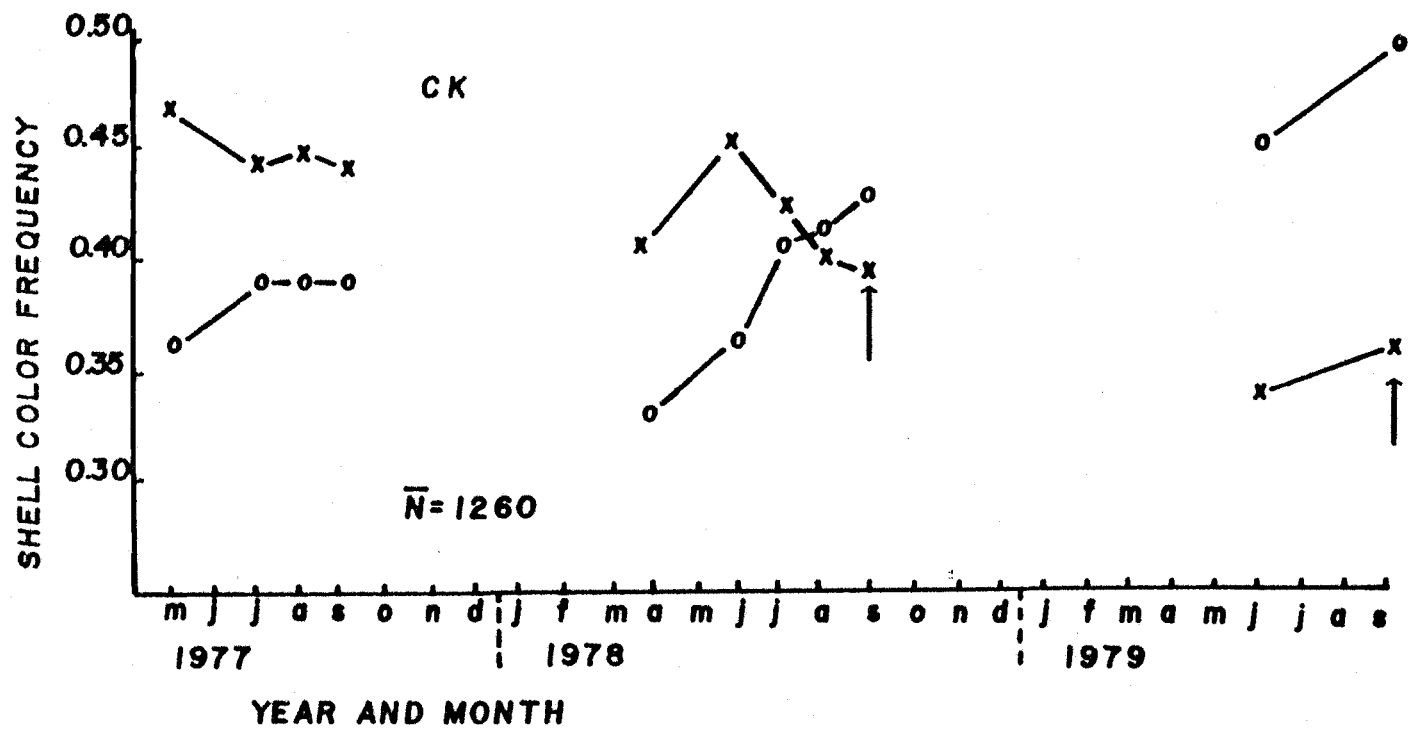


Figure 3. Continued.



III. THE ROLE OF MOVEMENT IN THE THAIS EMARGINATA SHELL COLOR POLYMORPHISM

Thais (Nucella) emarginata, a common rocky intertidal predatory gastropod of western North America, is highly polymorphic for shell color. In the previous paper, I described the polymorphism, established a genetic basis for it, examined geographic patterns of change in shell color frequencies and assessed micro and macrohabitat associations of the different shell color types. The predominant shell color categories of the Thais populations I examined were solid colored Black shells (B), and striped Grey-Black (GB), which together make up 70 - 90% of the snails in the populations I examined. These two common morphs were found to have a slight, but significant association with macrohabitat type (cobble vs. reef type areas), and it was suggested that this may be due to a differential response to wave action in these two macrohabitat types. I proposed that shell color, or genes closely linked to shell color, are important in the ecological dynamics of this animal.

In this paper, I report the results of an assessment of the association between shell color and movement. Movement was suspected to be important in the population dynamics of Thais from the results of previous study. This research explores the possibility of a relationship between the dynamics of movement and change in shell color frequencies.

The reasoning behind choosing movement for study was the following: a great deal is known about the natural history and ecology of this animal due to the efforts of previous workers (Connell, 1970; Emlen,

1966; Spight, 1972; Bertness, 1977). One common denominator of marking studies done with Thais is a very high disappearance rate of tagged animals, approaching 100% yearly turnover, indicating a very high adult mortality in the populations under study. However, if one takes the most liberal estimates of reproduction (Emlen, 1966; Spight, 1972), recruitment of young snails into the population via reproduction falls far short of replacing the number of lost individuals calculated from mark and recapture estimates. This suggested that either the marking method itself was influencing the loss rates, or that marked animals were moving out of the population.

In 1975, I tried a different marking method, one designed to disturb the animals as little as possible (see Methods). I found, as did the other studies, close to 100% turnover in a year. I also found that over 30% of the tagged snails had changed location before they disappeared. This result suggested that it was movement, not marking technique, that was responsible for the disappearance rates.

Movement is one of the most important and least studied phenomena in population biology. The role of movement in the ecological and genetical structure of natural populations is almost totally unknown. This is particularly disturbing in that rates of movement, or a lack of movement, are essentially what defines or delimits a population of organisms. Krebs, et al., 1973, were the first to show an association between genetic change and movement using two species of voles in southern Indiana. They found a correlation between genotypes at two blood protein loci and movement tendency. Further field studies of this type, establishing a relationship between genes and movement, seem to be

lacking.

In this study, I will underscore the importance of movement in the ecology of Thais emarginata. In addition, I will ask if there is an association between the dynamics of shell color frequencies and movement of Black and Grey-Black snails in an Oregon population of Thais.

Study Site and Methods

The site chosen for examining movement in Thais was Cascade Head located within the Cascade Head Scenic Research Area on the north central Oregon coast. The intertidal area at Cascade Head (Figure 1) is a southwest facing sandy beach with boulders lying on the beach up against a ledge, part of the Cascade Head bluff. Immediately to the south of the site is the mouth of the Salmon River. Exposure to wave action is not severe at Cascade Head due to the presence of three offshore islands protecting the site. Cascade Head was chosen for several reasons. The density of Thais at the site was very high (and remained so throughout the study). The linear nature of the habitat (Figure 1) limited movement to two directions, east and west. The presence of boulders surrounded by sand was ideal for the study of movement because the unambiguous scoring of a move from a boulder to a boulder or ledge was very easy. Finally, I thought that the presence of a cave to the west, and decreasing salinity to the east (upriver) would limit movement in such a way as to make it easier to follow moving snails.

Censuses of the shell color frequencies of all snails seen in the area were taken at varying intervals throughout the study (Figure 2).

This was done to see if any changes were occurring in overall shell color frequencies during the period of the study. A census was taken by starting at the east wall of the cave, proceeding east and recording the shell color of all snails seen in a fixed period of time.

During the summers of 1977 and 1978, a removal experiment was conducted at Cascade Head. A rock isolated by sand (Removal Rock; RR in Figure 1) was chosen and all snails seen on the rock were removed and replaced out of the study site. After the initial removals, it was assumed all snails on the rock moved there from elsewhere. The results presented here give an idea of the extent with which snails moved.

The movement study was conducted as follows: A boulder centrally located in the area, but surrounded by sand, was chosen and designated the movement rock (MR, Figure 1). Snails on this rock were painted with nail polish and shell colors recorded. Painting of unmarked snails on the movement rock continued throughout the study, and monthly estimates of the shell color frequencies of painted (non-moving) snails were taken. When a painted snail was found off of the movement rock (i.e. one that had moved), its shell color, shell length, microhabitat (whether on a barnacle, mussel, bare rock, or in a crevice), distance from the movement rock, and the direction it had moved were recorded. In addition, it was tagged with a colored numbered bee tag (available from Ch. Graze Kg., Postfach 2107, 7056 Weinstadt-Endersbach, West Germany) which was cemented on the shell with Loktite adhesive. As my interest was in undisturbed movement, tagging allowed assessment of individual snail movement after the initial move from the movement rock, and prevented the possibility of overestimating movement by counting the same snail more than once.

Results

Censuses

The results of the censuses (Figure 2) indicate that there was considerable change in frequencies of Black and Grey-Black snails at Cascade Head over the two and one half year period of the study. Analysis of these frequencies (Table 1) showed significant heterogeneity (G - test, $P < 0.001$) over time. There was a significant regression (Table 1) of both Black and Grey-Black shell color frequencies over time. Black snails have decreased in frequency, and Grey-Black snails have increased in frequency during the study.

Removals

During the summer of 1977, I removed all snails on the removal rock nine times after the initial removals. On the average, 246 snails were removed on each occasion. Removals were made two days apart in 1977 to check the speed of recolonization. Over 300 snails were removed on the first visit. Two days later there were over 150 snails found on the rock, indicating that recolonization is probably very fast.

During the spring and summer of 1978, the removal experiment was repeated on the same rock at Cascade Head. Twelve removals were conducted and, on the average, 45 snails were removed each visit. This drop in the number of snails removed suggests a great deal of variation in the number of snails moving from year to year. There was no corresponding drop in overall snail density at the site in 1978.

Movement

During the movement study (1978), 2194 snails were painted with

nail polish on the movement rock. Painting of unmarked animals continued monthly (Spring) and bi-monthly (Summer) throughout the study. Monthly estimates of the shell color frequencies of painted, non-moving snails were taken before additional unmarked snails were painted. An estimate of the frequencies of snails available for movement during a particular time interval includes those already on the movement rock plus those newly painted. These frequencies can be compared with those that actually moved and were tagged during the particular time interval in question to determine if there is an association between shell color and probability of movement. There was little overall tendency for the shell color frequencies of those available for movement and those that did move to be different (Table 2). However, on a month to month basis, there was a significant amount of heterogeneity (Total heterogeneity, $G = 272.9$, $P < 0.001$; Monthly heterogeneity, $G = 195.92$, $P < 0.001$) in shell color frequencies from both sample types.

One way to examine this heterogeneity is to compare the changes with those occurring in the population as a whole (from the population censuses, Figure 2), during the same time interval (Figure 3). Of the 24 pairwise comparisons of these frequency changes (painted vs. tagged, tagged vs. censuses, and painted vs. censuses), 18 were in the same direction. This indicates significant ($P < 0.03$) relationship between changes in overall morph frequency and changes in frequency of snails involved in the movement observations. This relationship between the dynamics of movement and the dynamics of morph frequency change in the population is an important one when attempting to assess the causes of change in the population, and further reinforces the importance of

movement in Thais, particularly in conjunction with the shell color polymorphism.

If movement is related to shell color frequency change, then a closer examination of those animals that moved and were tagged might provide some insight into patterns of movement behavior, correlated with shell color, which might affect the direction of overall frequency change in the population. Several variables were recorded on tagged snails including shell length, microhabitat type, distance moved, and direction moved. As mentioned previously, there seems to be little relationship between the shell color frequencies of painted snails available for movement and the frequencies of those that actually moved and were tagged. As documented previously, there is no apparent correlation between shell color of the tagged snails and microhabitat type for Black and Grey-Black snails. Also, the mean shell lengths of tagged Black and Grey-Black snails (B; $\bar{x} = 17.39 \pm 0.23$ mm; GB; $\bar{x} = 16.95 \pm 0.17$ mm) were not significantly different.

When a tagged snail was last seen, it had moved an average distance of 9.12 meters from the movement rock (Figure 4). The longest distance recorded was 85 meters. A Mann-Whitney U test indicated no significant differences in the distributions of the two morph types with respect to distance moved. Black snails had a slight tendency to be underrepresented in the short moves and Grey-Black snails in the long moves, but the differences were very minor.

The direction a snail had moved from the movement rock when last seen, because of the nature of the Cascade Head intertidal area (non-habitable space in two of four directions) can be reduced to a move east

or a move west. A comparison of the frequencies of the two morph types disappearing east and west (Table 3) showed that Black snails moved west (downstream) at a higher frequency than would be expected, and that Grey-Black snails moved east (upstream) more than would be expected if movement were random ($P < 0.05$).

An interpretation of this result, in light of overall frequency changes in the population, can best be made by examining the differential directions of movement within the context of the Cascade Head site. A snail moving east (the tendency for Grey-Black snails), eventually runs into a barrier to further movement due to decreased salinity from the presence of the river (Figure 5). A snail moving east, in effect, cannot leave the area. If it continues to survive and move, it must return to the site I was examining. A snail moving west (the tendency for Black snails), faces no such barrier to further movement (the cave did not impede movement west), and can continue moving in that direction for several kilometers.

If this scenario is correct, two predictions can be made. One is that there should be an overall reduction in the relative frequency of Black snails in the Cascade Head population. This is exactly what happened (Figure 2; Table 1).

Another prediction is that a snail moving east should stay in the population longer than one moving west. This can be examined by counting the number of days multiply recaptured snails moving in these two directions stayed in the population. The mean number of days a snail moving east stayed in the population is longer than for those moving west (Table 4). Though the distribution of days for all snails moving

east and west were not different, Black snails, taken alone, moving east versus west, had significantly different distributions of the number of days in the population ($P < 0.05$); the mean number of days a Black snail moving east stayed in the population was over 10 days longer than for a Black snail moving west.

Discussion

As stated in the introduction, one of my original interests in the Thais emarginata polymorphism was to determine whether movement rates might account for part of the very high disappearance rates of tagged snails previously documented in the literature. The answer to this question is yes. Thais emarginata has the capability to move often, over long distances, and survive (Figure 4). The results of both the movement and removal studies suggest that changing location is a common part of the lifestyle of this animal. When these data are taken into account, the near 100% yearly turnover of marked animals recorded by myself and others (using different marking techniques) are no longer at odds with the reproductive characteristics of Thais, as many disappearances are undoubtedly due to movement.

Examination of the influence of movement on the dynamics of shell color frequencies of Black and Grey-Black snails at Cascade Head (Figure 3) showed that there is a significant association between shell color changes in the population as a whole and those snails observed in the movement experiment. This is consistent with the idea that the dynamics of movement influence the dynamics of the shell color frequencies in the population as movement, after all, is an active process.

If the month to month change in frequency of a given morph was negative during a particular time interval, there were usually fewer snails of that shell color available to move (painted snails), and fewer actually moved (tagged snails) during the same time interval (Figure 3). This relationship suggests that the heterogeneity in shell color frequencies was real, and that movement is closely related to these changes.

Even more interesting (and more puzzling) is the relationship between the direction of movement and shell color. Grey-Black snails moved east at Cascade Head at a significantly higher frequency than expected, and Black snails moved west at a higher frequency than expected.

Within the context of the Cascade Head site (Figure 1), and the results of the population censuses (Figure 2), all of these data support the hypothesis that the process of movement is at least partially responsible for overall changes in shell color frequency at Cascade Head, and that differential directions of movement, predicting a steady loss in the frequency of Black snails and increase in the frequency of Grey-Black snails (the occurrence at Cascade Head), play a role in driving the direction of overall change.

There are important questions about these results that remain to be addressed. Why do snails move at all, what is the significance of the association between shell color and the direction of movement, and what is a biological population of Thais emarginata, in light of the movement results?

Why move?

Intuitively at least, changing habitats involves risk. In the rocky intertidal system, this risk can be interpreted as failure to find a suitable new habitat for resettling before becoming a meal for another organism, or dying from exposure.

If Thais movement is by choice, the possible gain from moving must outweigh the risk involved in order to make a move profitable. This suggests that changing microhabitat suitability at home, in terms of food supply, predation intensity, physical stresses, or conspecific density cause an animal to move. Work by Connell (1961), Emlen (1966), Paine (1969), Dayton (1971), Menge (1978), and others has shown that the rocky intertidal system can be quite variable in time and space. If things get bad enough, a snail could very simply drop off a rock and let the ocean carry it (hopefully) to a suitable new location.

On the other hand, movement may be involuntary. Emlen (1966) suggests that one major cause of mortality (disappearance of tagged snails) in the Thais populations he studied was the result of being knocked off a rock by a wave and washed away. All that is required for this to be consistent with the dynamics of overall movement reported here is for successful resettlement to be possible after being washed off by a wave, a requirement necessary for either voluntary or involuntary movement.

Bertness (1977) has shown that Thais emarginata exhibits a behavior termed photo-orthokinesis, which means snails have the ability to orient themselves in their environment with respect to sunlight and gravity. This suggests that Thais has, at least, the capability of finding a good

habitat in an unknown situation. This capability does not differentiate between voluntary and involuntary movement however, and the exact reason for movement of either kind await further study.

Why move in different directions?

This question is particularly puzzling in that the results of this study are somewhat unique in the ecological genetics of natural populations and it is difficult to find a context within which to place an association between phenotype and direction of movement. For Thais at Cascade Head, differential directions of movement of the common morphs led me to search for an environmental variable associated with the directions moved. One such variable is the direction of wave action. I postulated wave action to be important in the macrohabitat correlations of Black and Grey-Black snails reported previously.

Wave action has been shown to be important in the rocky intertidal system (Dayton, 1971; Connell, 1961, 1970; Menge, 1978), and for Thais emarginata in particular (Emlen, 1966; Miller, 1974). The direction of wave movement at Cascade Head is from west to east, the same direction as most Grey-Black snails moved and opposite to the direction that Black snails tended to move. It is not difficult to imagine that Black and Grey-Black snails are (whether by choice or not) responding differentially to this powerful environmental force, resulting in different directions of movement associated with shell color. For example, this behavior could simply be that the two morphs drop off a rock (or are washed off) at different points in the cycle of a wave hitting shore. A differential response to wave action due to shell color, or genes

closely linked to shell color loci, is the same behavior I suggested was responsible for the macrohabitat correlations found in the previous study, and underscores the possible influence of this important environmental variable on the population and genetical dynamics of Thais emarginata.

What is a population of Thais?

One final important question raised by the results of this study is, considering the high frequency of movement in Thais observed during this study, what is a biological population of Thais emarginata? If the definition of a population is taken to be a potentially interbreeding group of organisms of the same species, my results suggest that Thais may have a much larger population size than was previously suspected. Defining the limits to a population is difficult in any field study, and there exists the danger of misinterpretation of the data gained due to an artificial delineation of population size. Though it seems that the behaviors I was able to observe were sufficient to account for much of the change in shell color frequencies at the intertidal site I studied, my own results blurred any definition of population size, and the question of what is a biological population of Thais emarginata remains unanswered.

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TABLE 1. Analyses of the changes in shell color frequencies of Black and Grey-Black snails at Cascade Head, 1977 - 1979.

1. Test of the heterogeneity of shell color frequencies over time.

$$G = 676.66$$

$$22 \text{ d.f.}$$

$$P < 0.001$$

2. Regression analysis

Frequencies of Black snails over time

$$F_{(1,20)} = 25.96$$

$$N = 22$$

$$R^2 = 0.56$$

$$P < 0.01$$

$$Y = 0.37 - 0.0044 (X)$$

Frequencies of Grey-Black snails over time

$$F_{(1,20)} = 20.92$$

$$N = 22$$

$$R^2 = 0.51$$

$$P < 0.01$$

$$Y = 0.53 + 0.0053 (X)$$

TABLE 2. Analyses of the frequencies of painted and tagged Black and Grey-Black snails from the movement observations, Cascade Head, 1978.

1. Test of independence of shell color frequencies.

	Painted	Tagged
Black	851	71
Grey-Black	1379	136

$$\chi^2 = 1.20$$

$$P < 0.5$$

TABLE 3. Comparison of the frequencies of Black and Grey-Black snails that moved east and west at Cascade Head, 1978. Proportions of the total for each direction are in parentheses.

	East	West
Black	35 (0.29)	31 (0.45)
Grey-Black	85 (0.71)	38 (0.55)

$$\chi^2 = 4.79$$
$$P < 0.05$$

TABLE 4. A comparison of the number of days snails recaptured more than once stayed in the population for Black and Grey-Black snails that moved east and west at Cascade Head, 1978.

East Moves

Black snails	N = 18	
	\bar{X} = 74.56 Days	
	S.D. = 40.7 Days	
		Combined Totals
Grey-Black snails	N = 48	N = 66
	\bar{X} = 67.65 Days	\bar{X} = 69.53 Days
	S.D. = 43.25 Days	S.D. = 42.37 Days

West Moves

Black snails	N = 18	
	\bar{X} = 64.39 Days	
	S.D. = 51.05 Days	
		Combined Totals
Grey-Black snails	N = 27	N = 45
	\bar{X} = 66.22 Days	\bar{X} = 65.49 Days
	S.D. = 46.91 Days	S.D. = 48.01 Days

Mann - Whitney U	- - Combined Totals
	t = 0.8
	P < 0.40
	- - Black snails only
	t = 3.39
	P < 0.05

Fig. 1. Map of the Cascade Head study site. Cascade Head is a sandy beach next to a bluff with boulders lying on the beach.
MR = Movement Rock. RR = Removal Rock.

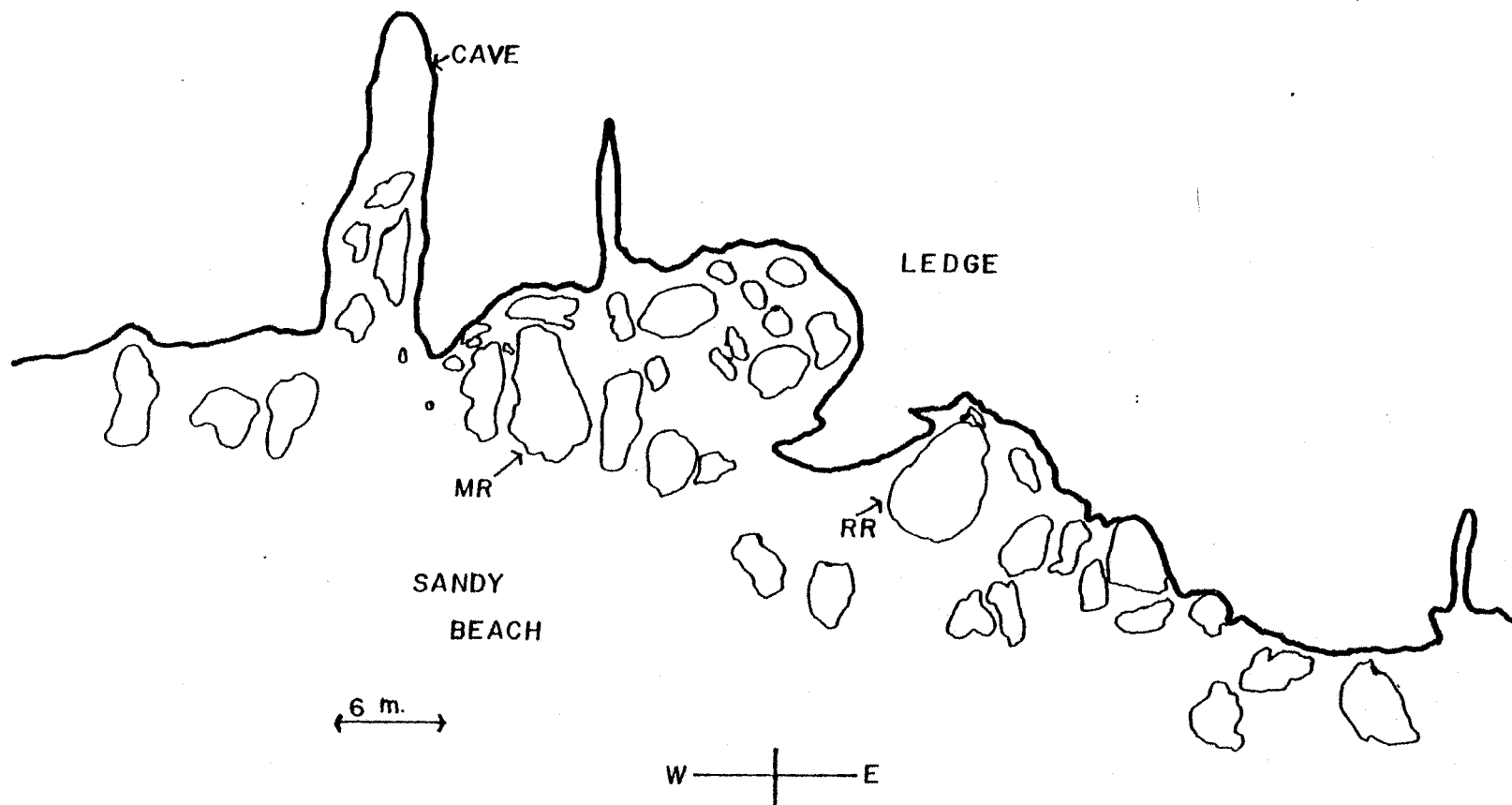


Fig. 2. Frequencies of Black and Grey-Black snails at Cascade Head, 1977 - 1979. X = Grey-Black; O = Black

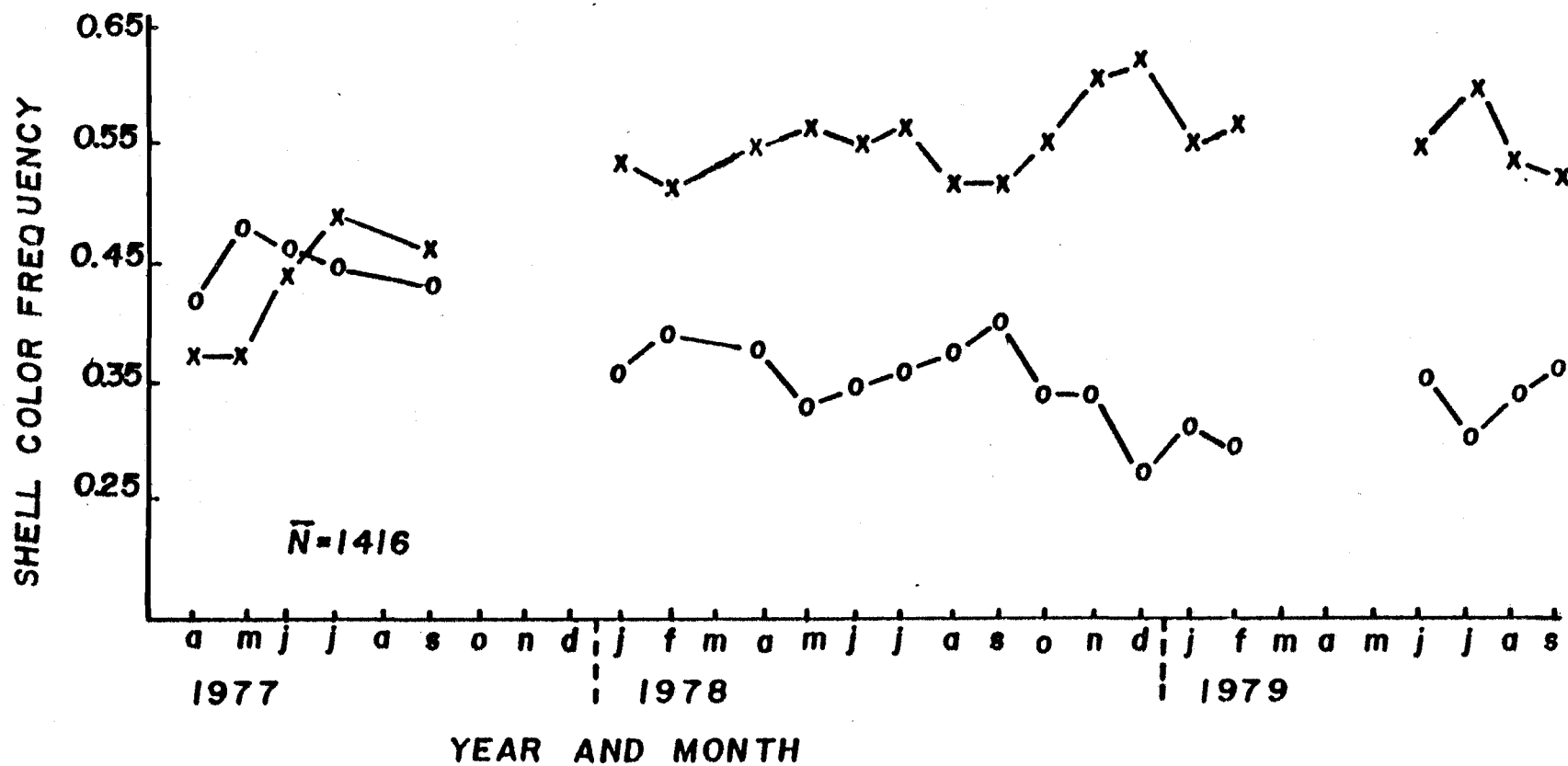


Fig. 3. Comparisons of the frequencies of censused, painted, and tagged Black and Grey-Black snails during the movement study.

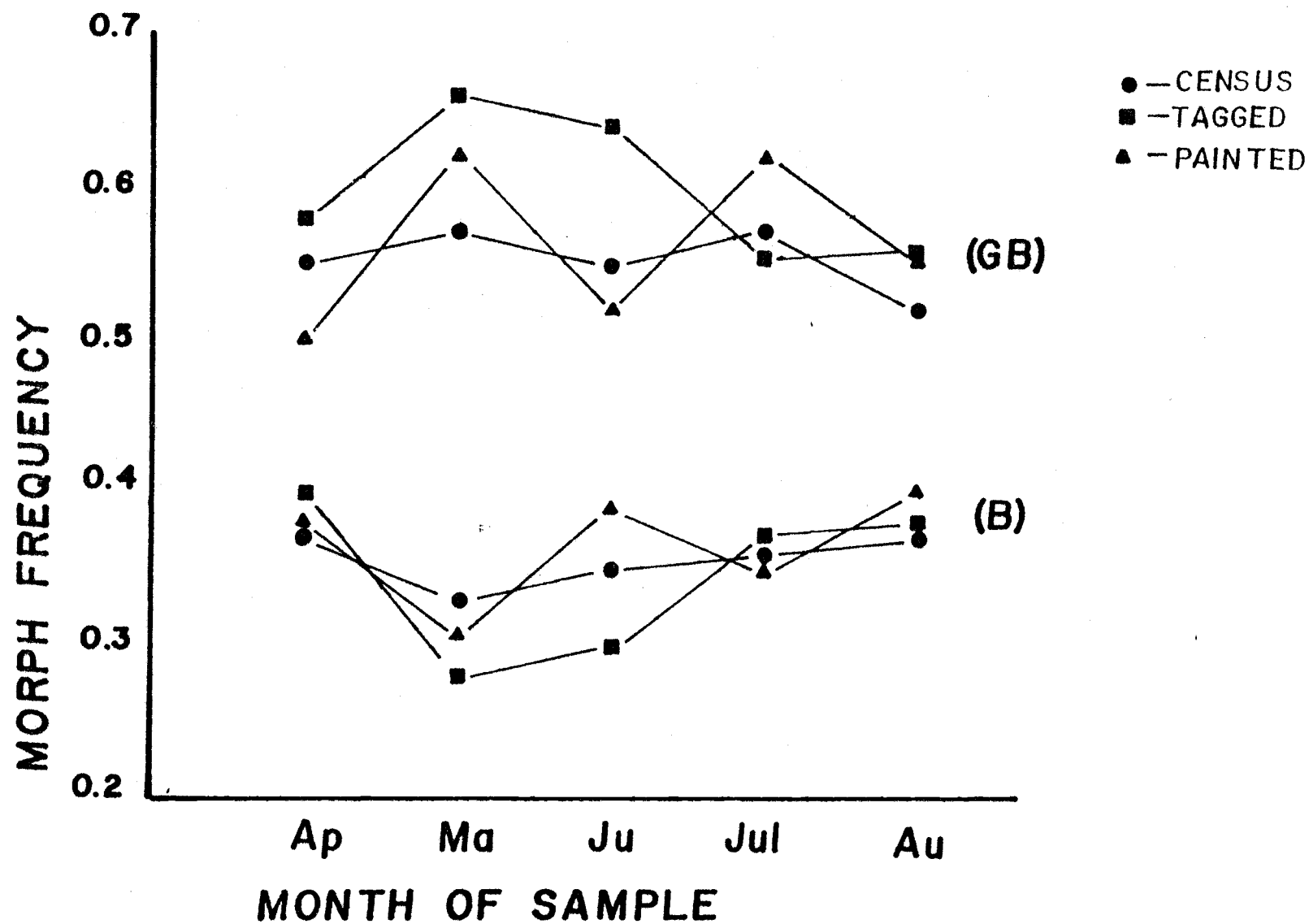


Fig. 4. Distribution of distances moved from the movement rock by tagged snails at Cascade Head, 1978.

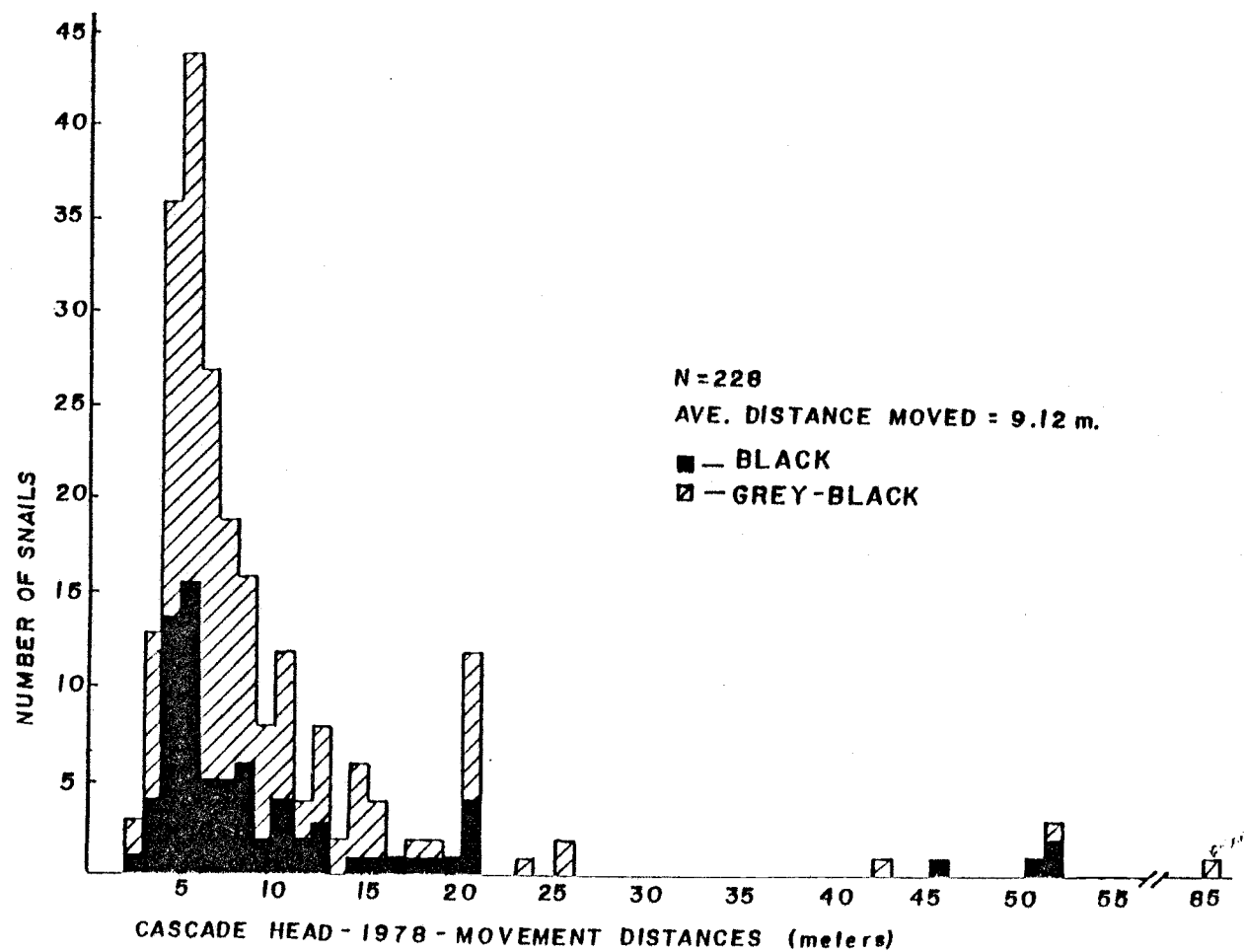


Fig. 5. Diagram of the consequences of movement in different directions at Cascade Head. Snails leave (1 and 4) the movement rock (MR), in both directions, east and west. Snails continuing west (5) face no barrier to further movement and surviving snails can continue to move in that direction. Snails moving east run into the barrier of the river (3), and surviving snails (2) that are moving must eventually return to the area of the movement rock.

