

Habitat Choice in the Intertidal Snail *Tegula funebris*

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Abstract

Intraspecific variation in habitat preference was studied in the black turban snail *Tegula funebris* (Adams, 1854), at two locations on the northern U.S. Pacific Coast. Studies in 1977 using a mass-marking technique showed that most snails found either above or in permanent tidepools at low tide return to their original habitats within a few days after experimental habitat reversal. This return is not due to homing behavior, but is apparently based on the recognition of ecological characteristics of the two habitats. Experiments in 1978 with individually-marked snails suggest that they prefer specific intertidal levels, and not merely above-pool or in-pool habitats. Theoretical models predict that this behavior could play a major role in the maintenance of genetic polymorphism in a species like *T. funebris*, whose intertidal environment is characterized by extreme spatial heterogeneity.

Introduction

Some animal species occurring in spatially heterogeneous environments exhibit intraspecific variation in habitat preference. An early example of habitat choice was discovered by Kettlewell (1955). He placed light and dark forms of a moth (*Biston betularia*) in a barrel lined with alternating strips of black and white paper, and found that they preferred the background on which they were cryptic. Habitat selection behavior has been found in other insects (Sargent, 1966; De Souza *et al.*, 1970; Trpis and Hausermann, 1975; Taylor and Powell, 1978; Cavener, 1979), gastropod molluscs (Sedlmair, 1956; Giesel 1970), and mammals (Wecker, 1963).

Habitat selection could play a major role in the maintenance of genetic polymorphism in natural populations, according to theoretical models (Hedrick *et al.*, 1976; Powell and Taylor, 1979). Levene (1953) was the first to point out that if individuals choose habitats in which their fitness is

highest, the severity of natural selection required to maintain a balanced polymorphism in a heterogeneous environment would be reduced. Conversely, if a polymorphism is being maintained by selection in a spatially heterogeneous environment, a selective advantage would accrue to individuals exhibiting habitat choice. This has led several authors (Maynard Smith, 1966; Silcock and Parsons, 1973; Taylor, 1975; Powell and Taylor, 1979) to propose that this type of selection is a force promoting the evolution of habitat choice.

The present report gives evidence for habitat selection in the black turban snail *Tegula funebris*. This species occurs in the intertidal zone from Alaska to mid-Baja California, and in many places dense populations of these snails can be found (Frank, 1975). The intertidal is a region of extreme spatial heterogeneity, and in parts of its range *T. funebris* has a wide vertical distribution within this zone (Fawcett, 1979). For these reasons, *T. funebris* is a useful model animal for studies of intertidal habitat choice.

Materials and Methods

Study Sites

Habitat selection studies were conducted at Cape Arago, Oregon (Latitude 43°20'N) and Mukkaw Bay, Washington (48°20'N). The Cape Arago population of *Tegula funebris* (Adams, 1854) occupied a large permanent tidepool about 0.5 m deep. Based on algal zonation (Ricketts and Calvin, 1968), the pool surface was estimated to be about 0.6 m above the mean of lower low water (MLLW), the zero datum of tide tables. The Mukkaw Bay study site was also a large permanent pool about 0.5 m deep. Based on algal zonation (Ricketts and Calvin, 1968), this pool appeared to be 0.25 to 0.5 m higher in the intertidal zone than the Cape Arago pool. At both sites, specimens of *T. funebris* were found in the pools and up to about 1.0 m above their surfaces on rocks exposed during low tides.

Mass-Marking Experiments

Habitat selection studies using a mass-marking technique were conducted during the summer of 1977. Approximately 200 snails were collected during low tide from each of two habitats, permanent tidepools and rocks above the pools. Snails were placed on paper towels for 20 to 30 min to allow their shells to dry, and then marked by painting a large area of each shell with quick-drying enamel paint ("Testors" trademark). One-half of the snails from each habitat were assigned to control groups, and one-half to experimental groups; each group was marked with a different color. After marking, control groups from each habitat were replaced in their original habitats, and experimental groups from each of the two habitats were placed in opposite habitats. Collection, marking, and replacement in the intertidal were completed during one morning low tide. Positions of marked snails (above-pool or in-pool) were recorded each morning during the low tide period for 6 d after marking.

Three patterns of distribution of the control and experimental groups are potentially possible after a period of undisturbed movement. First, if snails have no habitat preferences and move little, the pattern of distribution created by experimental manipulation would persist; both control and experimental groups would differ in distribution, and experimental groups would differ from their respective controls. Second, if snails have no habitat preferences but do move, all of the groups should have similar distributions. Third, if habitat choice occurs, distributions of the two control groups and the two experimental groups should differ, but each experimental group should match its respective control group. Tests of independence using the *G*-statistic (Sokal and Rohlf, 1969) were used to evaluate the statistical significance of differences in distribution between groups. Statistical tests were performed on the distributions observed on each day after marking. Since the snails were not disturbed after marking and experimental manipulation, however, only one truly independent test of habitat preference is represented by 1 wk of observation.

In the mass-marking experiments just described, habitats of snails were reversed in the snails' home pool. Therefore, any differential movement of the two groups could represent homing behavior, in which individuals return to familiar areas, rather than habitat choice based on recognition of ecological differences between above-pool and in-pool habitats. In order to distinguish between these two possibilities, 100 snails from each of the two habitats were marked and then placed in opposite habitats in another tidepool 3 m from their home pool. This pool was separated from the first by rocks rising about 1 m above the surfaces of the pools. Equal numbers of snails were first removed from both above and in the second pool to control for possible effects of changes in snail density on behavior. If homing behavior were the cause of the differential movement of experimentally-reversed groups, neither habitat should be recognized as familiar in this experiment, and movement should then be random with respect to

habitat. If habitat selection based on a preference for areas ecologically similar to the original habitat occurs, snails should prefer above-pool or in-pool habitats in an unfamiliar pool also.

At the end of the week-long observation period of the basic mass-marking experiment at Cape Arago, snails remained undisturbed for approximately 6 wk. On the 43rd and 44th days after marking, distributions of marked snails were again recorded. Marked snails observed on Day 43 were removed, and not re-counted on Day 44, so distributions on these two days can be pooled for statistical testing.

Individual-Marking Experiments

A problem with the mass-marking studies just described is that they cannot resolve fine-grained spatial preferences. Certain snails could prefer a narrow range of height above pools, for example, but they would be lumped with all other above-pool snails in the mass-marking studies. In order to examine habitat preferences in more detail, experiments with individually-marked snails were carried out at the two study sites during the summer of 1978.

In these experiments, the height of undisturbed snails above or below the pool surface was measured to the nearest centimeter on the first day of an experimental series. After measurement of original position, snails were placed in individually-numbered plastic bags and returned to the laboratory for marking. Snails were placed on paper towels for about 30 min to allow their shells to dry, and then individually-numbered plastic tags, made for marking honeybees, were glued to each shell with cyanoacrylate ester glue ("Superglue" trademark). These numbers were found to be highly permanent in salt water. Since the numbered tags are only about 2 mm in diameter, and very difficult to see on snails in pools under adverse lighting conditions, a portion of the shell of each snail was also painted with yellow enamel paint, as in the mass-marking studies, to make them easier to locate. Marked snails were held in an aquarium overnight, and returned to the study pool during the next morning low tide. All marked snails were replaced at the waterline of the study pool. After 48 h, the position of each marked snail that could be found was measured and recorded, and snails were once again moved to the waterline. Positions of snails which were not found 2 d after they were placed at the waterline were measured on the first subsequent day they could be found, and they were then restarted at the waterline. Position was recorded only if a snail had been undisturbed for at least 48 h. During the course of an experimental series most marked snails were recaptured at least once, and some three or four times. Since snails were replaced at the waterline after each recorded position measurement, a number of independent measures of position preference were obtained for most individuals.

Pearson correlation coefficients between independent measurements of each snail's position on all pairs of days

were calculated. If no habitat selection occurs, correlation coefficients are not expected to be statistically significant except by chance. Also, approximately as many correlations should be negative as positive, since a snail not practicing habitat choice should be as likely to go up as down when released at the waterline. If habitat selection occurs however, only positive correlations are expected, and many of them should be significant. The value of each correlation should give an indication of the strength of position preference.

Results

Mass-Marking Experiments

Fig. 1 shows the results of a basic mass-marking experiment at Cape Arago. *Tegula funebris* placed in contrasting habitats returned to their original habitats in significant numbers. Snails in control groups tended to remain in their original habitats, although 20 to 30% moved to the contrasting habitat. By Day 5, a pattern like that expected if snails choose their habitats was observed. Experimental groups matched their respective control groups in distribution (above-pool control vs experimental: $G=1.78$, degrees of freedom, $DF=1$, $P>0.10$; in-pool control vs experimental: $G=0.47$, $DF=1$, $P>0.10$). Significant differences in the distributions of both control groups ($G=14.37$, $DF=1$, $P<0.001$) and experimental groups ($G=11.43$, $DF=1$, $P<0.001$) were observed.

Fig. 2 shows the results of a similar experiment at Mukkaw Bay. By Day 3 the observed pattern of distribution matched that expected from habitat choice. Distributions of experimental groups and their respective control groups are statistically indistinguishable (above-pool control vs experimental: $G=0.15$, $DF=1$, $P>0.50$; in-pool control vs experimental: $G=0.35$, $DF=1$, $P>0.50$). Significant differences in the distributions of control groups ($G=11.08$, $DF=1$, $P<0.001$) and experimental groups ($G=14.45$, $DF=1$, $P<0.001$) were also observed.

Distributions of snails in the experiment designed to differentiate between habitat choice and homing are given in Table 1. Even in an unfamiliar pool, the majority of experimentally-displaced snails returned to the habitat ecologically similar to their original habitat.

Table 2 gives the pooled distributions of groups of snails approximately 6 wk after initial marking and experimental habitat reversal at Cape Arago. The pattern observed is that expected if snails choose their habitats. Significant differences in the distributions of control groups ($G=7.36$, $DF=1$, $P<0.01$) and experimental groups ($G=9.98$, $DF=1$, $P<0.001$) are observed. Experimental groups match their respective control groups in distribution (above-pool control vs experimental: $G=3.01$, $DF=1$, $P>0.10$; in-pool control vs experimental: $G=0.81$, $DF=1$, $P>0.10$).

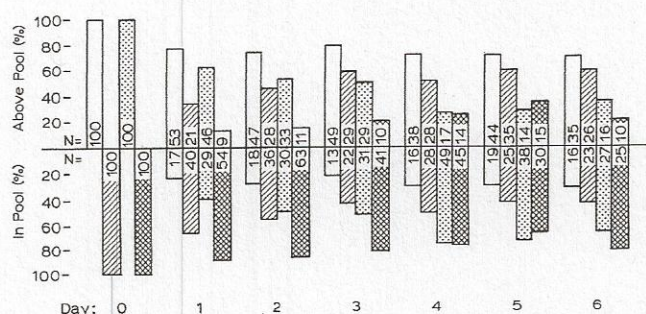


Fig. 1. *Tegula funebris*. Distribution of control and experimental groups with respect to tidepool surface at Cape Arago, Oregon. Groups are symbolized as follows: unshaded bars=above-pool control (snails found above pool and replaced there after marking); hatched bars=above-pool experimental (snails found above pool and placed in pool after marking); dotted bars=in-pool experimental (snails found in pool and placed above pool after marking); crosshatched bars=in-pool control (snails found in pool and replaced there after marking)

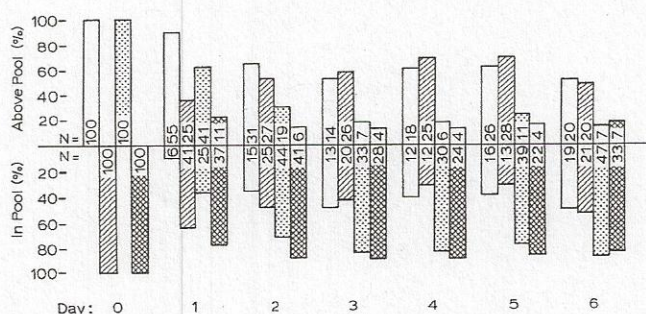


Fig. 2. *Tegula funebris*. Distribution of control and experimental groups with respect to tidepool surface at Mukkaw Bay, Washington. Symbols as in Fig. 1

Table 1. *Tegula funebris*. Distribution of experimental groups following habitat reversal in an unfamiliar tidepool, Cape Arago, Oregon

Day	Original habitat	Final habitat		N	Statistical comparison ^a
		Above (%)	In (%)		
0	Above	0	100	100	
	In	100	0	100	
1	Above	52	48	64	$G=1.45$, NS
	In	62	38	61	
2	Above	63	37	62	$G=10.88$, $P<0.001$
	In	34	66	65	
3	Above	59	41	46	$G=6.13$, $P<0.05$
	In	34	66	53	
4	Above	65	35	43	$G=5.38$, $P<0.05$
	In	39	61	38	
5	Above	56	44	39	$G=6.45$, $P<0.05$
	In	28	72	39	
6	Above	59	41	46	$G=6.95$, $P<0.05$
	In	30	70	37	

^a All degrees of freedom = 1

Table 2. *Tegula funebris*. Distribution of control and experimental groups 6 wk after habitat reversal, Cape Arago, Oregon. Above-pool control group: snails found above pool and replaced there after marking; above-pool experimental group: snails found above pool and placed in pool after marking; in-pool control group: snails found in pool and replaced there after marking; in-pool experimental group: snails found in pool and placed above pool after marking

Group	Final habitat		N
	Above (%)	In (%)	
Above-pool Control	77	23	31
Above-pool Experimental	95	5	19
In-pool Control	41	59	22
In-pool Experimental	54	46	24

Individual-Marking Experiments

Table 3 gives the correlation matrix resulting from an individual-marking experiment at Cape Arago. Nineteen of the 21 correlation coefficients which could be calculated are positive. This is a highly significant ($P < 0.001$) excess of positive values when compared to a binomial distribution based on the null hypothesis that one-half of the values should be negative and one-half positive, the expectation if habitat selection does not occur. Of the 19 positive correlations, 7 are statistically significant. Some of the correlations are quite high.

At Mukkaw Bay (Table 4), 14 of 15 correlation coefficients are positive, again a highly significant excess of positive values (binomial probability: $P < 0.001$). Seven of the 14 positive coefficients are statistically significant.

Table 3. *Tegula funebris*. Correlation coefficients (and sample sizes) between intertidal positions chosen by individually-marked snails at Cape Arago, Oregon

Day	Day						
	0	2	3	4	5	6	
2	0.496 ^c (52)						
3	0.118 (80)						
4	0.211 ^a (86)	0.328 ^a (28)					
5	0.107 (66)	0.328 (11)	0.203 (42)				
6	0.134 (70)	0.144 (20)	0.653 ^b (12)	0.028 (51)			
7	0.268 ^a (57)	0.753 ^a (6)	-0.337 ^a (30)	0.678 ^b (12)	0.199 (32)		
8	0.359 (21)		0.478 (3)	0.261 (13)	-0.729 (4)	0.126 (6)	

^a $P < 0.05$; ^b $P < 0.01$; ^c $P < 0.001$

Table 4. *Tegula funebris*. Correlation coefficients (and sample sizes) between intertidal positions chosen by individually-marked snails at Mukkaw Bay, Washington

Day	Day					
	0	2	3	4	5	
2	0.213 (32)					
3	0.251 ^b (122)					
4	0.297 ^a (46)	0.037 (19)				
5	0.386 ^c (92)	-0.411 (7)	0.252 ^a (71)			
6	0.277 ^a (42)	0.202 (6)	0.408 (10)	0.194 (19)		
7	0.214 (13)		0.529 ^b (20)	0.375 (5)	0.790 ^a (6)	

^a $P < 0.05$; ^b $P < 0.01$; ^c $P < 0.001$

Table 5. *Tegula funebris*. Correlation coefficients (and sample sizes) between intertidal positions chosen by individually-marked snails at two sites. Positions were recorded 3 to 4 wk apart. nd: no data

Day	Site	
	Cape Arago	Mukkaw Bay
0	0.073 (46)	0.372 ^b (58)
2	0.307 ^a (30)	0.270 (31)
3	nd	-0.056 (8)
4	nd	0.359 (19)
5	nd	0.183 (16)
6	nd	0.537 ^a (15)

^a $P < 0.05$; ^b $P < 0.01$

Table 5 gives correlations between positions of individual snails on several days and their positions approximately 1 mo later for both Cape Arago and Mukkaw Bay populations. At Cape Arago, both of the correlations which could be calculated are positive; one of these is significant ($P < 0.05$). At Mukkaw Bay, 5 of 6 correlations are positive, and 2 of the 5 positive correlations are significant.

Discussion

Results of the mass-marking experiments presented above show that, after experimental displacement, *Tegula funebris* tend to return to the intertidal habitat in which they were originally found. Habitat choice is not perfect, since 20 to 30% of snails in the control groups leave their original habitats, and roughly the same proportion of experimentally-displaced snails do not return.

Homing behavior has been described in several intertidal gastropods (Hewatt, 1940; Newell, 1958; Frank,

1964). In *Tegula funebris*, habitat choice appears to be due to the ecological similarity of the preferred habitat and the original habitat, and not to homing, since it occurs even in an unfamiliar pool (Table 1).

The time course of habitat selection can be seen in Figs. 1 and 2. At both study sites the movement of experimentally-displaced snails must begin almost immediately, since substantial numbers are again found in their original habitats just 1 d later. Movement appears to stabilize after 3 or 4 d. Habitat preferences persist for at least 6 wk (Table 2).

The results of the individual-marking experiments, in particular the significant excess of positive coefficients in the correlation matrices from both Cape Arago and Mukkaw Bay, confirm the general conclusion that habitat choice occurs. The many statistically significant correlations and the relatively large values of some coefficients indicate that individuals tend to return to approximately the same intertidal level where they were originally found. Thus, preferences appear to be more specific than merely for above-pool or in-pool habitats. Like the mass-marking experiments, individual-marking studies also show that habitat preferences persist for at least 1 mo (Table 5).

Individual-marking as well as mass-marking experiments show that habitat selection is not perfect. Not all of the correlations between individual positions on different days are positive. Many correlations are not significant, and even the significant positive correlations do not approach values of 1.0, the expected result if habitat preferences were absolute.

The intertidal position of *Tegula funebris* is influenced by the age and sex of snails, intertidal temperature contrasts at low tide, and the abundance of the predatory seastar *Pisaster ochraceus* (Paine, 1969; Fawcett, 1979; Byers, 1980, and unpublished data). These factors, and others not yet identified, could result in habitat preferences that are less than absolute.

Habitat selection behavior has been studied in *Tegula funebris* by Wara and Wright (1964) near Pacific Grove, California. In one marked population, snails originally found either in the low or high intertidal were released together in the mid-intertidal, and their movement was followed for 14 d. No vertical or horizontal separation of the two groups was observed; snails appeared to have no habitat preferences. A preliminary study using the mass-marking technique reported here was done at Pacific Grove, and no evidence for habitat selection was found (Byers, 1980), supporting the conclusion of Wara and Wright. Lack of habitat choice by black turban snails at Pacific Grove suggests the possibility of geographic differences in this behavior. Since life history features of *T. funebris* differ between Pacific Grove and the Oregon and Washington study sites of this paper (Frank, 1975), it is tempting to speculate that these aspects of the biology of the species might be related.

Theoretical models predict that genetic polymorphism and habitat selection might be associated (Hedrick *et al.*, 1976; Powell and Taylor, 1979). The existence of habitat

choice in *Tegula funebris* suggests the hypothesis that snails which prefer different habitats are genetically different. Evidence that snails' genotypes at two polymorphic enzyme loci are associated with differences in habitat selection has been obtained (Byers, 1980, and unpublished data).

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