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Movement Patterns of the Limpet *Lottia asmi* (Middendorff): Networking in California Rocky Intertidal Communities

by

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Abstract. Laboratory observations of marked specimens of *Lottia asmi* (Middendorff, 1847) and *Tegula funebralis* (A. Adams, 1854) over a 27-day period established that movement of limpets between snails was frequent and nocturnal. Limpets changed snails as many as 20 times and as few as 5 times during the study period. Every *T. funebralis* was occupied by 3 or more different limpets, and 5 snails were occupied by 10 or more individuals at different times. Patterns in these data suggest that some *T. funebralis* were ridden more often than others. The number of changes per night ranged between 3 and 11 (mean = 6.67) and time series analysis revealed no periodicity. Cohorts of limpets often occupied the same snail and some of these moved together as units between snails. Radular morphology, behavior, and ecology suggest that *L. asmi* is a more dynamic species than previously thought, and it appears that *L. asmi* is not a snail commensal but rather a carbonate associated species. Carbonate associates are most common in tropical seas where they are associated with corals and other carbonate habitats. In temperate and boreal regions they are commonly associated with coralline algae and other mollusks.

INTRODUCTION

The patellogastropod *Lottia asmi* (Middendorff, 1847) is easy to identify and characterize in California rocky intertidal communities (CARLTON & ROTH, 1975; ABBOTT & HADERLIE, 1980; RICKETTS *et al.,* 1985). The black, high-domed species is best known from the mid intertidal zone where it occurs on the shells of the trochid gastropod *Tegula funebralis* (A. Adams, 1854). Studies of the pair often treat *L. asmi* as a static organism, affixed to the whorls of its motile host. But, observations by GRANT (1933), F. H. TEST (1945), and EIKENBERRY & WICKIZER (1964) have suggested that *L. asmi* has a much more active life style.

The perception of *Lottia asmi* as an innocuous commensal on *Tegula funebralis* was first suspect when GRANT (1933) noted that specimens of *L. asmi* were sometimes found on rock surfaces, and she suggested that these individuals were in the process of transferring between snails. F. H. TEST (1945) published a 1937 study of the movement patterns of *L. asmi* and concluded that limpets rarely spent more than 24 hr on an individual snail. EIKENBERRY & WICKIZER (1964) studied transfer rates in laboratory aquaria and reported that about 75% of the limpets transferred at least once during their 13-hr observation period. Although both studies were of short duration, and were complicated by either poor field conditions or possible laboratory artifacts, it was evident that *L. asmi* was not uniquely associated with a specific *T. funebralis.*

This paper reports the results of a 27-day study of the movement patterns of *Lottia asmi.* The study was undertaken to annotate the earlier observations of high transfer rates, and to examine longer, time-series movement data for pattern. These data suggest that *L. asmi* is a more dynamic species than previously thought. Also, it appears that *L. asmi* is not a strict snail commensal but rather a carbonate associate, a species that occurs primarily or exclusively on carbonate substrates. Lottiidae associated with carbonate substrates are most common in carbonate-rich tropical seas (CHRISTIAENS, 1975; LINDBERG & VERMEIJ, 1985; LINDBERG, 1988). In temperate and boreal regions they are typically associated with coralline algae (MCLEAN, 1966; LINDBERG, 1983, 1988). In the Lottiidae, carbonate obligates form a morphological grade; within subclades the grade may be found in all members or widely scattered among several different groups. Abbreviations used in the text are as follows: LACMIP—Invertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California; USGSM—U.S. Geological Survey, Menlo Park, California; UCSC—University of California, Santa Cruz, California.

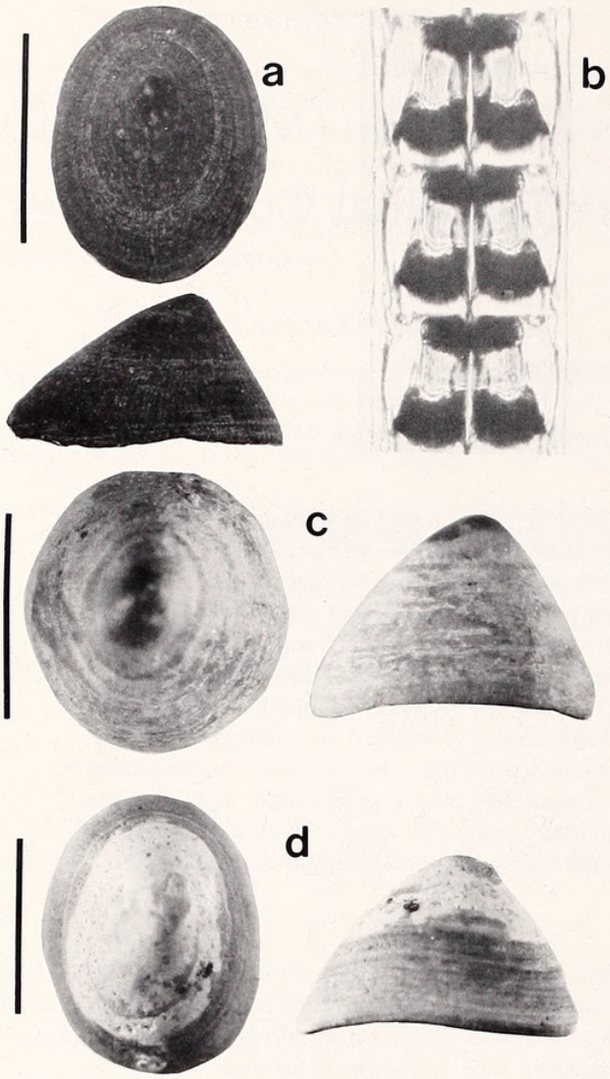


Figure 1

Recent and fossil *Lottia asmi* (Middendorff). Scale bars = 5 mm. a. Dorsal and lateral views of the shell of *Lottia asmi*; Recent, Davenport, Santa Cruz County, California. b. Dorsal view of the radula of *Lottia asmi*. c. Dorsal and lateral views of the shell of ?*Lottia asmi*; Pliocene, Los Angeles, Los Angeles County, California (LACMIP No. 8406). d. Dorsal and lateral views of the shell of *Lottia asmi*; Middle Pleistocene, San Nicolas Island, Ventura County, California (USGS Loc. No. M21663).

SPECIES, MATERIALS, AND METHODS

Species

Lottia asmi is a small (mean length <10 mm) northeastern Pacific lottiid (Figure 1a). It ranges from Cape Arago, Oregon (about 43°N) to Punta Pequeña, Baja California Sur, Mexico (26°N). Although the northern range limit of this species is often given as Sitka, Alaska (the supposed type locality), no well documented specimens have been collected north of Oregon (GRANT, 1933). *Lottia asmi* is often found on *Tegula funebralis,* but it is also common on mussels (*Mytilus californianus* and *M. edulis*) (LINDBERG, 1981) and sometimes on rock (GRANT, 1933; F. H. TEST, 1945; LINDBERG & PEARSE, in press). The radular tooth morphology of *L. asmi* is characteristic of lottiid species associated with carbonate substrates; all three pairs of outer lateral teeth are blunt and rounded, and the second pair are markedly broadened (Figure 1b). If *L. asmi* becomes stranded on rock substrates for several months, shell color and gross morphology change significantly, and the resultant shell morphology is similar to other northeastern Pacific lottiids (LINDBERG & PEARSE, in press); movement to these non-carbonate substrates produces no change in radular morphology.

Tegula funebralis is a mid intertidal species with diurnal and tidal mediated behavior (see review by ABBOTT & HADERLIE [1980]). It ranges from Vancouver Island, British Columbia, Canada (50°N) to Isla San Geronimo, Baja California Norte, Mexico (30°N) (MCLEAN, 1978). Because *Lottia asmi* extends farther south than *T. funebralis,* the southernmost specimens of *L. asmi* were probably collected from substrates other than *T. funebralis.*

The first putative specimen of *Lottia asmi* occurs in the Pliocene Fernando Formation of Los Angeles, California (Figure 1c) (>1.6 Ma). It differs from living specimens in having a more circular aperture. When viewed in profile, however, the aperture has a distinctive sigmodial shape that is shared with Recent specimens. The next record is from a Middle Pleistocene terrace on San Nicolas Island, Ventura County, California (Figure 1d) (VEDDER & NORRIS, 1963), about 0.6 Ma (MUHS, 1985). Subsequent records are lacking until the oxygen-isotope substage 5e of the last interglacial (Sangamon, approximately 0.120 Ma) (MUHS, 1985), and these records include many localities in southern California and Baja California Norte, Mexico (Lindberg, unpublished data). *Tegula funebralis* first appears in the upper Pico Formation (Early Pleistocene) near Ventura, California (GRANT & GALE, 1931), about 1.1 Ma (LAJOIE *et al.,* 1982).

Materials and Methods

Seventeen specimens of *Tegula funebralis,* each with a single specimen of *Lottia asmi* aboard, were collected at Pigeon Pt., San Mateo County, California on 14 February 1981. The limpets were carefully removed from the snails, and both were marked with small (approximately 2 mm × 2 mm), numbered squares of waterproof, plastic paper affixed to the apex of the shells with a cyanoacrylate-based glue. After measuring the limpets and snails to the nearest 0.1 mm with vernier calipers, a single limpet was randomly selected and placed on each *T. funebralis.* The trochids were then placed on concrete cinder blocks in an outdoor fiberglass tank equipped with a drip seawater system at the Long Marine Laboratory, UCSC. The drip seawater system was constructed of polyvinyl chloride (PVC) plastic pipe and fittings. Holes were drilled at intervals along the

Matrix A

T. funebralis

L. asmi	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	RK	A	B	C
1	1		1		3	1		3	1	1	1	2	2		1		2	1	12	19	20
2	3	1			1				1					1				2	5	7	6
3				1		3	1		1	1						1		1	6	8	7
4			1					1	2	1		1		2	1			2	7	9	9
5	1	1	1		1		1	1	1							1	1		9	9	
6			1		2	1							3		1		2		6	10	
7		3		1					1		1	1	1		3	1	1		9	13	
8	1	3	1	1	2			1					1				3		8	13	
9		1						1	2	1		1		1	2				7	9	
10	1	1	2			1	2	1	1			1		1	1		2		11	14	
11			1					1	3	2		3	1			2			7	13	
12		1			1	1			2			1			1	3	2		8	12	
13		3	1		2	1		2		1			1	1	2		3		10	17	
14	1	2	2		1			2				2			1		1		8	12	
15				1							1		1				2		4	5	
16		2	1	1	1				1			1	1		1	1	1		10	11	
A	6	10	10	5	9	6	3	9	11	6	3	9	8	5	10	6	11	4			
B	8	18	12	5	14	8	4	13	16	7	3	13	11	6	14	9	20	6			

Matrix B

T. funebralis

L. asmi	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	RK	D
1	1		1		3	1		3	2	2	2	3	4		1		3	1	27
2	10	1			3				1					1				10	26
3				1		10	1		3	3						4		5	27
4			1					3	2	1		1		8	1			10	27
5	2	2	6		1		2	1	1							10	1		26
6			8		3	2							3		1		8		25
7		6		3					1		2	6	1		4	2	1		26
8	2	6	6	1	2			3					1				6		27
9		2						1	12	4		1		4	2				26
10	3	1	7			1	2	1	3			3		3	1		2		27
11			1					2	10	4		4	2			4			27
12		3			1	1			2			1			1	11	5		25
13		5	1		5	1		2		1			1	1	2		8		27
14	3	9	2		1			3				3			3		2		26
15											19		1				6		27
16		6	1	1	1				2			1	1		2	10	1		26
C	21	41	34	7	20	16	5	19	39	15	23	23	14	17	18	41	43	26	

Figure 2

Data summaries. Matrix A (upper). The value in each cell of the large matrix is the number of times a numbered limpet (*Lottia asmi*) was found on each numbered snail (*Tegula funebralis*). The entries in column A are the total number of different snails ridden by each limpet and those in column B are the total number of transfers between snails by each limpet. Row A provides the number of different limpets found on each snail or on cinder block (RK); row B provides the total number of times a snail had limpets aboard or limpets were on RK. Data for time spent off *Tegula funebralis* are listed under RK (on cinder blocks) and column C lists the total number of transfers between all substrates (snails and rock). Matrix B (lower). The value in each cell of the large matrix is the total number of days a numbered limpet spent on each snail. Column D provides the number of observations of each limpet (includes RK occurrences; a complete data set = 27 observations). Row C provides total "limpet days" for each snail or RK.

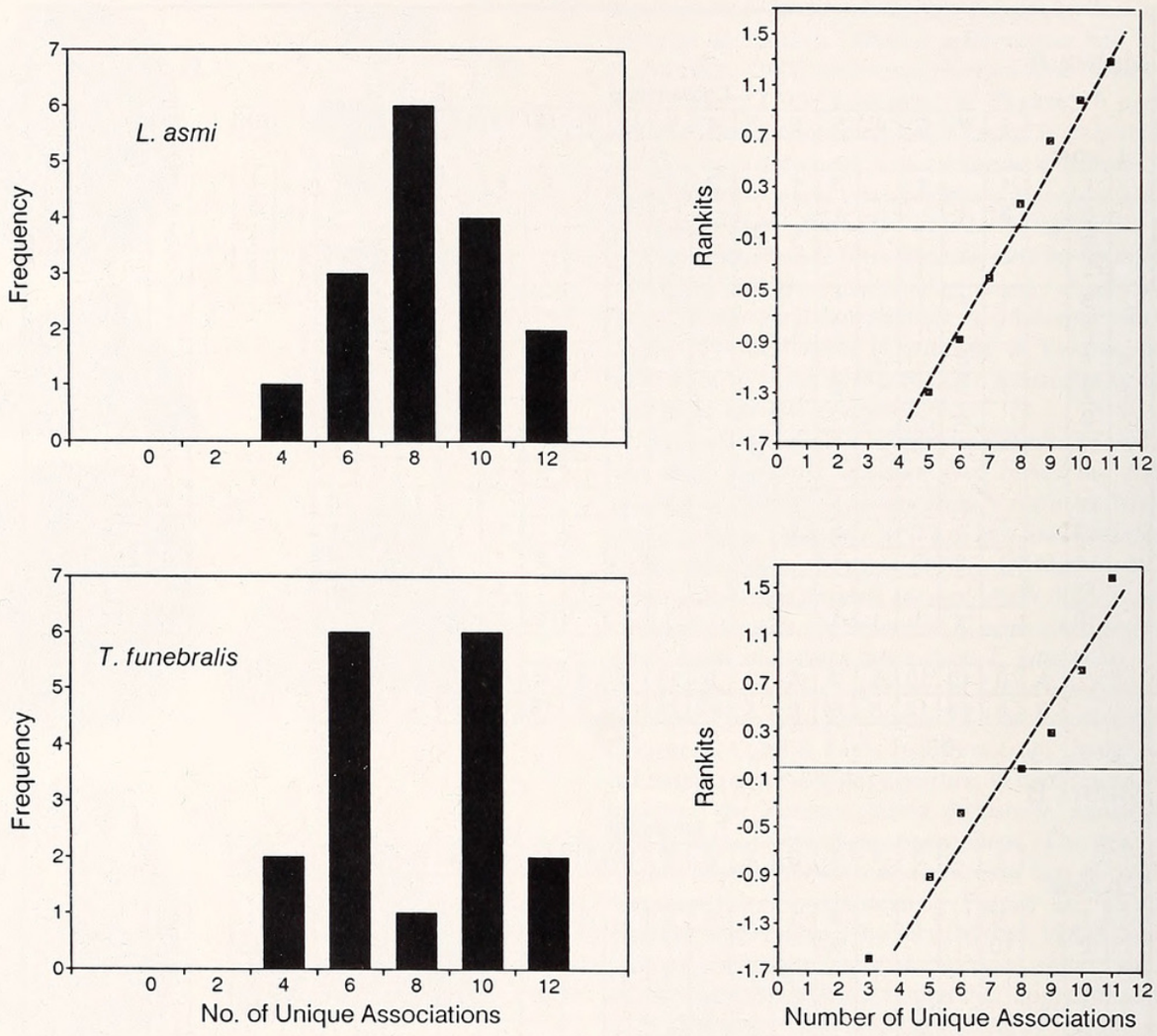


Figure 3

Frequency distributions of the number of unique associations formed by individual *Lottra asmi* with each *Tegula funebralis* (upper) and *vice versa* (lower). The figure to the right of each histogram plot presents a graphic test for normality of these data using rankits. In the case of *L. asmi* the deviation of the rankit values from a straight line suggests a normal or slightly leptokurtic frequency distribution; for *T. funebralis* the rankit values indicate bimodality in the data (see SOKAL & ROHLF, 1981:123).

pipe lengths from which seawater would drip down on the cinder blocks. The cinder blocks were set in sand and the runoff from the blocks percolated through the sand and exited the tank through a drain. Limpet position was recorded twice daily, once in the early morning and once in the late afternoon for 27 days (16 February to 15 March 1981). Limpet no. 17 was found dead on 17 February and therefore the results report the movements of only 16 limpets.

The raw data were analyzed by constructing two preliminary matrices. The first listed each limpet's position in the tank (*Tegula funebralis* number or rock) by date, while the second contained limpet numbers on *T. funebralis* by date. These matrices were used to produce two additional matrices that summarize the raw data. The first matrix reports the number of times a particular limpet was found on each *T. funebralis* (Figure 2, matrix A), while the second matrix gives the number of days a particular limpet was associated with a specific *T. funebralis* (Figure 2, matrix B). Selected patterns from these data matrices were further quantified, graphed, and tested for statistical significance (SPSS, INC., 1986). The mean number of days a particular limpet and snail were associated was calculated by dividing each cell in Figure 2, matrix B, by its corresponding cell in Figure 2, matrix A. The higher this value, the fewer the moves and the longer the visits.

The lateral surface area of the *Tegula funebralis* shells was estimated by modeling the shells as cones as follows:

$$\text{lateral surface area} = \pi rs$$

where r = the radius of the shell base and s = the slant height of the shell. The value of s was obtained by solving for the hypotenuse of a right triangle as follows:

$$s^2 = r^2 + b^2$$

where b = shell height. The surface area of the shell base was not included in the estimate because this region was seldom used by *Lottia asmi*.

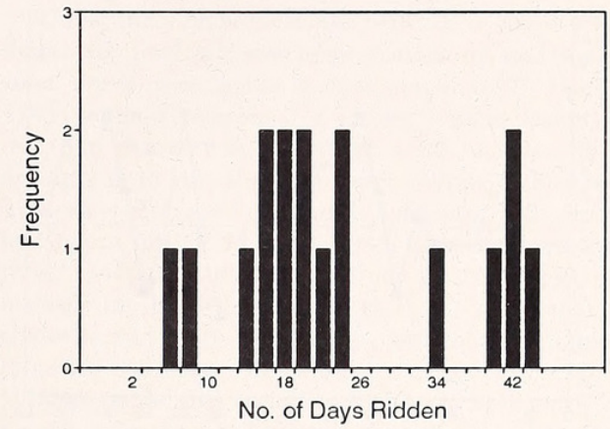
RESULTS

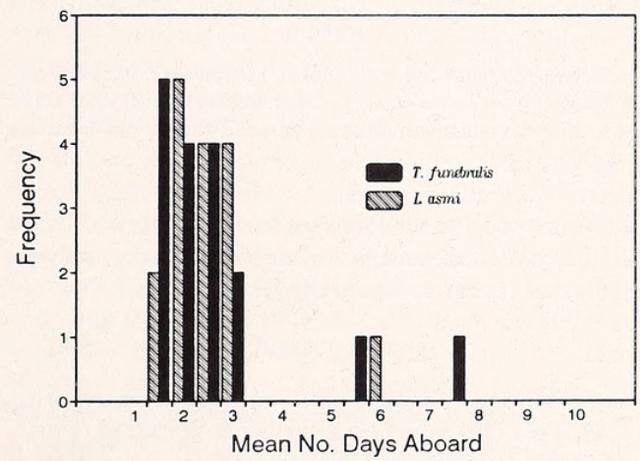
Lottia asmi moved between specimens of *Tegula funebralis* often during the study period. Limpets changed substrates as many as 20 times and as few as 5 times (Figure 2, matrix A). Every *T. funebralis* was occupied by 3 or more different limpets during the study period, and 5 snails were occupied by 10 or more (Figure 2, matrix A). The number of unique associations for limpets appears normally distributed, while the distribution for snails has a distinctly bimodal distribution (Figure 3). This latter distribution suggests that some *T. funebralis* were more "popular" than others with the limpets. The number of limpet days for each *T. funebralis* ranged between 5 and 43 (Figure 2, matrix B), and also shows a possibly bimodal trend (Figure 4). Whether these patterns resulted from the limpets' or snails' behavior is not known.

For *Lottia asmi* the ratio of days aboard to times visited varied between 1.4 and 6.0 (mean = 2.4). For *Tegula funebralis* the ratio varied between 1.3 and 7.7 (mean = 2.4). Both distributions are skewed to the left (Figure 5).

The twice-daily observations of the positions of numbered limpets and snails demonstrated that movement occurred at night; associations recorded during the morning were always still in place in the late afternoon. Although the experimental setting removed *Tegula funebralis* from tidal and other mass water movements, the drip system kept the substrate constantly wet, thus allowing the snails to move and graze at anytime. However, *Tegula funebralis* remained aggregated at the base and within the holes of the cinder blocks during the day. The minimum number of changes per night ranged between 3 and 11 (mean = 6.67) (Figure 6). Time-series analysis of the number of changes per night revealed that the series was stationary, but heteroscedastic; examination of the autocorrelation functions revealed no periodicity in the time series.

More than one limpet often occurred on each *Tegula funebralis*. Groups of 2 *Lottia asmi* formed 36 times on 14 of the *T. funebralis*, groups of 3 formed 10 times on 7 of the snails, and 4 snails had groups of 4 once during the study period (Table 1). Groups of two moved together as a unit 9 times, while groups of 3 or more never moved as units. The longest a group of 2 remained together was 9 days, for a group of 3 it was 10 days, and for a group of 4 it was 5 days. The longest period a *T. funebralis* went without a rider was 14 days and about 40% of the snails were bare at any given time (Table 1).





Explanation of Figures 4 and 5

Figure 4 (upper). Frequency distribution of the total number of days each *Tegula funebralis* had limpets (*Lottia asmi*) aboard during the 27-day study period. Values greater than 27 result when more than one limpet was present on the snail on the same day. Figure 5 (lower). Frequency distributions of the mean number of days each *L. asmi* spent aboard individual *T. funebralis* and the mean number of days each *T. funebralis* was ridden by individual *L. asmi*.

Four *Lottia asmi* moved onto the cinder blocks during the study period (Figure 2). Two of these limpets spent almost one-third of the study period on the cinder blocks (Figure 2, matrix B). The data for cinder block specimens most likely represent minimum values. Because the snails were not handled during the study, not all the specimens of *L. asmi* were accounted for each day (Figure 2, matrix B, column D) and missing specimens may have been overlooked among the clumps of algae on the cinder blocks. If the missing data represent additional cinder block specimens, then 11 *L. asmi* would have been on cinder blocks at sometime during the study for a total of 35 limpet-days (Figure 2, matrix A).

Regressions of total cohort days (Figure 7) and total limpet days (Figure 8) on shell surface area suggest that there is a positive relationship between these pairs of variables. In both cases, however, these trends are driven by

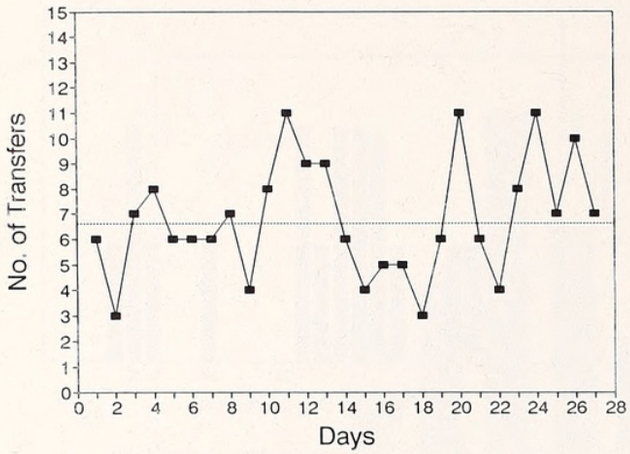


Figure 6

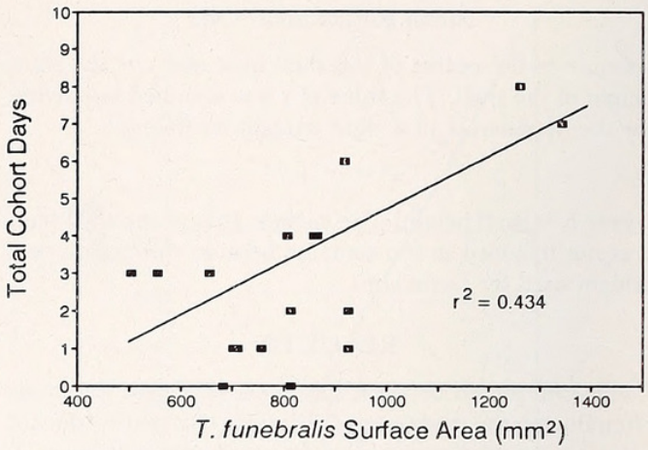
Time-series plot showing the number of transfers, between *Tegula funebralis* by *Lottia asmi,* per day during the 27-day study period. The dashed line indicates the mean number of transfers per night.

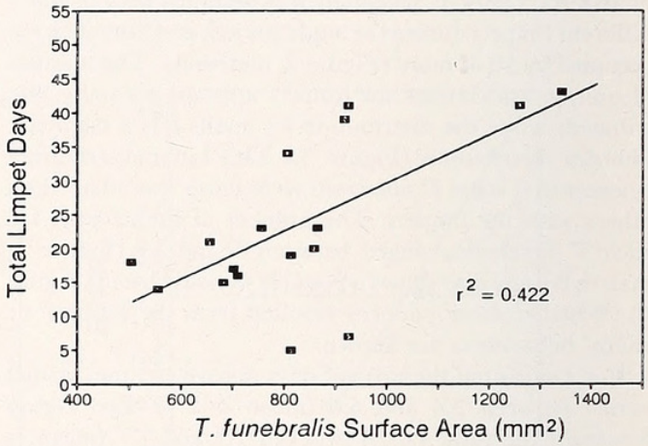
two specimens with shell surface areas in excess of 1000 mm^2. If these two specimens are removed from the analysis, the patterns appear substantially less linear.

DISCUSSION

Transfer rates in this study are lower than those reported by F. H. Test (1945) and Eikenberry & Wickizer (1964). F. H. Test (1945) reported that *Lottia asmi* transferred at least once every 24 hr and Eikenberry & Wickizer (1964) reported that 75% of their laboratory populations transferred overnight. In this study about 40% of the population transferred between *Tegula funebralis* nightly, and the minimum average transfer rate was about 6.7 transfers per day (Figure 6). F. H. Test (1945) states that his field observations were complicated by tag loss and this may have contributed to his higher rate. Eikenberry & Wickizer's (1964) study was done in laboratory bowls and aquaria and these conditions may have influenced snail and limpet movement.

The absence of periodicity in the time-series analysis suggests that limpet movement patterns are not correlated with tidal or lunar cycles, and rather are random. The possibility that certain *Tegula funebralis* are occupied more often by limpets than others is suggested by several trends (Figures 2, 3, 4; Table 1), but two different patterns of ridership produce these more popular snails. Some individuals (*e.g.,* snails 2, 3, 9, 17) were ridden by many different limpets (>10), often occurring simultaneously on the snail (Table 1), that remained on average for more than 3 days (Figure 2, matrix B). In other cases (snails 1, 11, 16) individuals were ridden a few times (<6), seldom by cohorts (Table 1), but had limpets that remained for 10 or more days. In summary, examination of the movement data revealed no unequivocal, statistically significant patterns.





Explanation of Figures 7 and 8

Figure 7 (upper). Scatterplot of the total number of days cohorts of *Lottia asmi* (≥2 limpets) spent on individual *Tegula funebralis* regressed against the lateral surface area of the snail's shell. Figure 8 (lower). Scatterplot of the total number of days each *T. funebralis* had limpets aboard during the 27-day study period (Figure 4) regressed against the lateral surface area of the snail's shell.

The behaviors of *Lottia asmi* and *Tegula funebralis* are ultimately responsible for the patterns present in the data. *Lottia asmi* can chemically locate *T. funebralis* both in field and laboratory settings (F. H. Test [1945] and Alleman [1968], respectively). Once a snail is located and boarded the snail's behavior will play a large role in determining limpet transfer rates. *Tegula funebralis* forms aggregations in different tidal and light conditions. Aggregations occur during daytime low tides and during nighttime high tides (Wara & Wright, 1964). When submerged during daylight high tides, the snails are active and scattered, but if water movement becomes too extreme, the snails will seek shelter (Kosin, 1964; Overholser, 1964; Abbott & Haderlie, 1980). During nighttime low tides snails are also active and dispersed (Lindberg, personal observations).

Table 1

Distribution of cohorts of *Lottia asmi* on *Tegula funebralis* and time periods unoccupied.

T. funebralis no.	Cohort size 2	3	4	Days bare
1	2	1	0	12
2	5	2	1	4
3	2	1	1	11
4	1	0	0	20
5	4	0	0	13
6	1	0	0	11
7	0	0	0	22
8	2	0	0	9
9	3	2	1	6
10	0	0	0	12
11	1	0	0	4
12	4	0	0	10
13	3	0	0	16
14	1	0	0	13
15	2	1	0	12
16	1	1	0	6
17	4	2	1	2
Totals	36	10	4	183

The aggregation behaviors of *Tegula funebralis* facilitate *Lottia asmi* transfers between snails. Therefore, once attached to the *T. funebralis* population, the snails' aggregation behavior guarantees that *L. asmi* can locate other suitable patches of microhabitat (*i.e.*, other *T. funebralis*) (also see Phillips *in* RICKETTS *et al.*, 1985).

The impetus for transfers likely results from the limited food reserves of the *Tegula funebralis* shell. EIKENBERRY & WICKIZER (1964) found that *Lottia asmi* ate between 2.7% and 7.0% of the algae on the shell of *T. funebralis* per hour. At the average grazing rate (4.7% shell algae eaten/hr) a limpet would denude a *T. funebralis* shell in 21.4 hr, and grazing is often so intense that the entire exterior surface of the *T. funebralis* shell become grooved (HICKMAN & MORRIS, 1985).

Riding the *Tegula funebralis* network is also a very efficient way for *Lottia asmi* to move about the mid intertidal zone. *Lottia asmi* moves at 12.8 mm/min (F. H. TEST, 1945) while *T. funebralis* is almost 4 times faster at 42 mm/min (ABBOTT & HADERLIE, 1980). *Lottia asmi* does not appear to ride the even faster hermit crab network. The rarity of *L. asmi* on dead *T. funebralis* shells occupied by *Pagurus* spp. (F. H. TEST, 1945; EIKENBERRY & WICKIZER, 1964) probably results from the crabs' aggressive intraspecific behavior (RICKETTS *et al.*, 1985) that precludes hermit crab aggregations, and therefore opportunities for the limpets to transfer.

Based on the first occurrences of *Lottia asmi* and *Tegula funebralis* in the fossil record of southern California, *L. asmi* may have been riding the *T. funebralis* network for over 1.0 million years. The gross morphology of the putative *L. asmi* from the Fernando Formation (Figure 1c) suggests an association with a *T. funebralis*-like snail had already been established by the Late Pliocene (more than 0.5 million years *before* the first appearance of *T. funebralis*). Although fossil specimens of *T. funebralis* date only from the Early Pleistocene (about 1.1 Ma), several *Tegula* spp. are common in Middle and Late Pliocene deposits in southern California (GRANT & GALE, 1931; L. G. Hertlein, unpublished MS), and could have provided substrates for Pliocene *L. asmi*. Non-epizoic fossil specimens of *L. asmi* are not known, but undoubtedly exist and likely have been misidentified (see LINDBERG & PEARSE, in press). Alternatively, the Fernando specimen may not be *L. asmi*; several other lottiid species are known to occur on trochid gastropods (BREWER, 1975; LINDBERG, 1981). The first unequivocal specimen of *L. asmi* (Figure 1d) appears in the Middle Pleistocene of San Nicolas Island off southern California (about 0.6 Ma or about 0.5 million years *after* the first appearance of *T. funebralis*).

Reappraisal of *L. asmi* as a Carbonate Obligate

The association of *Lottia asmi* with *Tegula funebralis*, and the morphological consequences for the limpet, have made *L. asmi* easy to recognize and characterize. A. R. G.

Table 2

Temperate northeastern Pacific carbonate associate species.

Taxon	Habitat	Latitudinal distribution
Acmaea mitra Rathke, 1833	Encrusting coralline algae	52°N to 30°N
Erginus sybaritica (Dall, 1871)	Encrusting coralline algae	60°N to 57°N
Erginus apicina (Dall, 1879)	Encrusting coralline algae	56°N to 53°N
Erginus moskalevi (Golikov & Kussakin, 1972)	Encrusting coralline algae	55°N to 53°N
Niveotectura conica (Gould, 1846)*	Encrusting coralline algae	55°N to 25°N
Lottia asmi (Middendorff, 1847)	Other mollusks	43°N to 26°N
Lottia triangularis (Carpenter, 1864)	Branching and encursting coralline algae	59°N to 34°N
Lottia sp. (undescribed)	Encrusting coralline algae	53°N to 38°N
Tectura rosacea (Carpenter, 1864)	Encrusting coralline algae	55°N to 29°N

* Although formerly regarded as junior synonym of *Acmaea mitra* (Rathke, 1833), the shell structure of the holotype of *Patella conica* Gould, 1846, clearly indicates that this species name is a senior synonym of *Scurria mitra* var. *funiculata* Carpenter, 1864.

TEST (1945:17) suggested that *L. asmi* was derived from *Lottia pelta* (Rathke, 1833) by "ecologic segregation and selection." Although she provided no characters to support the supposed relationship, Test proposed that dwarf specimens of *L. pelta* became associated with *T. funebralis* and subsequently became isolated from *L. pelta* populations. Test was unaware that many characters that she thought inviolable and extreme variants of the ancestral species were phenotypic expressions of living on *T. funebralis*. For example, the gross shell morphology (small size, dome-shape, *etc.*) and dark coloration only occur when the limpet is living on *T. funebralis* (LINDBERG & PEARSE, in press). Specimens of *L. asmi* from rock substrates are similar to most other eastern Pacific *Lottia* species, and the modification of the radula for carbonate feeding masks its ancestry. *Lottia asmi* was included in WALKER's (1968) study of the jaw, digestive system, and coelomic derivatives of several central California *Lottia* species, but the characters treated do little to resolve the ancestry of *L. asmi*. The general jaw morphology of *L. asmi* is substantially different from the other *Lottia* species examined by Walker. Salivary gland morphology grouped *L. asmi* with *L. pelta* and "*Collisella*" *scabra* (Gould, 1846), but *L. asmi* was the only species examined in which the posterior glands were very small and light green in color. Moreover, in *L. asmi* the hindgut was substantially longer than in the other species. Whether these characters are related to the carbonate feeding strategy of this species is not known.

The common occurrence of *Lottia asmi* on the shells of other mollusks, notably *Tegula funebralis, Mytilus edulis,* and *M. californianus,* and its rareness on non-carbonate substrates, combined with the morphology of the radular lateral teeth, suggest that *L. asmi* is a carbonate associate. Species that occur primarily or exclusively on carbonate substrates are broadly distributed in the Patellogastropoda (LINDBERG, 1988; Lindberg & Padilla, unpublished data). Carbonates associates may be present in an entire subclade (*e.g., Patelloida profunda* group [CHRISTIAENS, 1975; LINDBERG & VERMEIJ, 1985], *Erginus* spp. [LINDBERG, 1983; LINDBERG & MARINCOVICH, 1988]) or randomly scattered within a clade and clearly convergent (LINDBERG, 1988; Lindberg & Padilla, unpublished data). The shells of these species are typically colored by the pigments present in the carbonate substrates, and the radulae have broad, rounded second lateral teeth and the third lateral teeth also may be enlarged.

Carbonate substrates used by these limpets include both plants and animals. Epiphytic species are found on encrusting and branching calcareous algae, while epizoic species are most often found on the shells of other mollusks (*e.g.,* mussels, oysters, chitons) or on the skeletons of dead corals. The earliest record of this grade is from the Early Cretaceous of England where *Patelloida tenuistriata* (Michelin, 1838) lived on dead ammonite shells (AKPAN *et al.,* 1982). On the basis of the morphology of the rasp marks left on ammonite shell, its radular morphology was identical with that of living carbonate associated species (AKPAN *et al.,* 1982). Recently, ZINSMEISTER (1990) has reported an "acmaeid" limpet associated with a bivalve mollusk from the Late Cretaceous of Antarctica.

Extant carbonate associates living on mollusks are common in both tropical and temperate settings. In the Caribbean, *Lottia leucopleura* (Gmelin, 1791) often occurs on the trochid gastropod *Cittarium picta* (Linné, 1758) (PILSBRY, 1891). In Chile, *Scurria parasitica* (Orbigny, 1841) is so named because it lives on the shells of the gastropods *Scurria viridula* (Lamarck, 1819) and *Fissurella* spp. and on the chitons *Acanthopleura echinata* (Barnes, 1823) and *Enoplochiton niger* (Barnes, 1823) (MARINCOVICH, 1973). In tropical Australia, *Patelloida bellatula* (Iredale, 1929) occurs on *Lithothamnion,* coral, beach rock, and dead shells, and *Patelloida mimula* (Iredale, 1924) lives on oysters (*Saccostrea*) in tropical and temperate estuaries (PONDER & CREESE, 1980). In temperate Australia, *Patelloida mufria* (Hedley, 1915) and *Patelloida nigrosulcata* (Reeve, 1855) occur primarily on other gastropods (PONDER & CREESE, 1980). Members of the *Patelloida profunda* group are also present in Australia, and include *P. profunda calamus* (Crosse & Fischer, 1864) and *P. profunda ivani* (Christiaens, 1975). Northeastern Pacific carbonate associates are listed in Table 2.

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