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Population dynamics and spatial distribution of the terrestrial snail *Ovachlamys fulgens* (Stylommatophora: Helicarionidae) in a tropical environment

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Abstract: The introduced snail *Ovachlamys fulgens* (Stylommatophora: Helicarionidae) occurs on cultivated land habitats in Costa Rica, where its macrodistribution seems to be limited by annual mean temperature (20 - 27.6°C) and annual precipitation (1 530 - 3 034 and 3 420 - 8 000 mm, with no more than six dry months). This species can be found in litter and on vegetation up to 70 cm tall. Random quadrat field sampling was done in leaf litter and understory plants every three months for a total of five dates in Central Costa Rica. At least 150 plots of 25x25 cm were analyzed on each date. Abundance of living specimens and eggs was positively correlated with (1) litter abundance and depth, (2) litter and soil humidity, (3) relative humidity and (4) early morning temperature (6:30 AM), and negatively correlated with temperature later in the morning (10:00 AM). Besides these factors, living snail abundance was correlated with thickness of the herbaceous vegetation and with the occurrence of *Yucca elephantiphes* (in litter and understory). Egg abundance was also correlated with the sampling date, apparently because of changes in humidity. The correlation pattern of shell abundance was opposite to that of living specimens. Population size and number of empty shells throughout the year parallel the rainfall pattern. Reproduction takes place between May and November (wet season); and up to 92% of the specimens can be found aestivating between December and April (dry season). Clutch size averages three eggs. The maximum density of living specimens was reached in December (43.41 ind/m^2) and the minimum in March (8.30 ind/m^2). Shells decompose in an average of five months.

Key words: Land snail, distribution, microdistribution, *Ovachlamys*, Helicarionidae, reproduction, demography, shell decomposition, Costa Rica.

In Costa Rica, as in many other places, increased human activity has accelerated the introduction of snail species, enhancing the need to study the niches they occupy as well as the adaptations that allow their establishment in tropical countries. *Ovachlamys fulgens* was originally described from Loo Choo (Gude 1900) an archipelago also known as Liu Chi or Ryukyu Islands (Okinawa being the largest island of it). The archipelago is currently administrated by Japan (http://is3.hk.super.net/~csjwv/dytf.html), its subtropical weather has the following ranges: average temperature 22.4°C, minimum 13.6-26.1°C, maximum 18.6-31.1°C, yearly precipitation 2 036.8mm without dry months (data from Naha City, Okinawa Island) (http://jin.jcic.or.jp/stat/stats/01CEN12.html). This species has entered other countries in shipments of ornamental plants (F.G. Thompson, pers. comm. 1995). It may have become

established in Costa Rica in the last 15-20 years, with the massive cultivation of native and introduced ornamental plants. Currently, *O. fulgens* is considered an agricultural pest (Monge-Nájera 1996), but with the exception of a few discussions about its taxonomic classification and its life cycle, there appears to be no information on the ecology of the species.

Studies done in temperate habitats found that the microdistribution of leaf litter pulmonates depends on the amount of litter (Boag and Wishart 1982, Locasciulli and Boag 1987) and humidity (Boag 1985). The scanty information about tropical snails suggests that well-drained soils are also important (Peake 1968). This paper about Costa Rican *O. fulgens* reports on: 1- macrodistribution of the species, 2- microdistribution of individuals, shells and eggs, 3- the yearly changes in abundance, 4- reliability of the sampling procedure and 5- shell decay.

MATERIALS AND METHODS

Macrodistribution: The geographic distribution was plotted from the database of the Department of Malacology, Instituto Nacional de Biodiversidad (INBio) in Heredia, Costa Rica. Collecting sites include forested and cultivated areas.

Microdistribution:

Study area: Field work was done in an urban lot (12x18m^2) in Pavas, San José, Costa Rica (9°56'45"N, 84°07'15"W, 1075 masl). The biotic area classification is "subtropical, tropical, moist with 5-6 dry months" (Herrera and Gómez 1993). The soil is slightly alkaline (pH = 6.6) and calcium-rich (Ca^+=17.1 cmol(+)/l) (Centro de Investigaciones Agronómicas, Universidad de Costa Rica). The site, originally cleared for a coffee plantation, became an urban lot with secondary growth and grasses (*Pennisetum purpureum*). In 1982 an orchard was planted, mainly: *Persea americana* (avocado), *Citrus* spp. (lemon, tangerine, sour orange), *Mangifera indica* (mango), *Musa* sp. (plantain), *Psidium guajava* (guava), *Psidium friedrichsthalianum* (sour guava), *Yucca elephantipes* (yucca), *Annona muricata* (guanabana) and *Acnistus arborescens* (güitite). The only maintenance was mechanical mowing (about four times a year). The site was selected because it was the only Costa Rican habitat of *O. fulgens* known when the study began.

Field methods: Considering the body size of *O. fulgens*, site characteristics, ecological variables and time availability, the lot was divided into 3 984 quadrats (25x25cm^2). Sample size was determined by preliminary sampling and the equation presented by Southwood (1978). Five samplings of at least 150 quadrats each were done every three months with the assistance of a random number generator. Sampling was done in the following dates:

1= December 18; 1992 (beginning of dry season), 159 quadrats.

2= March 6-14; 1993 (dry season), 153 quadrats.

3= June 8-18; 1993 (wet season), 150 quadrats.

4= September 7-14; 1993 (wet season), 150 quadrats.

1= December 7-19; 1993 (beginning of dry season), 150 quadrats.

In each quadrat, quantitative and qualitative variables that potentially affected the abundance (or presence) of snails, shells and eggs were measured (Tables 2-6). Al molluscs seen without special optical equipment were collected for 5 min in each quadrat (see Villalobos *et al.* 1995, Emberton *et al.* 1996). The number of live individuals, shells and eggs of *O. fulgens* were recorded in each quadrat, as was the shell diameter of dead and live individuals (classified as "active" or "aestivating"). Live *O. fulgens* were returned to the original site after measuring. Plant cover was measured with a fixed point pattern (1cm between points) and soil moisture by weight difference after oven drying for 48hr at 90°C (moist weight divided by dry weight). Litter was divided in three levels: Z1 closest to the soil, leaves were black and retained more humidity and could only be classified as monocotyledons and dicotyledons

because of decomposition, Z2 brown dead leaves identifiable to family or species level; and Z3 freshly fallen leaves, green-yellow-brown, in many cases the layer was artificially produced when trees were routinely pruned. To analyze the effect of plants, only the most abundant species of each quadrat was considered. When abundance was assessed the following rating was used 0=absent, 1=absent-scarce, 2=scarce, 3=scarce-regular, 4=regular, 5=regular-abundant, 6=abundant, 7=very abundant. Abundance of fungal hyphae was limited to those visible to the naked eye.

Microhabitat temperature was measured on each sampling day at around 06:30 and 10:00 hours on areas with trees and without them at four levels: 1) in air 1 m above ground, 2) in herbaceous vegetation 3 cm above ground, 3) inside litter and 4) at a depth of 0.5 cm in the soil.

Spearman´s correlations were applied to estimate the correlation of the 34 quantitative variables with the number of shells, living snails and eggs of *O. fulgens* per quadrat. Chi-square was used for the analysis of the qualitative variables, but as the amount of cells with less than five data was high the data were modified as follows: the dependent variables were classified as 0 = absent and 1 = present, all grasses were merged into a single category, the same was done for Myrtaceae species, and categories with low frequencies were discarded.

Demography: The snails were classified as: Neonates (shell diameter $\leq$2.5mm), Juveniles (shell diameter 2.6 - 4.9 mm) and Adults (shell diameter $\geq$ 5.0mm) (Barrientos 1996, 1998). Living individuals were recorded separately from shells. Statistical analysis between the population demography and precipitation and temperature was not possible because only five data were available. For the comparison only precipitation and maximum temperature were considered, as these had the greatest range. The variation of the minimum temperature was of only 0.9 °C (17.9-18.8°C) and average temperature varied 1.2°C while the maximum temperature varied 2°C (25.9-27.9°C).

Correction factor: The reliability of the sampling procedure was tested in December, 1993, on 39 randomly selected 25x25cm^2 quadrats. After the standard visual count, all the vegetation and soil to a depth of 1 cm were collected and examined in the laboratory under 10x magnification. The correction factor was calculated as the total number of specimens divided by the mean number of visually counted specimens.

Shell decomposition: The decomposition time was measured for 23 shells, 5 mm or more in diameter, placed simultaneously in a mesh cage left in the field; this prevented exposure to macrofauna yet allowed the action of water and other climatic factors. Shells were examined monthly and classified as either intact, faded or broken.

Voucher *O. fulgens* were deposited in the Museum of Natural History, University of Florida and Instituto Nacional de Biodiversidad (INBio) catalogue numbers 1474249 (17 specimens) and 1474252 (19 specimens). Summary statistics follow this format: mean (sample size, $\pm$standard deviation, minimum-maximum).

RESULTS

Macrodistribution: The distribution of *O. fulgens* in Costa Rica (Fig. 1) is correlated with human presence and specially with agriculture (Table 1). Only in Pejibaye de Cartago and in Río Claro de Puntarenas (Table 1) was it found in a secondary forest, other samples were collected in gardens or plantations. In Fig. 1, specimens collected in San Ramón (see Table 1) seem to be inside a forested area, but it is crossed over by a road where plantations occur on both sides.

According to Herrera and Gómez (1993) the biotic units where *O. fulgens* has become established are "tropical", "subtropical" and "temperate" thermic provinces with the following annual means: 20-27.6°C, minimum 14.8-22.2°C and maximum 24.3-33.1°C. These are "humid" and "very humid" provinces with a hydric index of 20-300% and with precipitation that ranges between 1 530 - 3 034 mm and 3 420 - 8 000 mm and no more than six dry months (Herrera and Gómez 1993).

TABLE 1

Localities and vegetation types where Ovachlamys fulgens *has become established in Costa Rica and biotic units to which each locality belongs according to Herrera and Gómez (1993). The INBio database was the main source for localities and dominant vegetation.*

Locality, province	Geographic coordinates	Altitude (masl)	Dominant vegetation	Biotic Unit
Esquinas, Puntarenas	8°46'08"N 83°15'24"W	10	Araceae	Tropical, Tropical, very humid, without dry months
Río Claro, Puntarenas	8°40'49"N 83°04'01"W	100	Secondary forest	Tropical, Tropical, very humid, without dry months
San Luis, Limón	10°14'59"N 83°39'58"W	50	*Heliconia* spp.	Tropical, Tropical, very humid, without dry months
Suerre, Limón	10°11'20"N 83°45'09"W	330	Poaceae (Bamboo)	Tropical, Tropical, very humid, without dry months
Cuestillas, Alajuela	10°22'08"N 84°30'15"W	200	*Dracaena marginata*	Tropical, Tropical, humid with 1-2 dry months
San Isidro, San José	9°22'51"N 83°42'24"W	700	Orchidaceae Urban garden	Tropical, Tropical, humid with 3-4 dry months
San Ramón, Alajuela	10°12'43"N 84°32'14"W	930	*Dracaena marginata* var. *compacta*	Subtropical, Tropical, very humid, with 1-2 dry months
Turrialba, Cartago	9°54'03"N 83°41'03"W	700	Urban garden	Subtropical, Tropical, humid without dry season
Pavas, San José	9°56'44"N 84°07'20"W	1100	*Pennisetum purpureum* Urban garden	Subtropical, Tropical, humid with 5-6 dry months
Los Angeles, Heredia	9°59'30"N 84°04'01"W	1200	Poaceae	Subtropical, Tropical, humid with 5-6 dry months
Jardín Landcaster, Cartago	9°50'23"N 83°53'25"W	1350	Orchids	Template, Tropical, humid with 3-4 dry months
San Vito, Puntarenas	8°49'23"N 82°58'08"W	1010	Poaceae	Subtropical, Tropical, very humid with 1-2 dry months
Playa Blanca, Puntarenas	8°38'18"N 83°26'15"W	0	Poaceae	Tropical, Tropical, humid with 1-2 dry months
Jardín Botánico Las Cruces, Puntarenas	8°47'13"N 82°58'03"W	1160	Botanical garden	Subtropical, Tropical, very humid with 1-2 dry months
Siquirres, Limón	8°13'49"N 82°48'48"W	18	*Musa paradisiaca*	Tropical, Tropical, very humid without dry season
Pejibaye, Cartago	9°49'46"N 83°41'33"W	680	Forest edge	Subtropical, Tropical, very humid without dry season

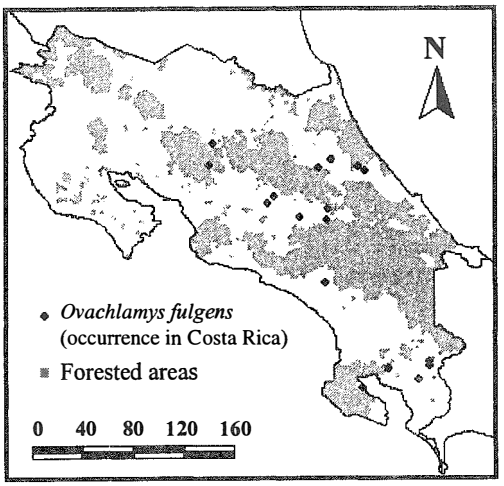


Fig. 1. Geographic distribution of *Ovachlamys fulgens* and Costa Rica forested areas(source: Atlas del Cambio de Cobertura de la Tierra en Costa Rica. 1979-1992. (MINAE, PNUMA, MAG, IGN y DGF). San José, 1996).

Microdistribution: For equivalent horizontal level and shading conditions, temperatures are higher at 10:00 than at 06:30 hours (Table 2). At 06:30 hours locations with trees have higher temperatures than those without trees, but the reverse is true at 10:00 hours (Table 2). The temperature depends on time of day and tree cover (Table 2). At 10:00, everywhere the temperature decreases in the following sequence: air > herbaceous vegetation > litter > soil. At 06:30 hours locations with trees have this temperature sequence: soil > litter > herbaceous vegetation > air. In the tree-less locations the sequence at this time is: soil > litter > air > herbaceous vegetation (Table 2). The thermically most stable location is the soil under trees, followed by soil without trees, litter with trees, herbaceous vegetation with trees, air in locations with trees, litter without trees, herbaceous vegetation without trees and finally the least stable temperatures were recorded in air from the tree-less locations.

TABLE 2

Descriptive statistic of temperatures measured at 06:30 hours (M) and at 10:00 hours (T) in an area without (S) and another with trees (C). The five samplings are included.

Variable	Mean	Standard deviation	Minimum	Maximum	Sample size
Air temperature TS	26.45	3.196	19.50	32.00	48
Air temperature TC	24.15	2.041	19.00	28.00	48
Litter temperature TS	25.89	5.914	18.75	43.00	48
Litter temperature TC	22.45	1.905	19.50	27.25	48
Soil temperature TS	21.01	1.171	18.75	25.50	48
Soil temperature TC	21.64	0.984	19.75	24.50	48
Temperature in herbaceous vegetation TS	26.10	5.043	19.50	40.00	48
Temperature in herbaceous vegetation TC	22.82	1.876	19.00	28.50	48
Air temperature MS	18.76	0.999	16.50	20.50	48
Air temperature MC	18.89	1.073	16.00	21.00	48
Litter temperature MS	18.88	0.901	16.75	20.50	48
Litter temperature MC	19.29	0.877	17.50	21.00	48
Soil temperature MS	19.35	0.775	18.00	20.75	48
Soil temperature MC	20.36	0.851	18.00	22.00	48
Temperature in herbaceous vegetation MS	18.55	0.907	16.25	20.25	48
Temperature in herbaceous vegetation MC	19.00	0.866	17.00	20.75	48

Quadrats were almost (95 %) completely covered by litter, but only 54 % of them had herbs (Table 3). The litter has twice as much humidity as the soil (Table 3). Relatively few quadrats had visible fungal hyphae and these were almost exclusively in the lower litter layers (Table 4). The herbs were mainly *P. purpureum*, *Impatiens walleriana* and *Blechum*

brownei (Table 5). Litter was dominated by grass blades and leaves of *P. americana* and *P. friedrichsthalianum* (Table 6).

Most live specimens were found in litter and on herbaceous vegetation in the first 50 cm above ground, while none were found inside the soil or at more than 70 cm above ground. Snail abundance was similar in the sections with and without trees (chi-quadrate x^2, $p > 0.05$). The factors most strongly correlated with the abundance of live snails were litter abundance in Z1 and Z2, litter and soil humidity, litter depth, herbaceous vegetation thickness, relative humidity (Table 7) and the herbaceous vegetation and litter (in Z2) composition (Table 8). In the last two cases snails seem to be more abundant in areas where *Y. elephantipes* occurs. The presence of live snails was: 1- negatively correlated with the temperature at 10:00am in the litter and vegetation of areas with trees and without them and in the soil of areas with trees, and 2- positively correlated with the temperature at 6:30 am in the air and herbaceous vegetation of areas with and without trees, and in the litter of areas without trees (Table 7).

TABLE 3

Descriptive statistic of quantitative variables (except temperatures). The five samplings are included.

Variable	Mean	Standard deviation	Minimum	Maximum	Sample size
Litter moisture rate	1.58	1.32	0.00	9.4	756
Soil moisture rate	0.78	0.74	0.01	8.7	740
Number of *O. fulgens* eggs	0.20	1.00	0.00	12.0	762
Maximal thickness of herbaceous vegetation (cm)	44.12	39.04	0.00	200.0	762
Minimal thickness of herbaceous vegetation (cm)	8.65	18.11	0.00	130.0	762
Mean thickness of herbaceous vegetation (cm)	26.39	25.79	0.00	140.0	762
Maximal depth of litter (cm)	14.35	13.97	0.00	100.0	762
Minimal depth of litter (cm)	6.05	7.03	0.00	70.0	761
Rate of litter cover	0.95	0.18	0.00	1.0	762
Mean depth of litter (cm)	10.19	9.75	0.00	75.0	761
Number of *O. fulgens* shells	0.27	0.83	0.00	10.0	762
Number of live *O. fulgens*	0.61	1.33	0.00	10.0	762
Rate of herbaceous cover	0.54	0.38	0.00	1.0	762
Relative humidity	68.17	15.65	44.00	100.00	36

TABLE 4

Frequency (%) of litter and hyphae abundance in levels Z1, Z2 and Z3. Abundance is divided into eight levels: 0= absent, 1= absent-scarce, 2= scarce, 3= scarce-regular, 4= regular, 5= regular –abundant, 6= abundant, 7= very abundant.

Variable	Category								Sample size
	0	1	2	3	4	5	6	7	
Litter abundance in Z1	2.5	10.5	19.2	13.8	21.0	10.0	11.0	8.3	734
Litter abundance in Z2	0.4	6.4	14.7	12.5	23.0	13.3	15.2	10.6	732
Litter abundance in Z3	37.3	17.6	12.9	5.0	10.0	3.4	4.9	6.2	740
Abundance of hyphae in Z1	72.7	5.0	3.7	1.4	2.4	1.3	1.4	2.0	685
Abundance of hyphae in Z2	82.3	1.2	1.4	0.9	1.6	0.8	1.2	0.5	685
Abundance of hyphae in Z3	89.8	0.0	0.0	0.0	0.0	0.0	0.0	0.1	685

TABLE 5

Frequency (%) of occurrence of plants as dominant species on the composition of herbaceous vegetation. Species with low frequencies were discarded (see Materials and Methods).

Plant species	Frequency of occurrence
Grasses, mainly	
Pennisetum purpureum	34.6
Impatiens walleriana	20.9
Blechum brownei	13.1
Absent	10.4
Calopogonium galactioides	9.7
Yucca elephantipes	3.5
Achyranthes aspera	3.3

TABLE 6

Frequency (%) of occurrence of plants as dominant species in the composition of litter in three levels. Only species with higher frequencies were included (see materials and methods).

Species of plant	Litter level		
	Z1	Z2	Z3
Absent	2.5	0.4	38.3
Monocotyledons (mainly grasses for Z2 and Z3)	45.2	38.5	58.9
Dicotyledons	29.5	——	——
Monocotyledons and dicotyledons	22.1	——	——
Persea americana	——	18.1	——
Annona muricata	——	7.2	——
Musa sp.	——	1.9	——
Psidium friedrichsthalianum + Psidium guajava	——	15.9	——
Citrus sp.	——	1.9	——
Yucca elephantipes	——	2.8	——
Wood	——	1.7	——
Mangifera indica	——	9.6	——

Eggs were found in soil crevices 1 cm deep or less or in the litter closest to the soil. Egg abundance was strongly correlated with litter abundance in Z1 and Z2, litter and soil humidity, litter depth, sampling date and relative humidity. The egg occurrence was: 1- negatively correlated with the temperature in herbaceous vegetation of an area with trees at 10:00 am and 2- positively correlated with the temperature at 6:30 am in the litter of areas with trees and without trees and in the soil in an area without trees (Table 7).

The factors most strongly (negatively) correlated with the presence of shells were the temperature at 6:30 am in the soil and litter of areas with trees and in the soil of areas without trees (Table 7).

Demography: The small sample size prevented statistic analysis but the general pattern of population dynamics shows correlation with the annual rain cycle (Fig. 2), with some time lag. The maximum temperature also seems to have influence on the population dynamics. December 1992 was a very dry and cool month as well as the onset of the dry season, snail population was high, but many aestivating individuals were found. Similarly, the population increase became noteworthy shortly after the first rains. March 1993, although wetter less dry, had the highest temperature of the year and also the fewest amount of live snails. In June 1993 precipitation as well as the snail population rose and the temperature decreased. The same pattern was kept in September 1993.

TABLE 7

Spearman´s correlations between quantitative variables and amount of eggs, shells and living snails. Temperatures were measured at 06:30 hours (T) and at 10:00 hours (M) in an area without (D) and one with trees (P). Litter and hyphae abundance were measured in level Z1, Z2 and Z3 (see Materials and Methods).

Variable	Eggs R (p) N	Shells R (p) N	Living snails R (p) N
Litter abundance in Z1	0.15960 (0.0001*) 734	0.06477 (0.0795) 734	0.18738 (0.0001*) 734
Litter abundance in Z2	0.14104 (0.0001*) 732	0.06844 (0.0642) 732	0.24039 (0.0001*) 732
Litter abundance in Z3	0.01811 (0.6228) 740	0.03896 (0.2899) 740	0.03833 (0.2978) 740
Litter moisture rate	0.25317 (0.0001*) 756	0.00941 (0.7962) 756	0.23498 (0.0001*) 756
Soil moisture rate	0.10850 (0.0031*) 740	0.09414 (0.0104) 740	0.19066 (0.0001*) 740
Maximal thickness of herbaceous vegetation	0.01513 (0.6767) 762	0.03838 (0.2901) 762	0.09657 (0.0076*) 762
Minimal thickness of herbaceous vegetation	0.00024 (0.9948) 762	0.04422 (0.2228) 762	0.04242 (0.2422) 762
Mean thickness of herbaceous vegetation	0.01361 (0.7076) 762	0.04136 (0.2541) 762	0.09528 (0.0085*) 762
Abundance of hyphae in Z1	-0.07322 (0.0554) 685	-0.03009 (0.4317) 685	-0.09693 (0.0111) 685
Abundance of hyphae in Z2	-0.03232 (0.3984) 685	-0.01349 (0.7246) 685	-0.07264 (0.0574) 685
Abundance of hyphae in Z3	-0.00952 (0.8037) 685	-0.01730 (0.6513) 685	-0.02431 (0.5253) 685
Maximal depth of litter	0.10542 (0.0036*) 762	0.03661 (0.3129) 762	0.22297 (0.0001*) 762
Minimal depth of litter	0.14548 (0.0001*) 761	0.03850 (0.2888) 761	0.15884 (0.0001*) 761
Rate of litter cover	0.07358 (0.0423) 762	-0.04100 (0.2583) 762	0.07077 (0.0508) 762
Mean depth of litter	0.12289 (0.0007*) 761	0.03902 (0.2824) 761	0.22318 (0.0001*) 761
Date of sampling	0.22361 (0.0001*) 762	-0.07556 (0.0370) 762	0.00088 (0.9807) 762
Rate of herbaceous cover	0.01627 (0.6538) 762	0.05802 (0.1095) 762	0.04209 (0.2458) 762
Relative humidity	0.17685 (0.0001*) 597	-0.00399 (0.9224) 597	0.21797 (0.0001*) 597
Air Temperature MD	-0.00327 (0.9288) 751	0.03254 (0.3732) 751	-0.04872 (0.1823) 751
Air temperature MP	0.06549 (0.0729) 751	0.00170 (0.9630) 751	-0.00480 (0.8955) 751
Litter temperature MD	-0.02823 (0.4398) 751	0.02920 (0.4243) 751	-0.12304 (0.0007*) 751
Litter temperature MP	-0.05504 (0.1318) 751	0.02220 (0.5436) 751	-0.10317 (0.0047*) 751
Soil temperature MD	0.03597 (0.3250) 751	-0.03686 (0.3131) 751	-0.07338 (0.0444) 751
Soil temperature MP	-0.01252 (0.7320) 751	0.00829 (0.8206) 751	-0.10004 (0.0061*) 751
Temperature in herbaceous vegetation MD	-0.06510 (0.0746) 751	0.00609 (0.8677) 751	-0.13846 (0.0001*)751
Temperature in herbaceous vegetation MP	-0.12745 (0.0005*) 751	0.05233 (0.1520) 751	-0.13058 (0.0003*)751
Air temperature TD	-0.02244 (0.5392) 751	0.00409 (0.9110) 751	0.12123 (0.0009*) 751
Air temperature TP	0.04363 (0.2323) 751	-0.00712 (0.8456) 751	0.11299 (0.0019*) 751
Litter temperature TD	0.11713 (0.0013*) 751	-0.05237 (0.1516) 751	0.10940 (0.0027*) 751
Litter temperature TP	0.12587 (0.0005*) 751	-0.10308 (0.0047*) 751	0.06929 (0.0577) 751
Soil temperature TD	0.13814 (0.0001*) 751	-0.09855 (0.0069*) 751	0.04481 (0.2200) 751
Soil temperature TP	0.04570 (0.2109) 751	-0.13163 (0.0003*) 751	-0.02160 (0.5545) 751
Temperature in herbaceous vegetation TD	0.06219 (0.0886) 751	-0.02016 (0.5812) 751	0.10812 (0.0030*) 751
Temperature in herbaceous vegetation TP	-0.01416 (0.6985) 751	0.02045 (0.5759) 751	0.10223 (0.0050*) 751

N= sample size, R= correlation coefficient, p= probability, * = p less than 0.01.

TABLE 8

Chi-square analysis for qualitative variables with egg, shell and living Ovachlamys fulgens *amount. Composition were measured in level Z1, Z2 and Z3 (see Materials and Methods).*

Variables	Freedom degree	Value	Probability	Sample Size
Egg amount by litter composition in Z1	3	1.870	0.600	745
Shell amount by litter composition in Z1	3	4.687	0.196	745
Living snail amount by litter composition in Z1	3	0.274	0.965	745
Egg amount by litter composition in Z2	9	4.944	0.839	737
Shell amount by litter composition in Z2	9	13.974	0.123	737
Living snail amount by litter composition Z2	9	32.545	0.000*	737
Egg amount by litter composition in Z3	1	0.003	0.957	733
Shell amount by litter composition in Z3	1	0.288	0.592	733
Living snail amount by litter composition inZ3	1	0.001	0.973	733
Egg amount by composition of herbaceous vegetation	8	11.906	0.155	722
Shell amount by composition of herbaceous vegetation	8	16.216	0.039	722
Living snail amount by composition of herbaceous vegetation	8	29.621	0.000*	722

Neonates is the group that during the dry season decreases most and also the one that increases most dramatically (followed by juveniles) with the rains. Neonates and juveniles decrease proportionatelly as they are recruited to the adult class (Fig. 2).

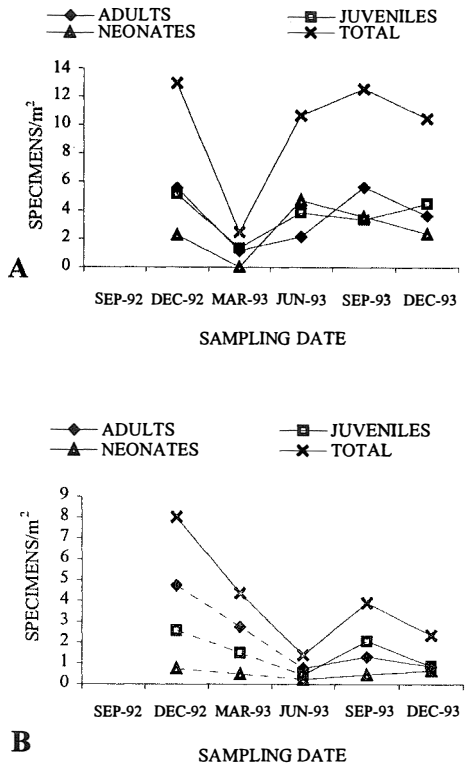
Empty shell density has two important differences from the living population (Fig. 2): 1) between the second and third sampling it decreased as the population increased and 2) it never recovered its initial level. Nevertheless, the general empty shell density parallels the curve of living animal density (Fig. 2). Live snail density ranged from 8.30 ind/m^2 in March to 43.41 ind/m^2 in December.

The presence of *O. fulgens* eggs is also affected by rain: 57.2% of eggs were found in the September 1993 sampling, 34.9% in June 1993 and only 7.9% in December 1992 (n=152). The mean clutch size was 2.6 eggs (60, $\pm$0.978, 1-5 eggs).

The lowest proportion of aestivating individuals was recorded in June (1.0%; n= 100) and September 1993 (0.9%, n=116). The proportion increased for the December (1992 and 1993) samplings, that is the dry season onsets: 12.7% (n=126) and 18.4% (n=98) respectively. The greatest proportion was in March 1993 with 91.7% aestivating (n= 24). To prepare for aestivation, these molluscs retract the head and then the foot into the shell. They are found adhering to litter leaves and grass blades. The adherent mucus is limited to the aperture edge and does not form an epiphragm (n= 58). They could end aestivation abruptly, becoming active almost immediately (5 - 10 sec) when experimentally separated from the substrate.

A single case of predation was observed: an ant carrying an *O. fulgens* egg (some endoparasites were also observed but these in specimens collected in San Luis, Limón province (Table 1). Courtship and copulation were not seen.

Sampling correction factor: Visual counts underestimated the number of live and dead *O. fulgens* in the field, nevertheless it was statistically different only with dead neonates (U-Mann-Whitney for neonates shells, n-shells found in the field= 39, n-shells found in the laboratory = 39, p= 0.0065*). The correction factor for live animals is 3.36 and for shells 15.33. Dead neonates were the most likely to be misrepresented in the counts; adult counts were closer to the real numbers (Table 9).



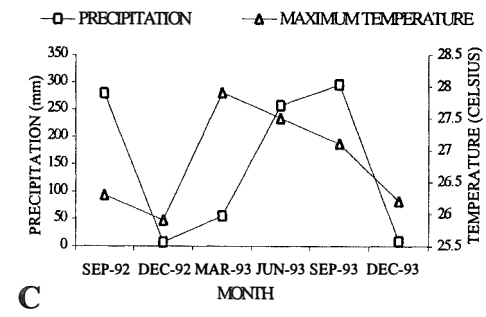


Fig. 2. Density of *Ovachlamys fulgens* for 13 months. Values not corrected for undersampling (see Appendixes 1 and 2 for descriptive statistics). A- live snails. B- Empty shells (adult, juvenile and neonate data from March 1993 are intrapolated –denoted with an interrupted line–). C. Annual rain precipitation and maximum temperature in Pavas, San José, Costa Rica.

Shell decomposition: Shell decomposition is a gradual process that begins with death. The decomposing soft parts often leave a black stain in the first body whorls; the stain is gradually reduced and finally disappears. At this time the periostracum is not decomposed and the shells are translucent amber in color. This part of the process was labeled "intact" and takes tree months (Fig. 3). Next, the shells "faded", the periostracum is lost, beginning at the apex (only once was a shell totally white before it began to break apart). Then the apex is lost; the process lasts ten months and follows a normal curve (Fig. 3) although the curve ascent occurs in the first three months. The third or "broken" stage occurs after the apex is broken, the shells lose the periostracum and fragments to disappearance. The 23 shells sample required more than ten months for all to disintegrate (Fig. 3); the mean was 147.5 days (23, ±102.6, 28-310 days).

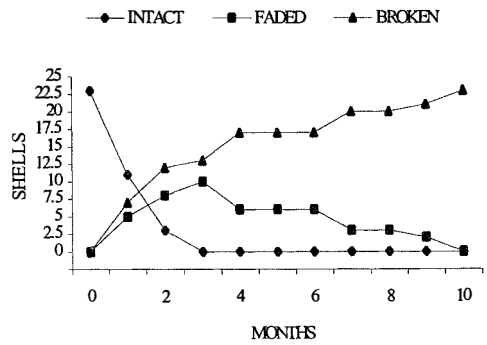


Fig. 3. Disintegration of *Ovachlamys fulgens* shells.

TABLE 9

Descriptive statistic of Ovachlamys fulgens *visually detected in the field and those detected in the laboratory in ind/m²*

Variable	Mean	Standard deviation	Minimum	Maximum	Sample size
Adult shells detected in the field	1.64	6.14	0	32	39
Adult shells detected in the laboratory	2.05	5.42	0	16	39
Juvenile shells detected in the field	0	0	0	0	39
Juvenile shells detected in the laboratory	8.21	13.17	0	16	39
Neonate shells detected in the field	0	0	0	0	39
Neonate shells detected in the laboratory	21.33	54.11	0	304	39
Adult specimens detected in the field	2.87	9.62	0	48	39
Adult specimens detected in the laboratory	3.69	15.77	0	96	39
Juvenile specimens detected in the field	1.23	7.69	0	48	39
Juvenile specimens detected in the laboratory	4.92	12.80	0	64	39
Neonate specimens detected in the field	0	0	0	0	39
Neonate specimens detected in the laboratory	0.61	1.33	0	16	39

DISCUSSION

Macrodistribution: In Costa Rica *O. fulgens* is correlated with agricultural plantations and with secondary growth vegetation; thus it is probably benefited by deforestation. Nevertheless, it may also become established in forest remnants close to plantations.

The macrodistribution of *O. fulgens* appears to be limited by temperature and humidity because it has not been found in regions with annual means below 20°C and above 27.6°C and annual precipitation below 1530mm. The data from Naha (the only city in the Liu Chiu Islands with meteorological data available) fully agree with these ranges. For this reason, the species will probably fail to colonize the northern Pacific region (Nicoya, basically), and the highlands above 1700masl. The only biotic zones still open to establishment are those classified as "temperate, tropical very humid" mainly on the bases of the mountain ranges in the center and south of Costa Rica.

Microdistribution: According to this study the number of eggs and live snails of *O. fulgens* increase with the increase of temperature during the morning (6:30 am) and with the decrease of temperature later in the morning (10:00am) showing a tendency to thermic stability. Exactly the opposite situation was found in the case of empty shell, a fact which supports the last conclusion. Apparently the thermic stability that tree cover gives is not significant for the abundance of *O. fulgens*, making the species more suitable to colonize cultivated areas. Similarly to the findings of Boag (1985), thermic stability appears to determine substrate selection of adults.

Other factors clearly correlated with occurrence of eggs and live snails were humidity of litter and soil and season (for eggs only), as reported for temperate species (Boag 1985, Locasciulli and Boag 1987, Nilsson *et al.* 1988). High relative humidity is also an important factor for snail and egg abundance, an expected result due to the hygroscopic nature of the eggs and to the snails' slime trail production. This study suggests that *O. fulgens* lays eggs in the soil probably not only because it is, thermically, the most stable microhabitat available, but also because these can take advantage of the increased moisture during the rainy season (see Barrientos 1998). Degen *et al.* 1992 found that the desert snail *Trochoidea seetzenii* markedly selects microhabitats with stable humidity, but this study suggests that *O. fulgens* prefers moister soil and litter, not the more stable. The results of this study do not support Peake's (1968) opinion that well drained soils favor the presence of molluscs.

Litter depth and abundance also affected eggs and living *O. fulgens* abundance. Abramsky *et al.* (1990, 1992) stated that the factors determining abundance of desert species are predation, oviposition sites and habitat heterogeneity. Brown and Lodge (1993) stressed the relationship between abundance and habitat structural complexity, the latter increases the area that can be colonized. In the present study, the factors listed by Abramsky *et al.* (1990, 1992) and Brown and Lodge (1993) are the result of litter depth and abundance because thicker litter has more sites to colonize, lay eggs in and hide from predators.

It has been shown that the litter from each tree species generates significant differences in the soil composition (*e.g.* phosphorus concentrations, pH values, etc.) (Orians *et al.* 1996) and that some types of leaf litter leaves are not adequate for snail oviposition (Barrientos 1996, 1998) or feeding (Van Es and Boag 1981, Boag and Wishart 1982, Molgaard 1986, Laurens *et al.* 1987, Speiser and Rowell-Rahier 1991, Stamol 1993). Besides this, Chatfield (1975) found that *Discus rotundatus* feeds mainly on green algae. On the contrary, the same author found that in high density populations of Helicid snails the most frequent food plants were usually the common ones in the plant community, in a more opportunistic way. Chatfield's (1975) findings support an extrapolation: more diverse forests (or litter layers) make specialization less desirable, although this could also be true in a tropical forest due to its high diversity, in this study the taxonomic composition of the litter apparently had a significant effect on the microdistribution of *O. fulgens*. Although not the most abundant plant, *Y. elephantipes* litter was very abundant, had "long live" and kept high moisture levels (of the layers not exposed to sun), any of these factors could favor the abundance of *O. fulgens*. Before establishing if this result was produced due to dietary needs or to any of the other characteristics mentioned above, laboratory experiments should be conducted. Chatfield (1975) and Locasciulli and Boag (1987) suggested that litter molluscs benefit from the presence of fungal hyphae but for *O. fulgens* seems to have no effect on them (Barrientos 1996, 1998), at least for hyphae visible to the naked eye.

The different results of the analysis of living snails' and shells' tendencies suggest that those categories should not be considered together as some authors have done (see Coppois 1984). Shell occurrence can be the result of factors that operated in the past but that may be currently absent such as foliage shadow, litter accumulation and transport by water currents or predators (Abramsky *et al.* 1990).

Demography: The density curve for live snails has the expected shape: it follows, with some lag, the precipitation curve and is inverse to the maximum temperature curve. A similar pattern was found by Kralka (1986) for *Euconulus fulvus*, *Nesovitrea electrina*, *Discus cronkhiteri* and *Vertigo gouldii* for precipitation and population dynamics in north temperate zones. In Cuba Alonso and Berovides (1991) found for *Zachrysia guanensis* that the higher the moisture and temperature the greater its abundance. Costa Rican *O. fulgens* are more abundant when daily temperature variation is minimal, not during periods of high temperature. In fact, low precipitation (followed by high temperature) seems to have a higher impact in the population demography. The species is abundant but does not reach the extremely high densities of 2500ind/m^2 reported for *Bradybaena similaris* in southern Brazil (Reichholf 1986).

The density of dead snails (empty shells) does not fluctuate as expected because, if shells require a mean of five months to disintegrate, the curve should climb in the dry season, remain stable the next five months and progressively decline until the next dry season. However, the shell curve follows, with some lag, that of living snails, suggesting that in nature the shells disintegrate in less than five months. Shell density should not be used for extrapolation of live snail demography until more species with different shell sizes and thickness as well as larger samplings are tested.

The timing of egg laying correlates with high humidity, consistent with the need of recently laid eggs to absorb water from the surroundings (Barrientos 1996, 1998). Most stylommatophorans behave similarly; for example, *Sphincterochila zonata*, *S. prophetarumare* and *Helminthoglypta arrosa* prepare physiologically while aestivating to lay eggs with the first spring rains (Van der Laan 1981, Hodgson and Shachak 1991). Field clutches have fewer eggs than laboratory clutches (Barrientos 1996, 1998), possiblly reflecting the effect of predators and competition in the field.

Aestivation is similar to that of other terrestrial molluscs and represents a physiological defense against environmentally difficult periods, for instance low humidity in Mediterranean and Caribbean species (Hyman 1967, Lazaridou-Dimitriadou and Saunders 1986, Dallas *et al.* 1991, Bidart *et al.* 1992, Ward and Slotow 1992). Apparently, in the field *O. fulgens* also begins aestivation when humidity decreases significantly. *O. fulgens* reproduced and did not aestivate during the dry months when kept in moist terraria (Barrientos 1996, 1998), but a different behavior has been reported for other species like *Trochoidea seetzeni* (Ward and Slotow 1992). This makes of *O. fulgens* a very successful pest in artificially irrigated plantations. In the dry season the most affected group was that of snails with a shell diameter under 2.5mm; the most probable reason being that their volume/surface ratio is lower and thus water loss higher (see Waite 1987). The reason for lack of an epiphragm requires more research because it could be an alternate system to close the shell aperture, as in members of the genera *Pararhytida* and *Rhytidopsis* (Charopidae), which have pseudo-opercules (Solem *et al.* 1984).

The underestimation of live and dead *O. fulgens* was not as high as in *Succinea costaricana* (Villalobos *et al.* 1995). These results suggest that, when shells smaller than 2.5 mm in diameter want to be included in the analysis, ecological samplings should be done by collecting the soil and plants and sorting them in the laboratory.

Only two types of predators (ants and nematodes) were seen in the field but *O. fulgens* populations may be controlled by rodents, lizards, birds and carabid coleopterans, known to feed on other snails (Sirby 1984, Bishton 1986, Abramsky *et al.* 1992, Digweed 1993). Some molluscs attacked by ants have developed defensive behaviors (Gotwald 1972) and *O. fulgens* shields itself with the shell when disturbed (pers. observ.) or jumps using its caudal horn and the posterior part of the foot as a catapult (Barrientos 1998).

RESUMEN

El caracol introducido *Ovachlamys fulgens* (Stylommatophora: Helicarionidae) habita regiones cultivadas de Costa Rica y su distribución está limitada por temperaturas anuales entre 20 y 27.6°C y precipitaciones anuales entre 1530-3034 y 3420-8000 mm con no más de seis meses secos. Esta especie habita en la hojarasca y en la cobertura herbácea hasta a 70 cm de altura. Se realizaron cinco muestreos; uno cada tres meses. En cada muestreo se analizaron un mínimo de 150 parcelas aleatorias de 25 x25 cm. Los factores que determinan la abundancia de individuos y huevos fueron la abundancia y profundidad de la hojarasca, la humedad del mantillo y del suelo, y la humedad relativa. Éstos a su vez estuvieron positivamente correlacionados con la temperatura a primeras horas de la mañana (6:30 am) y negativamente con la temperatura a media mañana (10:00 am). Aparte de estos factores, los caracoles tambien estuvieron correlacionados con el grosor de la capa herbácea y con la presencia de*Yucca elephantipes* tanto en el mantillo como en la vegetación. Los huevos tambien se vieron afectados por la época del año, debido a su propiedad higroscópica. La abundancia de conchas se correlacionó únicamente con la temperatura, en patrón contrario al de los huevos. Tanto la población como la cantidad de conchas siguieron, con un leve retraso, la curva de lluvias de la zona a lo largo del año. La época reproductiva abarca los meses de mayo a noviembre (época lluviosa); y durante los meses de diciembre a abril (época seca) se puede encontrar hasta el 92% de los especímenes estivando. En condiciones naturales la camada promedio tiene tres huevos. Los caracoles vivos tuvieron una densidad máxima de 12.92 ind/m^2 (en diciembre) y mínima de 2.47 ind/m^2 (en marzo; estos valores deben multiplicarse por el factor de corrección 3.36). En condiciones experimentales las conchas tardaron intactas dos meses y su descomposición total se produjo en cinco meses en promedio.

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Appendix 1

Descriptive demographic statistic for live Ovachlamys fulgens *for 13 months. Data in individuals/m² (see Fig. 2A). Values not corrected for undersampling.*

Sampling 1 (December 1992)

Variable	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	156	5.54	15.38	0	96
Juveniles	156	5.13	12.72	0	80
Neonates	156	2.26	8.42	0	80
Total	156	12.92	27.33	0	176

Sampling 2 (March 1993)

Variable	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	155	1.14	4.51	0	32
Juveniles	155	1.34	6.04	0	48
Neonates	155	0.00	0.00	0	0
Total	155	2.48	7.98	0	48

Sampling 3 (June 1993)

Variables	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	150	2.13	7.34	0	64
Juveniles	150	3.84	9.58	0	64
Neonates	150	4.69	13.69	0	112
Total	150	10.67	23.05	0	144

Sampling 4 (September 1993)

Variable	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	148	5.62	15.49	0	112
Juveniles	148	3.35	8.19	0	48
Neonates	148	3.57	10.02	0	64
Total	148	12.54	23.79	0	128

Sampling 5 (December 1993)

Variables	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	150	3.63	8.52	0	64
Juveniles	150	4.48	11.59	0	80
Neonates	150	2.35	8.57	0	80
Total	150	10.45	18.54	0	96

Appendix 2

Descriptive statistics of Ovachlamys fulgens *empty shell density for 13 months. Data in individuals/m² (see Fig. 2B). Values not corrected for undersampling. Only total value available for the March 1993 sampling.*

Sampling 1 (December 1992)

Variable	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	156	4.72	11.81	0	64
Juveniles	156	2.56	8.03	0	48
Neonates	156	0.72	3.79	0	32
Total	156	8.00	19.11	0	112

Sampling 3 (June 1993)

Variable	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	150	0.75	3.39	0	16
Juveniles	150	0.43	2.59	0	16
Neonates	150	0.21	1.84	0	16
Total	150	1.39	4.88	0	32

Sampling 4 (September 1993)

Variables	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	148	1.30	4.38	0	16
Juveniles	148	2.05	7.05	0	48
Neonates	148	0.43	3.20	0	32
Total	148	3.78	9.02	0	48

Sampling 5 (December 1993)

Variable	Sample size	Mean	Standard deviation	Minimum	Maximum
Adults	150	0.85	3.61	0	16
Juveniles	150	0.85	3.61	0	16
Neonates	150	0.64	3.65	0	32
Total	150	2.35	5.98	0	32