Factors Affecting the Structure and Distribution of Terrestrial Pulmonata

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Abstracts Soil $CaCO_3$ levels were determined for six ecosystems in Washtenaw and Wayne Counties, Michigan and in Linn County, Iowa; and correlation between these results and the shell thickness of certain terrestrial snails was made. Species used were *Anguispira alternata* (Say), *Triodopsis multilineata* (Say), and *T. albolabris* (Say). Two ecosystems had high $CaCO_3$ levels (120-144 ppm), three had intermediate levels (93-99ppm) and one had a low level (40 ppm). Width/thickness ratios of live and cast shells showed that those in high calcium ecosystems had thicker shells than those in low calcium ecosystems, though there were large deviations in the thickness values. Population density of the snails seemed to be influenced by the calcium level, but predators, cover, and moisture conditions were also observed as important limiting factors. Species distribution studies showed that the maximum number of species was found when soil $CaCO_3$ levels were between 99 and 120 ppm, with a decrease in number of species in low calcium ecosystems. These correlations seem to indicate that at some point in the food chain of the terrestrial snail, calcium is passed on to the snail at levels reflecting the levels of calcium in the ecosystem.

INTRODUCTION

One of the factors having a definite effect on mollusks is the amount of dissolved salts, specifically calcium carbonate, in the water of the ecosystem. Allee et al. (1949) stated that northern Wisconsin lakes that are intermediate in hardness (10 to 20 ppm of bound carbonates) have the largest number of aquatic snail species and that those lakes with the hardest waters (over 30 ppm) have the greatest number of individual aquatic snails. Studies of land snails in Ireland by Atkins and Lebour (1923) showed that there was an optimal soil pH (7.0) for snails with calcareous shells, but not for those with hyaline shells.

The effects of various concentrations of calcium on shell thickness have been discussed by Pennak (1953) who stated that the thickness of the shells of certain species of aquatic snails is directly related to the amount of calcium in the water. Since the terrestrial Pulmonata lack gills (Baker, 1939) and also can not absorb calcium through their integument as has been demonstrated for some marine mollusks (Johnson, 1963), the effects of calcium concentration on the terrestrial pulmonata could be quite different. A search of the literature showed that most of the studies to date have been on either marine or fresh water mollusks.

The purpose of this study was to determine whether three species of terrestrial Pulmonata, *Anguispira alternata* (Say), *Triodopsis albolabris* (Say), and *Triodopsis multilineata* (Say), also show a variation in the thickness of their shell correlated with differences in the calcium concentration of the ecosystem. Species and population distribution studies were also made in an effort to determine possible factors affecting land snail distribution.

Areas Studied

The six areas studied were:

1. the Cemetery River Flat (C. R. F.), a flood plain behind Highland Cemetery, T3S/R7E/S4, City of Ypsilanti, Washtenaw County, Michigan,

2. the Lower Huron Area (L. H. A.), specifically the river flat known as the Paw Paw Trail Area in Lower Huron Metropolitan Park, T3S/R8E/S36, Van Buren Township, Wayne County, Michigan,

3. the slopes and low areas surrounding the pond on the Loesell Field Laboratory (L. F. L.), T3S/R7E/S4, Ypsilanti Township, Washtenaw County, Michigan,

4. the Curtis Road Woods (C. R. W.), a beech-maple forest north of Ypsilanti, T1S/R7E/S21, Salem Township, Washtenaw County, Michigan,

5. Cedar River South (C. R. S.), specifically the flood plain north of the Cedar River and south of Otis Road, south of Cedar Rapids, Iowa, T83N/R7W/S36, Rapids Township, Linn County, Iowa,

6. Cedar River North (C. R. N.) specifically the flood plain east of the Cedar River just below the dock ramp, T83N/R7W-/S17, Rapids Township, Linn County, Iowa.

The first two areas listed above supported deciduous forests in the flood plain of the Huron River. Both were primarily mixtures of *Ulmus americana L.*, *Tilia* spp., *Quercus* spp., *Crataegus* spp., *Acer* spp., *and Populus deltoides* Marsh. *Platanus occidentalis* L. was, however, more common in the Lower Huron Area. The first ecosystem, the Cemetery River Flats, showed a great variation in leaf litter composition. In the Lower Huron Area, *Platanus occidentalis* contributed the most to the leaf duff in the microhabitats studied. Because of the larger leaves and thicker growth of the sycamores, the leaf duff on the forest floor ranged from one-half inch to two inches during the early summer in the Lower Huron Area. On the forest floor of the Cemetery River Flat, at the same date, the leaf duff ranged from zero to one inch in depth.

The shrubs and bushes of the transgressive stratum were not significantly different in the two areas. They were primarily saplings of the large trees, plus a mixture of *Viburnum* spp., *Cornus* spp., and *Ribes* spp., shrubs. The herbaceous ground cover in the two areas was essentially similar.

The soil of both areas is Griffin loam (Veatch, Wheeting, and Bauer, 1930). Griffin loam is bottomland soil, poorly drained, and is often the alluvium of a nearby river or stream. The surface soil is brown, sandy loam, moderately high in organic matter

(Veatch et al., 1930). A profile description of Griffin loam by Striker et al. (1961) states that the A_p and C_{2g} horizon (26 inches plus) is calcareous.

A third area studied, the forest around the Loesell Field Laboratory pond, differed markedly from the other two areas. The land was of higher elevation and was better drained. The trees and shrubs included many of the river bottom genera (except sycamore) plus hickories (*Carya* spp.) with the oaks predominating. There was much less herbaceous plant cover. Oak leaves predominated in the forest floor leaf duff.

The soil of the Loesell Field Laboratory is Miami Silt Loam except for patches of Greenwood Peat in the marshy areas (Veatch et al., 1930). Miami Silt Loam is not high in organic matter. The A horizon is neutral to slightly acid, the B horizon is neutral to strongly acid, and the C horizon calcareous, giving an alkaline reaction.

The fourth area studied was a beech-maple forest on Curtis Road, north of Ypsilanti, Michigan. The soil surface was nearly level and the drainage ranged from good to poor. *Fagus grandifolia* and *Acer saccharum* were the predominant trees, although some *Ulmus americana* and *Fraxinus spp.* were also found. Few saplings or shrubs were found and herbaceous cover was sparse. Leaves of the above trees predominated in the leaf duff of the forest floor.

The soil of the woods is Conover Loam, with a small area of Fox Sandy Loam. The two soils are quite similar, both having slightly acid A and B horizons, and calcareous C horizons.

The Cedar River areas were wooded flood plains bordering the Cedar River. *Ulmus americana* L., *Populus* spp. and *Acer* spp., especially *Acer negundo*, were common in the overstory in both areas. The Cedar River South study area had more shrubs and brush, particularly *Ribes* spp. and *Smilax* spp. than did the northern area. Leaves of the above species made up the leaf duff which ranged from zero to 1.5 inches in both areas. The herbaceous ground cover was similar to that of the other flood plains studied.

Soil in both Cedar River areas was neutral to slightly alkaline in the A horizon (Table 1). Cedar River North had a calcerous A horizon ranging from one inch to more than a foot, with a sandy B horizon. Cedar River South was the same except that the A horizon rarely exceeded eight inches.

Methods

The collections and tests in the study were made in the spring and early summer of 1963 in the first four ecosystems listed above. The latter two areas were studied in the spring of 1966. The species distribution study was made at the same times.

Soil samples of 100 cc were collected from the A horizon between a depth of zero and two inches. No leaf duff was included. These samples were mixed with 250 ml of distilled water and allowed to equilibrate. The water was then decanted, filtered, and tested. The water tests for calcium carbonate concentration were made both with standard soap solution and with a Calgon water hardness test kit in the first four areas. For the latter two areas, a Hellige-Truog soil kit was used. Tests for pH were made on some samples.

Because of the scarcity of live snails, some of the shells studied were empty cast shells. A comparison between live and cast shells from each area showed no significant difference since any shell showing evidence of erosion was not used.

The width (diameter) and thickness of the shell wall were measured with micrometer calipers. The width measurement differed from that of standard terminology because many shells had damaged outer lips. Therefore, the width was not taken at the widest part of the shell. Instead the width measurement for all the shells was taken at the widest part from the parietal wall across the umbilicus. The thickness measurement of the shell wall was always taken on a section of the wall at the ventral (basal) surface of the body whorl 1 to 5 mm within aperture.

By use of these two measurements, a width to thickness ratio (W/T) was calculated, as was the standard error. The lower the W/T ratio the thicker the shell. The species studied for shell thickness were *Anguispira alternata* (Say), *Triodopsis multilineata* (Say), and *T. albolobris* (Say). The taxonomy of Burch (1962) was used.

Species and population distribution was studied by the use of quadrats one meter square located by a modified transect method. A number of quadrats were sampled along the transect and the values averaged. Counts of number of species and total number per square meter were made and the total number of species in a given study area was determined.

Results

As shown in Table 1, the level of calcium carbonate in the soil varied from 40.8 to 144 ppm in the six ecosystems. There appeared to be two high-level calcium ecosystems (Cemetery River Flat and Cedar River North), three medium-level ecosystems (Cedar River South, Lower Huron Area, and Curtis Road Woods), and one low-level ecosystem (Loesell Field Laboratory).

Table 1. $CaCO_3$ levels and pH in the six habitats.

Area	No. Samples Tested	pH	ppm $CaCO_3$	Standard Error (ppm)
Cemetery River Flat	10	7.7	144.	± 9.6
Lower Huron Area	3		96.3	± 2.3
Loesell Field Lab.	1		40.8	
Curtis Road Woods	4		93.2	±13.0
Cedar River South	3	7.5	99.	±13.0
Cedar River North	3	7.5	120.	±19.9

Width/thickness studies, shown in Tables 2 and 3 and plotted on Figure 1, show values ranging from 46.2:1 to 62.2:1 for *A. alternata* and ranging from 62.8:1 to 115:1 for the *Triodopsis* species. As seen on Figure 1, the ratios for both genera decrease with an increase in the calcium carbonate level, with the exception of the Cedar River North sample. Since the size of the ratio is inversely proportional to the thickness of the shell, this indicates a thickening of the shells as the calcium carbonate level increases.

Table 2. Comparison of Shell W/T Measurements of *Anguispira alternata* with standard deviation (S.D.), and standard error (S.E.).

Area	No. Measured	Shell Condition	Mean W/T For Area	S.D.	S.E.
Cemetery River Flat	60	cast	46.2:1	9.4	±1.2
Lower Huron Area	60	cast & live	51.9:1	12.2	±1.58
Curtis Road Woods	2	live	53.0:1	6.3	±4.4
Cedar River South	33	live & cast	62.2:1	16.9	±2.9
Cedar River North	42	live & cast	55.5:1	15.4	±2.4

Table 3. Comparison of Shell W/T Measurements in *Triodopsis* species in six ecosystems, with mean values, standard deviations, and standard errors of the mean.

Area	No. Measured	Shell Condition	Mean W/T For Area	S.D.	S.E.
Cemetery River Flat	9	cast	62.8:1	6.7	± 2.2
Lower Huron Area	5	live & cast	70.7:1	23.8	±10.6
Curtis Road Woods	8	live	73.1:1	9.1	± 4.1
Loesell Field Lab.	1	live	115:1		
Cedar River South	19	live & cast	64.5:1	15.2	± 3.5
Cedar River North	35	live	68.3:1	11.0	± 1.8

Triodopsis multilineata was the species measured in all study areas except Curtis Road Woods and Loesell Field Lab, where *T. albolabris* was the only *Triodopsis* species found. The only shell found in the low-calcium area (Loesell Field Lab) was extremely thin. Because of the small sample in this area, it is difficult to draw structural conclusions, and distribution studies in this area were impossible.

Distribution studies, shown on Table 4, showed a greater number of species in the high calcium ecosystems. Number of snails per one-meter quadrat varies greatly and was undoubtedly due to other factors. One of these factors was the large number of large *Triodopsis* shells found with the inner spire chewed out, probably by shrews or carnivores.

As shown on Figure 2, both the number of individuals per square meter and the number of species in the ecosystem in-

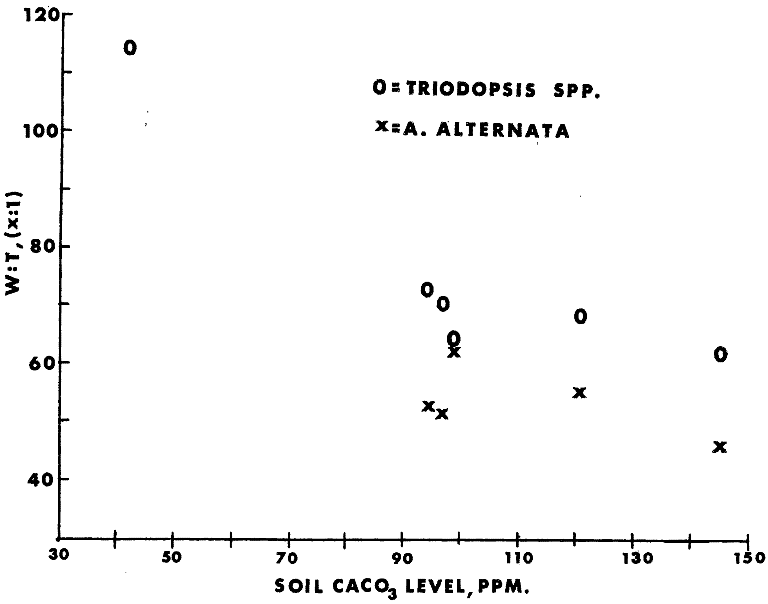

Fig. 1. Relation of shell thickness (W/T) to soil $CaCO_3$ levels for *A. alternata* and *Triodopsis* spp.

Table 4. Population size and species count in the six habitats studied.

$CaCO_3$ Conc Level	ppm.	Area	No. Species	No. Quad. Sampled	A. alternata	Triodopsis	Others	Total
	144	C.R.F.	3	6	.16	0	7.3	7.46
High								
	120	C.R.N.	5	8	.6	4.6	3.8	9.0
	99.	C.R.S.	5	8	4.4	.4	5.6	10.4
Med.	96.3	L.H.A.	4	4	4.0	.25	3.0	7.25
	93.3	C.R.W.	3	4	.50	2.0	.33	2.83
Low	40.8	L.F.L.	1	6	0	0	0	0

crease as the calcium carbonate level approaches 100 ppm. At levels greater than 120 ppm fewer species and individuals are found, though this is based on a single study. Figure 1 illustrates that, in a similar manner, shell thickness no longer increases greatly after the calcium concentration has reached a certain level.

Either *A. alternata* or one of the *Triodopsis* species was predominant in each area studied (Table 4). In no study were both present in large numbers in the same habitat. In only one area, Cedar River North, were both species of *Triodopsis* found together. Here *T. multilineata* was the predominate species, with four *T. albolabris* also in the sample. Other species found in this

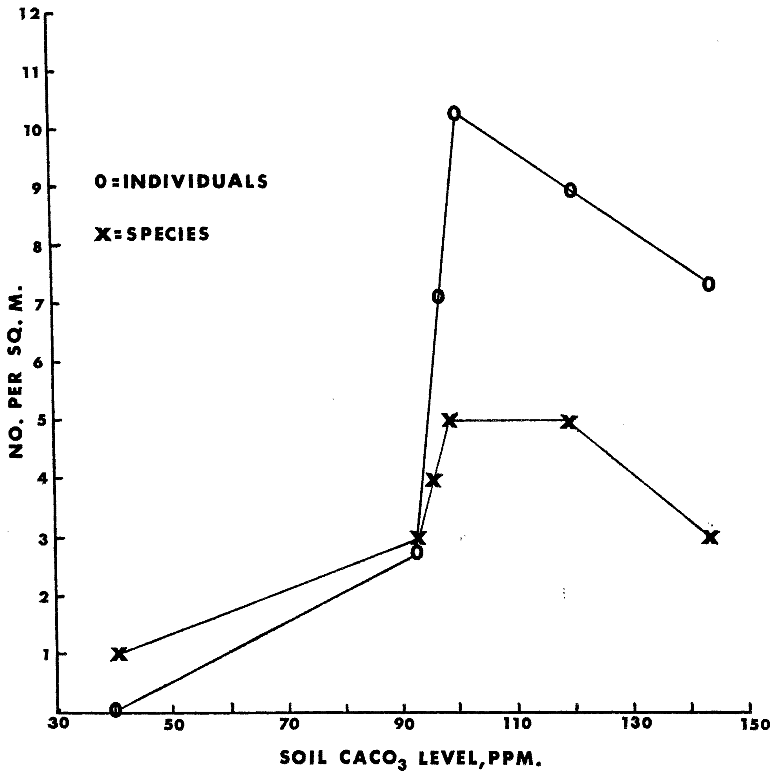

Fig. 2. Relation of species distribution and mean population size to soil $CaCO_3$ in the observed species of terrestrial pulmonata.

area were *Succinea* spp., *Discus cronkhitei* (Newcomb) and *A. alternata.*

Species found in the Cedar River South habitat were *A. alternata, T. multilineata, Succinea* spp., *Discus cronkhitei,* and *Retinella electrina* (Gould). Cemetery River Flat species included *A. alternata, T. multilineata,* and *Hygromia striolata* (*Pfieffer*). Lower Huron Area had four species: *A. alternata, T. tridentata* (Say), *T. multilineata,* and *H. striolata.* Curtis Road Woods species included *A. alternata, T. albolabris* and *H. striolata.*

Discussion

Several trends can be seen in the data presented. As the soil water hardness, expressed as calcium carbonate concentration, increases, the shell thickness tends to increase. There is, however, a considerable range of thickness within each group studied. The two Cedar River areas and the Lower Huron area showed the greatest range of W/T values. The two Cedar River areas also had a greater variation in their calcium carbonate levels, though this was not true for the Lower Huron Area.

Measurements of *A. alternata* from the Cedar River study areas do not fit into the pattern shown in Figure 2. They are thinner (have higher W/T values) than the shells from the areas lower in calcium. Only the Cedar River North samples varied from the pattern in *Triodopsis* species. Throughout the study, the shells of genus *Triodopsis* were consistently thinner in proportion to the *A. alternata* shells.

The variation in shell thickness, expressed as standard deviation, indicates little difference between the mean values for shell thickness in the high and medium calcium areas. Apparently, as long as sufficient calcium is passed through the food chain, shell thickness does not differ greatly in relation to width. Only when the calcium is low does shell thickness appear to decrease. The effects of soil calcium level higher than 144 ppm can not be concluded from the data.

As stated under AREAS STUDIED above, the low calcium concentration was only one of the differences between the Loesell Field Lab study area and the other areas. However, though these other factors (vegetation, soil, ground cover) may have influenced the sparse distribution of snail species in the area, it is probable that the calcium concentration was a major cause of the extreme thinness of the shells.

Distribution of species in both genera was extremely varied both between the ecosystems studied and also within the individual habitats sampled. There seems to be no immediate explanation of why *A. alternata* was the predominant species in the Cedar River South area as opposed to *T. multilineata* being predominant in the Cedar River North area. These two areas were essentially similar except for the higher calcium and slightly lower elevation of the Cedar River North area. A third difference was evidence of more predation by shrews and carnivores on the larger *T. multilineata* snails in the Cedar River South area.

The number of snails per square meter followed a definite pattern, being highest when the soil calcium carbonate level was about 100 ppm. However, it was found in most areas that leaf cover and moisture of the forest floor, amount of downed timber and its degree of decomposition, and frequency of flooding played a great role in determining distribution of the snails in any given ecosystem.

It can be inferred that the calcium level can act as a limiting factor on the snail population when this level is extremely high or extremely low. Quite possibly the optimum level differs from species to species, though there is no definite evidence of this in the data.

Species distribution, unlike population distribution, seemed to follow a more consistent trend. $CaCO_3$ levels between 99 ppm and 120 ppm produced the greatest number of species. Although other factors in the ecosystem may also have determined this range, a definite relationship seems to exist between soil $CaCO_3$ levels and number of species present in the ecosystem .

Conclusions

1. On the basis of the data, it can be inferred that the shells of *A. alternata*, *T. multilineata*, and *T. albolabris* are thicker in areas of higher calcium concentration than shells of the same species living in similar ecosystems with lower calcium concentrations. A relatively large range of thickness may also be expected within a given ecosystem.

2. The small change in shell thickness between 93 and 144 ppm indicates that this soil calcium carbonate level falls within the optimal range for the above species of snails.

3. The terrestrial snail population in the Loesell Field Laboratory is extremely low compared with the other ecosystems. The extreme thinness of the the only terrestrial snail shell found in this area appears to be related to the low calcium concentration, which may also limit the success of the snail population.

4. Population distribution studies showed that although population density was related to soil $CaCO_3$ levels, many other biotic and abiotic factors in the ecosystem influenced these figures.

5. Species distribution studies showed that the maximum number of species was found when soil $CaCO_3$ levels were between 99 and 120 ppm.

6. Because terrestrial snails have no gills to absorb calcium and have been shown not to absorb it through their integument, the above conclusions seem to indicate that some link in the food chain of the snail is capable of passing calcium on to the snail at levels reflecting the levels of calcium in the soil.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders Co. Philadelphia.

Atkins, W. R. G. and M. V. Lebur. 1923. The Hydrogen-Lon Concentration in the Soil and of Natural Waters in Relation to the Distribution of Snails. Proc. Roy. Dub. Soc. 17:233-240.

Baker, F. C. 1939. Field Book of Illinois Land Snails. Ill. Nat. Hist. Survey, Manual 2. Urbana, Ill.

Burch, J. B. 1962. The Eastern Land Snails. Wm. C. Brown Co. Dubuque, Iowa.

Johnson, R. F. 1963. The Source of Carbonate in Molluscan Shell Formation. Papers of the Twenty-sixth Annual Meeting of the Am. Soc. of Limnologists and Oceanographers. Ann Arbor. Mich.

Pennak, R. O. 1953. Fresh-water Invertebrates of the United States. Ronald Press. New York.

Striker, M. M., A. E. Taylor, L. J. Bartellk, L. S. Robertson, C. Shoaw, and A. W. McAllister. 1961. Soil Survey of Lenawee County, Michigan. U. S. Government Printing Office, Wash., D. C.

Veatch, J. O., L. C. Wheeting, and A. Bauer. 1930. Soil Survey of Washtenaw County, Michigan. U. S. Dept. Agric., Bur. Chem. & Soils, Ser. 1930. No. 2.