THE DISTRIBUTION AND REACTIONS OF THE LAND SNAILS
IN THE
VICINITY OF COLUMBIA MISSOURI

by

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PART ONE

I. Introduction

The following study was undertaken at the suggestion of Dr. G. S. Dodds, with the intent of discovering the factors which determine the distribution of a group of our local fauna, the land gastropods. This group has been a favorite object of study with naturalists for the past century, and a great mass of literature exists on isolated collections made the country over. In Missouri a certain amount of collecting has been done, probably exhausting largely the possibilities so far as species are concerned. However, some interesting additions to our knowledge of the regional distribution have been added in the course of the present study, as will be noted later. Greger (1905) has made extensive collections in Callaway County, Pilsbry and Ferriss (1906) in the Ozark Region, and Sampson (1913) over most of the State. There are besides, more general collections, as those of Binney (1885), in which mention is made of Missouri shells. Heretofore no attempt has been made to correlate the information scattered thru these papers, or to study the distribution from an ecological standpoint, and there has not been an intensive study of a single region in Missouri.

Before any attempt is made to determine the factors of distribution, one must learn the facts of distribution. The first part of this study is largely a study of the snail associations, and the second an experimental attempt to discover what factors of physiology or behavior underlie

the peculiarities of distribution learned in the first part of the work. The second part has not been carried to completion for lack of time and for other reasons mentioned later.

Several studies similar to the first part of the work have been made in other regions (Ruthven 1904, Adams 1906, F.C.Baker 1908, H.B.Baker 1910). Shelford in his Animal Communities (1912) includes the land snails. So far as I can discover, however, there has been no experimental work done with this end in view except that of Shelford on the "Reactions of animals to a gradient of evaporating power of air" (1913).

I am deeply indebted to Mr. Bryant Walker of Detroit, Michigan, for making identifications of the snails for me.

II. The Physiography of the Region

The region studied lies in Boone County, Missouri, south and west of Columbia. It consists of the valley of the Hinkson, from the College Road Bridge to the Round Hole about one mile below the Providence Road Bridge, and the slopes and ravines running down to it.

Boone County represents the meeting point of two distinct geological formations, that of the coal measures to the north, and the lower carboniferous limestone to the south. The district studied lies wholly in the latter region. The Hinkson Creek is a rather mature river valley in the limestone. It meanders back and forth across a fairly broad flood-plain, cutting alternately against the bases of the limestone bluffs, and across the valley. In places the

ravines have developed into broad secondary valleys, and the transition from flood-plain into uplands is much more gradual. The low hills on the north side of the valley southwest connect the alluvial flat with the upland plain. On the opposite side several deep ravines enter, on whose slopes is the most nearly virgin forest of the area.

III. The Flora

The prevailing vegetation of the region is mesophytic. Taking the county as a whole, it is a region of tension between the deciduous forest and the prairie. In the region studied however the forest dominates completely, the prairie region lying to the north over the coal measures. Along the river some hydrophytic plants are found, viz., the willows, poplars, sycamores, swamp-oaks and maples. On the upper edge of the limestone bluffs, and often on the upper part of their faces, the vegetation is xerophytic, but on the whole the associations are mesophytic, and the climax forest is the deciduous forest of the Ozark plateau (Daniels 1907).

It is hard to separate the hydrophytic forests of the river banks from the alluvial forests of the flood-plain. The alluvial forests grade very gradually into those of the midlands and uplands. No sharp distinctions exist. The river maples (Acer dasycarpus), the basswood (Tilia americana), the poplar (Platanus occidentalis), are characteristic of the alluvial forests. On the slopes white oak, (Quercus alba), the chestnut oak (Q. acuminata), the sugar-maple (Acer saccharinum), and the black walnut (Juglans nigra) are the dominant forms. The nettle associations (Urtica gracilis) are

typical of the alluvial zone, but may also obtain on the moist bluffs on the south side of the area. On the uplands, on the bluffs, and in the broader secondary valleys the climax forest is found. The oak society is primary, the white oaks dominating. The various hickories come next and then the walnuts. As a matter of fact, however, very little of the climax forest is left, probably none in its entirety. What has not been cleared rather vigorously has been pastured so heavily that the vegetation of the floor has been disturbed.

IV. Habitat Studies

a) Of the alluvial zone

1. Along the banks of the Hinkson there are occasional sand-flats, covered by willows and a few sycamores. These flats are entirely covered during high water, and the smaller plants either have not been able to obtain a footing, or, as is more likely, have been covered by sand deposited during the floods. Here on the trunks of the trees Succinea grovenori is found in rather large numbers. A few specimens of Castrodonata ligera were taken from moist leaves under the willows. Polygyra fraterna and P. monodon were found under the drift. Agriolimax campestris was also taken from similar situations. Zonitoides arborea and Vitrea indentata were found in bunches of as many as thirty in rotting driftwood.

2. East of Providence Road Bridge there is a sand and mud flat of apparently somewhat greater age than 1. It is covered by a dense thicket of willows, under which the lyne grass (Elymus) grows profusely. This flat also is

flooded during the winter and spring. Here on the bases of the willows Succinea grovenori was found many times.

b) Of the flood-plain

3. Back of the flats is a flood-plain varying in width depending on the distance between the creek and the bluffs. Most of this flood-plain is now in cultivation or in pasture. But along the river-band there are some places which represent approximately the primary condition. Also at the foot of the bluffs there are occasional clumps of willows, probably representing an actual stage in the genesis of the flood-plain forest. One such thicket composed largely of willows, ragweed and ironweed, with some buckbrush encroaching from the hillside, is south of Providence Road Bridge, near the mouth of a small stream emptying into the Hinkson. On this flat in September some thirty Gastrodonta ligera were observed. There are practically no plants on the floor, the large, tall weeds making such a dense shade that the smaller plants cannot compete. The amount of humus is small, a condition which seems to hold very often for the habitat of this snail.

4. At other places on the flood-plain the forest is fairly well developed. East of Providence Road Bridge on the south side of the creek is a narrow flat below the moist bluffs. Here the forest is well developed. The sycamore is the dominant tree. There are also large poplars, river-maples, and occasional birches and lindens. On the forest floor the nettles reach a large size. Here were found Polygyra thyroides in large numbers, P. profunda

almost as commonly, P.hirsuta and P.appressa occasionally, and Agriolimax campestris frequently. Bifidaria procera was found once on a grapevine about three feet from the ground. No other small shells were found, which is somewhat surprising, altho a great amount of searching was not done.

The forest here on the flat is continuous with that of the hillside, and apparently the same continuity holds for the molluscan population,

5. West of Providence Road Bridge on the north side there is a narrow strip of the flood-plain forest left along the bank of the creek. Here are elms and sycamores, quite large. The plain back from the river has evidently been under cultivation for a long time. Between the cultivated land and the sycamore-elm forest is a zone of young walnuts and poison elms, with a rather large amount of green-brier and ivy climbing into their branches. On the floor is a dense growth of nettles. Polygyra thyroides was abundant here after a rain. One individual of P.albolabris alleni and three of P.clausea have been taken here. In a rotting log a number of Zonitiodes arborea and a few Philomyona carolinensis were found.

6. One part of the flood-plain not in cultivation and yet a secondary community is the Bois D'arc hedge on the east side of Providence Road north of the bridge. There are a few elms and wild cherries in the hedge, and poison ivy has covered the stumps of other old elms. On the path under the hedge large numbers of Succinea grovenori

were found copulating in July. Agriolimax campestris was also very common here, it being very difficult to walk in the path dewy mornings without stepping on them. In the leaves Bifidaria armifera was extremely abundant. Gastrodonta ligera and Polygyra thyroides were found occasionally and P. clausa once. Under the bark and in the soft wood of the old stumps most of the above shells were found, especially Succinea grovenori and Bifidaria armifera. Zonitoides arborea was common, Euconulus fulvus and Pupoides marginata occasional, and Bifidaria contracta rare. This hedge was the richest both in individuals and in species of any place studied on the flood-plain.

c) Of the Secondary Valleys

7. A secondary valley, which has been eroded almost to base-level centers the main valley north of Providence Road Bridge. A more or less intermittent stream flows along the east side of this valley, being fed at the edge of the flood-plain by Rollin's Spring. Practically the entire valley has been cleared and pastured, but certain large trees have been left, giving it a park-like appearance. There is very little zonation along the stream tho where it runs close to the hillside it is more or less shaded and a carpet of moss develops on the rocky bank. At one such place the only specimens of Succinea concordialis in the collection were found. The elms and a few sycamores grow on the edge of the stream, and are often undercut by the spring freshets. On the roots of

such a tree were found two individuals of Succinea ovalis also the only ones collected. In the drift which accumulates along the bank during the freshets, many shells of Strobilops labyrinthica, Bifidaria armifera and Polygyra hirsuta were found. This probably does not represent a normal habitat, since the snails may have been washed down from the hillside.

8. The bases of the large elms, walnuts and sycamores left in the clearings of this valley were rich in snails, both in numbers and species. The leaves accumulate at the bases of the trunks and form a heavy humus, and often a thicket of gooseberry protects it from the stock pastured here. In such localities, either in the leaves or on the trunks, the following snails were fairly abundant: Succinea avara, Polygyra fraterna, Pyramidula alternata (young), Agriolimax campestris, Pupoides marginata, Bifidaria armifera, Zonitoides arborea, Vitrea indentata. In lesser numbers were found, Vitrea significans, Bifidaria contracta and Strobilops labyrinthica.

9. The sides of this valley have been largely cleared at some time in the past, only clumps of the larger shade trees being left, as hackberry, walnut, butternut, and the oaks. There has developed, however, a dense thicket of the younger trees, indicating that the sylvan element is again gaining control, and will eventually dominate. In such thickets, especially the moist, rocky ones, Polygyra thyroides, Pyramidula solitaria and P. alternata, and Vitrea indentata are common. Bifidaria armifera, Polygyra albolabris alleni, and

Zonitoides arborea are occasional. Philomycus carolinensis is found in rotting logs.

d) Of the mesophytic forests.

10. At other places the flood-plain of the Hinkson extends to the base of the bluffs. On the left bank of the Hinkson, south of Providence Bridge, such a condition exists. Here, according to Daniels, is the nearest approach to the primeval conditions to be found in this region. The bluffs, tho fairly steep, are quite moist, and are well covered by white oaks, hard maples, and some walnuts, elms, etc. On the floor the nettles are often so thick as to make collecting an unpleasant task. On these slopes among the mulch or under the moist ledges are found: Polygyra thyroides, P.albolabris alleni, P.appressa, P.profundus, Pyramidula solitaria and alternata, in large numbers; Polygyra hirsuta, Gastrodonta ligera, Circinaria concava, Bifidaria armifera, and Agriolimax campestris fairly abundantly; Polygyra elevata, P.fraterna, Pupoides marginata, Strobilops labyrinthica, Vitrea indentata, and Philomycus carolinensis occasionally; Bifidaria contracta and Gastrodonta demissa rarely.

Most of the above also inhabit dead logs and starting bark. With them were a fairly large number of individuals of the following species: Strobilops labyrinthica, Bifidaria contracta and armifera. A few dead shells of Helicodiscus lineatus were found.

e) Of the forest margin

11. The forest margin has not been thoroly studied at any place in this region. To the east of Providence Bridge, south

of the river and at the top of the bluff, the forest passes rather abruptly into grassland, evidently cultivated at some time in the past. Here among the leaves at the forest margin were frequently found Polygyra profunda, P.thyroides, P.albolabris alleni, and P.hirsuta. Circinaria concava was occasionally taken. Near the remains of an old campfire Bifidaria armifera and Agriolimax campestris were quite numerous.

f) Of moist rocks

12. Just below the place just mentioned there is a fairly steep bluff, not very high, facing the north. This bluff is quite moist the summer thru. A few young white oaks stand at the top. On the slopes are maples, black oaks, wild plums, wild cherry, dog-wood, grapevines, and poison ivy, while the rocks are more or less covered with liverworts and mosses. In July there were more individuals on the under side of the rocks than anywhere in the region studied. The following species were very abundant: Polygyra thyroides, P.albolabris alleni, P.appressa, P.hirsuta, Pyramidula alternata. This habitat probably corresponds physiologically with the climax forest (10).

g) Of dry forests

13. The mesophytic forest evidently once covered most of the bluffs in the region.. In places like the vicinity of Heart Rock, west of Rollin's Spring, the upland has been entirely cleared, except for certain trees of economic value, as the oaks and hickories. The grasses cover the parks completely, and the whole region is in pasture. No snails were found on

this upland. The slopes here are still covered by the large trees, oaks, hackberry, walnut, and maples, with pawpaw and redbud at the foot, but the whole region has been so severely pastured that the vegetation of the forest floor has been almost completely destroyed. The pasturing has disturbed the humus which is collecting, and the end result is not only that the slope is more exposed to drying, but that the running off of the surface water is not retarded, so that less sinks into the soil. The bluffs are rapidly becoming drier, and the smaller molluscan population is almost entirely depleted.

Pyramidula solitaria and alternata are still very common, the latter being found most frequently on the face of the rocks. Polygyra elevata was collected in large numbers early in the spring, but since then none have been found. P. appressa is also common on the rocks, and has been collected in other places similar to this in even larger numbers. P. thyroides has been found but once, and then not strictly within the area, being under a rotting log at the top of the bluff. P. albolabris alleni occurs occasionally on the rocks. Circinaria concava and Gastrodonta ligera have been collected but once. Vitrea indentata and Zonitoides arborea are found occasionally in the pawpaw-redbud thicket at the bottom, and Vitrea significans once.

h) Of dry slopes and hilltops

14. At other places the bluff is too steep for the flora to gain much of a foothold. The bare rock extends almost from the top to the bottom. The typical forest obtains at the bottom, but the slopes are practically bare. The cryptogams, viz., the lichens, form the only important part of the flora.

Occasionally a few rock ferns, waterleaf, bedstraw, Virginia creeper and ivy are found. No shells except an occasional Pyramidula alternata have been taken from such places. This species seems more tolerant to dryness than any of our snails.

15. On College Road opposite the Chicken Farm is a dry hilltop which has been partly cleared. An old quarry lies below, and there are a number of cut stones in the clearing. On the edge of the clearing is a bramble thicket composed largely of blackberry and gooseberry, with some sumach and buckbrush. Under the stones lying here a large number of molluscs were found. Young Pyramidula alternata were abundant, as were Agriolimax campestris, Bifidaria armifera, Vallonia pulchella, Pupoides marginata, Strobilops labyrinthica. Euconulus fulvus and Vitrea indentata were found fairly frequently, Pupoides marginata, Bifidaria contracta, B. procera, and the young of Succinea avara were found only rarely.

1) Secondary communities

16. On Ashland Gravel, opposite the University Farm, is an old stone fence. It is shaded in places by huge elms. Under the stones and leaves along the fence Vallonia pulchella was found quite frequently, Pupoides marginata, Bifidaria contracta and B. procera occasionally.

17. On a walk opposite the residence of the Dean of the Agricultural College, on College Avenue, on October sixth, 1915, over sixteen hundred shells of Vallonia pulchella

were collected. Among them were a relatively small number of specimens of Bifidaria procera and Pupoides marginata.

18. On the walks of the Agricultural Campus, thruout the summer and autumn of 1915, the slug Agriolimax campestris was found, and occasionally a specimen of Limax maximus was taken from such places.. The latter is also often found in the greenhouses here. The past summer was unusually moist and cool, and the slugs multiplied accordingly. They would get on the granitoid walks at night and remain there in the morning. Unless the walks happened to be moist, they were stimulated to secrete mucus, and if they happened to be headed across the walk, as frequently happened, they often succumbed to the exhaustion caused by the excessive stimulation.

TABLE ONE Showing the distribution of the snails by habitats

	Flats	Flood- plain	Second. Valley	Mesoph. Forest	Forest Margin	Dry Forest
<i>Polygyra profunda</i>	*	FC	Oc	C	FC	*
<i>P.albolabris alleni</i>	*	FC	Oc	C	FC	FC
<i>P.elevata</i>	*	*	*	Oc	*	FC
<i>P.appressa</i>	*	FC	*	C	*	C
<i>P.thyroides</i>	*	C	C	Oc	FC	VC
<i>P.claus</i>	*	R	*	*	*	*
<i>P.hirsuta</i>	*	Oc	*	FC	FC	*
<i>P.fraterna</i>	Oc	*	FC	Oc	*	FC
<i>P.monodon</i>	R	*	*	*	*	*
<i>Circinaria concava</i>	*	*	*	FC	Oc	R
<i>Vitrea indentata</i>	C	Oc	FC	FC	*	FC
<i>V.significans</i>	*	*	Oc	FC	*	R
<i>Eoconulus fulvus</i>	*	Oc	*	*	*	FC
<i>Zonitoides arborea</i>	C	C	FC	Oc	*	R
<i>Gastrodonta demissa</i>	*	R	*	R	*	*
<i>G.ligera</i>	FC	C	*	FC	*	R
<i>Agriolimax campestris</i>	C	C	Oc	Oc	C	C
<i>Philomycus carolinensis</i>	FC	FC	FC	Oc	*	*
<i>Pyramidula alternata</i>	*	C	C	C	*	VC
<i>P.solitaria</i>	*	*	C	C	*	VC
<i>Helicodiscus lineatus</i>	*	*	*	?	*	*
<i>Succinea concordialis</i>	*	*	FC	*	*	*
<i>S.ovalis</i>	*	*	R	*	*	*
<i>S.avana</i>	*	*	FC	*	Oc	*
<i>S.grovenori</i>	FC	C	*	*	*	*

Table One continued

	Flats	Flood- plain	Second. Valley	Mesoph. Forest	Forest Margin	Dry Forest
<i>Strobilops</i>	*	*	Oc	C	*	FC
<i>labyrinthica</i>						
<i>Pupoides</i>	*	FC	C	Oc	*	FC
<i>marginata</i>						
<i>Bifidaria</i>	*	VC	C	FC	C	C
<i>armifera</i>						
<i>B.contracta</i>	*	C	Oc	R	*	Oc
<i>B.procera</i>	*	*	*	*	*	R
<i>Vallonia</i>	*	*	*	*	*	C
<i>pulchella</i>						

Signs and abbreviations:- C-- common, FC--fairly common,
 O-- occasional, R-- rare, VC-- very common, %-- dead shells
 only, *-- no snails collected in this region.

V. Discussion and Conclusions

The most striking thing to be noticed in the above table is that always the molluscan fauna is large both in numbers and species where the moisture content of the atmosphere is considerable. It was not practical in the limited time available to make measurements of the evaporating power of the air, but the observational evidence lends support to this view. In the first place, it was on the moist and shaded ledges where moisture-loving plants, as the liverworts and mosses, were abundant, that the greatest number of specimens were found (12). The region having the next greatest number is the moist climax forest (10), while the dry bluffs were practically lacking in a molluscan fauna. The relative evaporating power of the atmosphere in different habitats has been studied by several investigators, principally botanists, viz., Transeau 1906, Sherff 1912, Shimek 1911 (see Shelford 1913, page 165 et seq.). Transeau found that the evaporation in a typical mesophytic forest was about twenty per cent less than in an open forest, while in a ravine forest it was about forty-five per cent less than in the same open forest. In all of them it was very much less than in the open prairie.

It is also true that the relative rate of evaporation varies more or less directly as the height from the ground (see Shelford l.c., p.165). In the same way the snails are seldom found at all out of the subterranean stratum of the leaves and humus, except when the air above is more or less saturated with moisture temporarily as by a shower. It is almost always necessary to stir up the leaves and humus to

find the inhabitants, except under the conditions mentioned above. In the spring, or after the fall rains begin, when the relative humidity is high most of the time, they may be found almost any time crawling on the rocks or leaves and bases of the trees; but in the summer they are active only when there is an abundance of moisture in the air.

Another way of putting the first point is to say that the snails are found in similar numbers in a series of habitats which resemble each other in only one point, i.e., a low evaporating power of air. The forest floor, the moss-covered crevices in the bluffs, and the decaying logs scattered all thru the area bear more or less the same fauna. For example, the young of Pyramidula alternata can be found readily in any of these situations. Polygyra appressa, P. thyroides, and P. albolabris alleni have a similar distribution. The smaller shells are distributed after the same fashion (Table II), except that they are seldom found on the rocks, probably because of the lack of food.

Still another confirmation of the view that the moisture content of the air is the determining factor, is the fact that the clearing and pasturing of the forest, (making an open forest) causes the ground to become drier, for reasons mentioned above--the disappearance of the herbaceous vegetation and the disturbance of the mold causes the surface water to be less retarded in the run-off, and this means that less sinks into the ground. In such places, while there may be a large number of dead shells, the live snails are almost entirely absent, those that are still to be found being those which are most tolerant to dryness.

In conclusion, we may say that the snail's habitat is determined by the moisture content of the atmosphere, and that in this region most of the snails may be found where the physical conditions are such as to afford a habitat having an atmosphere with a relatively high moisture content. This conclusion is borne out by the following facts:-1. The snails are found most abundantly in places possessing a relatively high amount of moisture; 2. They are most active in wet weather; 3. They are found in a series of habitats agreeing only in the possession of a large amount of moisture; 4. Clearing of the forests results in drying, and the death of the snail population.

Finally the experimental results demonstrate that moisture is the important factor.

TABLE TWO showing the distribution of forms found in
decaying wood and started bark thruout the area

	Flats	Flood- plain	Cleared ravines	Climax forest	Dry forest
Strobilops			*	*	*
labyrinthica					
Succinea avara			*		*
Pyramidula		*	*	*	*
alternata					
Bifidaria					*
procera					
B.armifera		*	*	*	*
B.contracta		*	*	*	*
Pupoides		*	*	*	*
marginata					
Zonitoides	*	*	*	*	
arborea					
Vitrea	*		*	*	*
indentata					
V.significans			*	*	
Gastrodonta		*		*	
demissa					
Polygyra	*		*	*	
freterna					
P.thyreoides				*	*
P.hirsuta			*		
P.appressa		*		*	
P.albolabris					*
alleni					
Agriolimax				*	**
campestris					
Euconulus		*	*		*
fulvus					
Vallonia					**
pulchella					

*-- the snail occurs here.

PART TWO

I. Introduction

With a view to determining the validity of the conclusion that the evaporation rate of the atmosphere is the determining factor in the distribution of the snail, a series of experiments was planned and partially carried out. A complete account of the behavior of the snail has not been obtained, and only those results are given which seem to have some bearing on the question of distribution.

II. Difficulties recognised by earlier workers

There are certain serious difficulties encountered in the study of the snail which have been recognized by several investigators. Frandsen (1901), working on the response of the slug to directive stimuli, found that the reactions of an individual varied both in intensity and character with variations in the intensity of the stimulus, and probably (he says) also in response to indeterminable physiological states. Cole (1906), studying image formation in various types of eyes, used *Helix pomatia* Linné. He says, "It soon became evident that these snails were by no means uniformly positive to light, so it was necessary to test them each time ---- to be sure of the state of the animal. It was furthermore found that they appeared to become fatigued very quickly, and apparently this was often accompanied by a change in the character of the --- response. ---Finally the method was adopted of making trials each day. ---The responses were so irregular and apparently so dependent on the physiological

state of the animal that no definite conclusions could be drawn." Shelford (1913) working on the reactions of certain animals to gradients of evaporating power of air, exposed several species of molluscs to such gradients. He says (page 92) "Snails and slugs are not good for gradient experiments of short duration, because of their sluggishness." Inactive animals became active after being in moist air from ten minutes to fourteen hours. "The experiments were carried far enough to show that activity may be induced in faint light, by air saturated with moisture, but it is clear that other factors are concerned, because occasionally it is not induced, and when it is, frequently does not continue." He was evidently facing the question of the physiological state again.

III. Behavior of the snails in a dry atmosphere

One of the most striking things to be noticed in the behavior of the snail is its constant response to dryness or lack of moisture by withdrawing into its shell and remaining there. Shelford (loc. cit.) devised some very elaborate apparatus in his work. It was not possible to erect any such complicated apparatus in this laboratory, but a simple apparatus was devised, in which a short series of experiments was performed. It consisted essentially of two air chambers of equal size thru which currents of air were drawn at as nearly as possible the same rate. One current before entering its chamber was made to bubble thru concentrated sulfuric acid and then over fused potassium hydroxide, which removed all the moisture. The other bubbled thru water. In running an experiment two snails from the same habitat,

collected at the same time, and in as nearly the same physiological condition as possible were placed in the two tubes respectively. Then the air currents were turned on and the activities of the two snails noted. Some half-dozen experiments were run, each of from twenty-four hours to four days duration. The snail in the tube thru which the moist air was being drawn invariably remained active longer than the snail in the dry air. The latter would have a period of intermittent activity lasting from three to seven hours, while the snail in the moist air would remain active twenty-four hours or longer. While no quantitative results were obtained, it seems clear that moist air stimulates the snail to activity. As noted more than once above, this is exactly what we find in the snail's normal behavior. It is found in places where the evaporation rate is relatively low, and is active only on days when the humidity of the air is high. This same fact is often noted in the laboratory. The snails have been kept in boxes filled with earth and covered with gauze. Whenever they are to be used for experiments it is necessary to saturate the gauze with water, some thirty minutes to an hour before they are wanted. Only when this is done will they be active enough to be used in experimental work.

IV. Behavior in response to light stimuli

In order to be able to draw any definite conclusions from laboratory experiments, working with animals which show these variations in physiological states, we must of necessity consider the responses which the animal shows in its natural

environment. Very little attention has been given to this side of such work. Miss Dawson (1909) working on the 'Biology of Physa' has given this point more emphasis than any other worker. Judging from the conditions in which we find the snails in the field, active on moist days or in moist places, inactive and seeking seclusion on dry days, we should expect to find the following peculiarities in response:-

- (1) a negative response to strong light at all times;
- (2) a positive response to weak light in a moisture saturated atmosphere;
- (3) a negative response to gravity in a weak light and in a moisture saturated atmosphere;
- (4) a positive response to gravity in a strong light and in a dry atmosphere.

The difficulty in experimental work along these lines lies not only in the variations in physiological states mentioned by other workers, but also in the fact that the snail can reach a place of weak light, low evaporation rate, and no stimulus from gravity, simply by forming an epiphragm, which not only closes the opening of its shell, but also, if it happens to be on a relatively smooth substratum, effectually fastens it to this substratum and does away with the use of muscular response to the pull of gravity. Furthermore the snail retracts more or less readily into its shell at the appearance of anything new in its environment. The shier snails, as Pyramidula solitaria and Circinaria concava, retire very quickly when handled, and will not come out of the shell for long periods of time. Polygyra thyroides will, on the other hand, stand a good deal of handling. For this reason it

has been used almost entirely in the experimental work. Nevertheless, the same difficulty holds in a large measure with it, and it has been impossible, even with this snail, to obtain a series of results, such as the responses to light of varying intensity, since it became inactive before enough trials could be made to remove the very large experimental error. This difficulty can in general be partially avoided by considering such a response to be negative to light, positive to gravity, and as a sign that the moisture content of the air is not satisfactory. When these conditions were all kept the same, however, as was usually the case, the change in sign of response must be due to some change in physiological state.

The variations of behavior caused by such variations in internal conditions have long been recognized. (See Jennings 1906 and Allee 1912 for summary of the literature.) Recently Tashiro (1913) has devised a method of determining the physiological state as evidenced by the rate of carbon dioxide production. Childs (1913) measures the general metabolic conditions by the survival time in protoplasmic poisons. Allee (1912-13-14) using both these methods has studied the relation existing between metabolic states and behavior: viz., rheotaxis. He finds that the per-cent of positive rheotactic responses is in direct proportion to the rate of metabolism. Such exact analysis was out of the question in this work, so that thus far the exact causes of the apparent inconsistencies of behavior remain undiscovered.

Experiments on phototaxis in an atmosphere holding from fifty to fifty-six per cent of its possible moisture, and us-

ing a light varying in intensity from .0019 C.M. to 280 C.M. seem to show a preponderance of negative responses. Only selected experiments are given. The method of procedure was as follows:- the snails were put on a clean glass plate, and then into the dark box at a measured distance from the opening for the light at one end of the box. The long axis of the snail was placed at right angles to the rays of light. The right and left sides were exposed alternately. A sheet of paper with a circle graduated in degrees was placed under the plate. The light was turned on for a stated time, generally two minutes, and the deviation from the original position noted in degrees. The sums of all the trials at any one time were averaged, and then converted into percentages, considering 90 degrees as 100 per cent. The percentage of indefinite responses was obtained by comparing the number of indefinite responses with the total number of trials.

Table III.

Conditions. Temperature 72 degrees Farenheit, humidity 51 per cent., intensity of light .0025 C.M.

Polygyra thyroides	#1	Positive 57 per cent.
"	" #2	Negative 61 " "
"	" #3	Positive 65 " "
"	" #4	Positive 17 " "
		and Negative 65 per cent.

Thus out of four snails, as nearly alike in condition as possible, so far as could be determined, the responses of two are very definitely positive, of another just as definitely

negative, and the fourth not definitely either.

Table IV, showing the responses to a series of varying intensities.

Conditions, Temperature 72 degrees Farenheit, Humidity 54 per cent, Intensity of light varying.

Intensity	Positive	Negative	Indefinite
.0018 C.M.	34%	22.5%	25%
.0156 C.M.	0%	0.0%	100%
.0625 C.M.	0%	16.0%	67%
3.500 C.M.	0%	41.0%	25%

It will be noted that the snail was positive only to the light of weakest intensity.

Table V, showing all the responses of one snail thruout the study.

Intensity	Positive	Negative	Indefinite
280 C.M.	28%	10%	62%
85 C.M.	48%	0	0
70 C.M.	not studied with this snail		
16 C.M.	68%	0	0
8 C.M.	not studied with this snail		
3.5 C.M. (a)	61%	4%	0
3.5 C.M. (b)	0	85%	0
.5 C.M.	not studied with this snail		
.0625 C.M.	0	51%	40%
.0031 C.M.	57%	0	0
.0018 C.M.	2.5%	16%	50%

The only conclusion to be drawn from such a table is that such a table averaging the results obtained from experiments performed under several different physiological states does not tell us anything. We can merely say that the snails are positively phototactic, negatively phototactic, or indifferent to light stimuli, depending on their condition at the time of experimentation.

V. Behavior in response to gravitational stimuli

Not enough experiments on geotaxis have been made to warrant definite conclusions. In the jars in the laboratory the snails nearly always collected near the top, but the experiments in the dark gave a positive response.

Table VI.

Conditions, Temperature 73 degrees Farenheit, Humidity 56%,
Plate at angle of 45 degrees.

Positive 51% Negative 0 Indefinite 33%

Plate at angle of 90 degrees

Positive 70% Negative 0 Indefinite 0

One series combining the effects of light and gravity was performed. The snail was proved positive to light, and positive to gravity. When put on an inclined plate so that it could not respond positively to both light and gravity, gravity seemed to control the response.

Table VII, showing the effects of light and gravity combined.
Conditions, Temperature 65 degrees Farenheit, Humidity 55%.

a. To light of 3.5 C.M.

Positive 68% Negative 5% Indefinite 0

b. To gravity, plate at 45 degree angle

Positive 90% Negative 0 Indefinite 0

c. To light of 3.5 C.M. and gravity

1. At 45 degree angle

Positive (to light) 0 Negative 100% Indefinite 0

2. At 23 degree angle

Positive (to light) 0 Negative 94% Indefinite 0

Obviously here gravity controls the response.

The experiments were stopped about the middle of November, because, tho it was still possible by saturating the atmosphere in the boxes to get a few snails to come out of their shells, they gave no satisfactory responses, and soon withdrew into their shells again. Most of them are now (Febru-

ary) buried below the surface, and there is little indication of the rather large population in each box. There is evidently a seasonal rythm which the artificial conditions of the laboratory could not displace. It is a well known fact that these rythms are quite marked in some animals and are not dependent on the weather conditions, e.g., the exact calendar migrations of some of the warblers.

VI. Summary and conclusions

In conclusion we may say (1) that the snail is unfavorable for experimental study, because of the variations in physiological state, and the consequent variations in response to constant stimuli; (2) that the snail is relatively inactive in a dry atmosphere, and is stimulated to activity by the presence of a relatively large amount of moisture in the atmosphere; (3) that in an atmosphere from 50% to 56% saturated the snail is generally positive to artificial lights of from .0006 C.M. to .06 C.M., and may be positive to lights of stronger intensities, tho generally negative; (4) that the snail is positively geotactic in the absence of other stimuli; (5) that in the presence of both light and gravitational stimuli the latter seems to control the response; (6) that there is a period of inactivity thru the winter which cannot be displaced by the artificial conditions of the laboratory.

If these conclusions be compared with the ones predicted on page 25, it will be seen that they do not completely fulfill them. Only one experiment with strong light, about 280 C.M., was tried. The snails seemed unable to orient them-

selves, apparently being dazzled. The second prediction, that they would prove positive to lights of low intensities, was realized. The converse of the third, that they would be negative to the stimulus of gravity under the experimental conditions, was determined. It was not possible to test the fourth because of the inactivity of the snails in dry air. It seems then that we are compelled to conclude that the moisture content of the atmosphere is the important factor in determining the habitats and distribution of the land snails.

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LIST OF SPECIES

1. Polygyra profunda Say. Sampson, in his preliminary list of the mollusca of Missouri, records this form only from the Post-Pliocene. It has been taken in the course of this study in rather large numbers at several places:- among the nettles in the flood-plain forest (4), again among the nettles in the climax forest (10), and in the fallen leaves of the young maples along the forest margin (11). It seems to require more moisture than most of the other *Polygyra*.

Shelford (1912) finds *P. profunda* in the flood-plain forest and in the climax forest of the savanna region.

2. Polygyra albolabris elleni Weth. This species is one of the most common and widely distributed in the area. It was found only once in the flood-plain.(5). Occasionally it occurs on the slopes of the secondary valley under the shaded ledges (9). In the climax forest (10) it was quite common, as it was in the forest margin (11). The drier bluffs do not seem so well suited, as it was found only once or twice in such situations.

3. Polygyra elevata Say. *Polygyra elevata* was found in large numbers on the drier bluffs (13) in April, and once or twice in the climax forest (10). The dead shells are to be found almost anywhere on the bluffs, but it is not certain that they have been occupied at any recent date. It is not possible to make any assertions as to the habitat preferences with this small number of data, and no statement can be found in the literature at hand.

4. Polygyra appressa Say. This snail is interesting in that it occurs very frequently as an albino. Collections from parts of this area show nearly fifty per cent with non-pigmented shell. The species is occasionally found on the floor of the flood-plain forest (4) but occurs in greatest abundance on the bluffs, being found in large numbers in the climax forest (10), on the under side of moist ledges (11), as well as on the drier bluffs (13, and several other similar localities not included in these records).

5. Polygyra thyroides Say. This is the most abundant species of the region, being fairly plentiful over almost the entire district. It seems adapted to a greater variety of conditions than any other. It was common in the flood-plain forests (4, 5, and 6), in the thickets of the secondary valleys (9), in the climax forest (10), among the leaves at the forest margin (11), under the moist rocks (12), and occasionally on the drier bluffs (13).

6. Polygyra clausa Say. *P. clausa*, judging from the collections made in the course of this work, is the rarest of the snails of the region, with the exception of *Gastrodonta demissa*. There are five shells in the collection, two of them young ones. All of these shells came from the flood-plain (5 and 6). Baker (1912) says that this snail is found in moist woods, under logs and debris of all kinds.

7. Polygyra hirsuta Say. This species was first found in a clump of drift, very dry at the time, on the bank of the small stream in the secondary valley studied. Later it was found to be

fairly abundant in the climax forest (10). On one trip to the moist bluff described in (12) some fifteen shells were taken in a very small area. It has since been found in the forest margin, but never in the drier forests.

8. Polygyra fraterna Say. This snail was found occasionally in almost all parts of the region studied, tho never in any numbers anywhere. One shell was found on the sand flat, under a rotting log (1). An occasional specimen was found in the secondary valley (8), and in the moist forest it was fairly abundant (11).

9. Polygyra monodon Rackett. This small shell was taken only once in the district studied, being found in company with a few P. fraterna and a number of Philomycus carolinensis under a rotting log on the sand flat (1).

10. Circinaria concava Say. This snail is of a very retiring disposition and is not common anywhere, but has been found several times in the moister parts of the district. It is carnivorous, living on the other molluscs, none of which are exempt from its attacks. It has been found most often in the moist forest (10), occasionally in th forest margin (11), and once deep in a pocket of leaf mold on the dry bluff (13).

11. Vitrea indentata Say. Next to Zonitoides arborea, with which it is often found, this is the most common of the Zonitidae in this region. Rotting logs seem to furnish the essential factors for its habitat, and it is found wherever such conditions obtain. It has been found in these logs on the sand-flats (1), in the clearings of the secondary valleys (8),

in the moist forests (10). It has also been found on the floor of this same forest, around the bases of the trees and in the thickets (8 and 9), at the edge of the dry forest (13), and under the stones on a dry hilltop (15).

12. Vitrea significans Bld. This snail is given by Pilsbry and Ferriss (1906) as a member of the Ozarkian fauna, Sampson does not mention it in his 'Preliminary List of the Molluses of Missouri' (1913). Its occurrence in this region, north of the Missouri River, is an interesting extension of its range. Its habitat is quite similar to that of V. indentata. It was found at the base of trees in the clearings of the secondary valleys (8), under started bark in the moist forest (10), and once in the pawpaw-redbud thicket at the bottom of the dry bluff (13).

13. Euconulus fulvus Drap. This tiny shell in all probability occurs more often than the records would indicate. It was found in common with other Zonitidae under started bark and in decaying logs -- on the flood-plain (6) and under rocks on a dry hilltop (15). It is given by H.B. Baker (1908) as an inhabitant both of dry and moist woods, and by Bryant Walker (1909) as an inhabitant of dry hills.

14. Zonitoides arborea Say. This is the most common of the Zonitidae in this region. It also occurs most frequently under started bark and in decaying logs. It was found on the sand-flats (1), in the flood-plain forest (5), in the clearings on the flood-plain (6), in the secondary valleys both at the base of the trees (8) and in the moist thickets (9), on the forest floor (10), and occasionally in the dry thickets (13).

15. Gastrodonta demissa Binn. According to Mr. Bryant Walker, there is one shell of this species in the Crandall Collection from Pettis County, now in his possession. It is not mentioned as an inhabitant of the state by Sampson (loc.cit.) Snails of this species have been taken at two different times in the course of this study, one adult and two young snails having been found on the forest floor in the climax forest (10), and one adult from the cleared forest south-west of the area included in these notes. According to F.C. Baker (1903) it is found near bodies of water, under moist logs or in the depths of brush-heaps.

16. Gastrodonta ligera Say. The shells of this species collected here seldom conform to the type, being smaller and heavier. It occurs commonly on the flood-plain (1,3 and 6), not at all in the secondary valleys, fairly frequently at the foot of the bluffs that are covered by the moist forests (10), rarely in the pawpaw-redbud thicket where the flood-plain and the dry bluff meet. (13). One shell, found in a bed of wild ginger on the moist bluff (12) conformed to the type described from the east and north.

17. Agriolimax campestris Say. This slug was found universally distributed thruout the area. Wherever molluscs could live, this one was common. For this reason it is often omitted from the records of collections.

18. Limax maximus Linné. This slug is not native, and is largely confined to the region of gardens and greenhouses.

19. Philomycus carolinensis Bosc. This slug was found in the moister parts of the area, always in rotting wood, e.g., in the flood-plain forest (5), in the moist thickets along the sides of the secondary valleys (9), and in the moist forest (10).

20. Pyramidula alternata Say. The Pyramidulas were not found on the flood-plain at all. In the secondary valleys the young were found both on the bases of the trees (8), and on the more moist rocks along the sides of the valley, moving about actively on days when no other snails were in evidence. In the thickets the adults were frequently found (9). They were abundant as well in the moist forest (10), on the moist rocks (12), and very abundant in the dry forests (13). On bluffs where no other snail was to be found, still this one could be found not infrequently (14). There were a few on the dry hill-top under the stones (15).

21. Pyramidula solitaria Say. This Pyramidula was not so widely distributed, being found only in the moister localities, seemingly preferring rocky situations, i.e., the moist thickets along the secondary valleys (9), in the climax forest (10), and in the cleared forest (13). There are two varieties from this region, represented by the shells from (10) and (13) respectively. Those from (10) are much larger, heavier, and more elevated than those from (13).

22. Helicodiscus lineatus Say. Only the dead shells of this snail were found in the dead logs in the climax forest (10). No conclusion can be drawn from such records. Judging from the literature it is rather widely distributed thruout territory habited by the land molluscs.

23. Succinea concordialis Gld. None of the Succinea were found very abundantly in this study, this one being collected but once. Then it was found on the mossy banks of the small stream that runs thru the secondary valley (7).

24. Succinea ovalis Say. Two specimens of this species were collected on the base of the trunk of a tree overhanging the stream just mentioned, at the point where the stream leaves the valley to cut across the flood-plain (7).

25. Succinea avara Say. A large number of dead shells of this species were found under the stones on the dry hilltop at (15). Young snails identified as S. avara were found about the bases of the trees in the clearings of the secondary valley (8), as well as with the dead shells mentioned above.

26. Succinea grovenori Lea. This was the most abundant of the Succinea in this region. It was found on the trunks of trees and in drift on the sand flats (1 and 2), and along the Bois D'arc hedge on the flood-plain, where they were breeding (3). The preference seems to be for low ground near the water.

27. Strobulops labyrinthica Say. Like Euconulus fulvus, this little shell probably often escapes observation. It is said to prey on Euconulus. In this study it was found in clumps of dry drift along the small stream in the secondary valley (7), in moss on the rocks back from this stream, in the leaves and under bark in the moist forest (10), and under the rocks on the dry hilltop (15).

28. Pupoides marginata Say. All of the smaller shells have more or less the same distribution (see Table II), being found in dead wood and under started bark, and varying chiefly in numbers. P. marginata is one of the most abundant. It was found on the flood-plain (5), in the secondary valley (8), on the floor of the climax forest (10), on the dry hilltop (15), and in the stone fence (16) as well as with the colony of Vallonia mentioned later.

29. Bifidaria armifera Say. This small snail occurs in the largest numbers of any of the Pupillidae. Its location of greatest abundance was along the Bois D'arc hedge on the flood-plain (6). It was also found in drifts along the stream and about the bases of the trees in the secondary valley (7 and 8), in the thickets in the same region (9), in the moist forest (10), in the forest margin (11), and on the dry hilltops (15).

30. Bifidaria contracta Say. This tiny shell generally occurs in company with B. armifera. It was found occasionally with its larger relative along the above mentioned hedge on the flood-plain (6), about the base of trees in the secondary valley (8), under stones on the dry hilltop and along the old fence on Ashland Gravel. (16).

31. Bifidaria procera Gld. This shell was found only a few times, once on a grapevine at the edge of the flood-plain forest (4), several times under the stones on the dry hilltop and along the old fence mentioned above. (15 and 16), and with the colony of Vallonia pulchella referred to below.

32. Vallonia pulchella Müll. This little shell, which is found all over the world, was not discovered until the end of the summer, being found then on the dry hilltop, under the stone fence, and in the colony mentioned in the description of Habitat 17. Mr. Bryant Walker says that both he and Mr. Clapp have observed this habit of collecting in large numbers.

UNIVERSITY OF MISSOURI
COLUMBIA

DEPARTMENT OF PHYSIOLOGY

May 16, 1916.

Professor Walter Miller,
Dean of the Graduate School,
University of Missouri.

Dear Sir:-

I take pleasure in recommending the thesis of Mr. Erwin Ellis Nelson as partial fulfillment of the requirements for the Master's degree. The effort to correlate the distribution of the snails in their natural habitats and the physiologic responses by which this distribution was attained, is a valuable one. Mr. Nelson's results, both on the faunistic side and the physiological side, are worthy of being permanently recorded. His physiological results have been obtained in spite of difficulties which to my mind are even greater than would be supposed by most persons reading his account of them. I am particularly interested by the evidence that these molluses, with such primitive organs for sight, are responsive to such faint intensities of light.

I would like to suggest that the two parts of this paper would be better tied together, and the conclusions stated on page 18 would become more obvious, if a classification of the numbered habitats were made on the basis of their comparative humidity, and then a table of the distribution of the species made out on the basis of this new grouping of the habitats, but otherwise handled about like the table already presented on page 16.

In the experiments on light responses, the units should be "candle meters" and not "candle power".

Minor errata for the literature list, etc., I am reporting directly to Mr. Nelson.

Sincerely yours,

Addison Gulik

UNIVERSITY OF MISSOURI
COLUMBIA

ZOOLOGICAL LABORATORY

The thesis of Mr. Erwin Ellis Nelson,
entitled "The Distribution and Reactions
of the Land Snails in the Vicinity of
Columbia, Missouri" is approved and
recommended for acceptance in partial
fulfillment of the requirements for the
degree of Master of Arts.

George Rejman

May 10, 1916

UNIVERSITY OF MISSOURI
COLUMBIA

ZOOLOGICAL LABORATORY

May 29 - 1916.

Dr. Walter Miller

Dean of the Graduate School.

Dear Sir:

I am returning my thesis, - Minor errors noted by Dr. Gulick have been corrected. - The other point suggested in his letter to you is one that I cannot remedy because of insufficient data.

Sincerely yours,

Erwin E. Nelson.

University of Missouri - Columbia

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