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INTRODUCTION

The ecology of those snails which are the intermediate hosts for the economically important trematode parasites has been particularly emphasized in recent years (Abbott, 1946; McMullen, *et al.*, 1951; Richie, *et al.*, 1951). Although the role of *Lymnaea humilis* Say (Hubendick, 1951) in the transmission of the liver fluke *Fascioloides magna* Bassi to ruminants is established (Swales, 1935), there is still much to be learned of the behavior and habitat preferences of this snail. An appreciation of the natural history of this and other snails may provide information which can be applied in the prevention and control of diseases caused by this group of trematode parasites. It is partly for this reason that the present study of *L. humilis* was undertaken. Studies on the gross anatomy of *L. humilis* have already been reported (McCraw, 1957).

The Lymnaeidae are an ecologically diverse group, and members of this family of snails are found in many of the various habitats of basommatophoran pulmonates. Although lymnaeids are largely dependent upon atmospheric oxygen, at least one species is able to live submerged on the bottom of large bodies of water throughout its life (Cheatum, 1934). Others are found in streams or ponds which are temporary or semipermanent. *L. humilis* approaches some of the Ellobiidae (*Carychium*) in its habits insofar as it is able to spend much of its life out of water in a damp environment breathing atmospheric oxygen and deriving sustenance from the organisms in moist soil or mud.

The systematic position of *L. humilis* has been investigated by Hubendick (*l.c.*). As a result of critical study, he concluded that a considerable number of the small lymnaeids recognized by F. C. Baker (1911) as separate species should now be linked to *L. humilis*; *doddsi* Baker, *umbilicata* Adams, *cyclostoma* Walker, *parva* Lea, *parva sterki* Baker, *owascoensis* Baker, *pilsbryi* Hemphill, *ferruginea* Haldeman, *humilis modicella* Say, *humilis rustica* Lea, *obrussa* Say, *obrussa peninsulae* Walker, *obrussa exigua* Lea, *obrussa decampi* Streng, *galbana* Say, and *petoskeyensis* Walker. Hubendick (1951) was hesitant to link *caperata* Say with *Lymnaea humilis*. *L. caperata* is recognized as a pond or woodland pool inhabitant.

L. humilis was studied in three selected areas. Two of these were on the Raisin River, southwest of Ann Arbor, Michigan. One of these localities was located three miles southeast of Clinton, at Newburg, in Lenawee County; the other was located about one mile northwest of Clinton in Washtenaw County. The two stations are designated as the Newburg and Clinton habitats, respectively. The third area was Crane

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Pond, one of several ponds on the Edwin S. George Reserve, about 30 miles west of Ann Arbor.

At Newburg, where there was an exceedingly large colony on an extensive mud flat, quantitative samples were gathered. These quantitative samples were taken 25 cm. apart along a line at right angle to the edge of the water and extending as far as 20 feet out on the bottom of stream and on land until *L. humilis* were no longer found. The snails were harvested using a circular metal container whose opening covered an area of 50 sq. cm. A section of mud or sand was removed by pushing the container about one inch into the soil and slicing this with a flat trowel. The samples were then placed upright in glass jars of the same diameter and these were filled with water to within about two inches of the top and covered. All the snails in each of these samples were measured. Usually within 12 hours most or all of the snails had climbed out of the water onto the walls of the jars. These samples were checked at least three times and when no more could be found the water was drained off carefully and the mud examined. Each successive quantitative series was made parallel to the other in a direction away from the previous one to ensure that the area to be sampled was not one which had been disturbed during previous collecting. Neither the Clinton area nor Crane Pond were sampled quantitatively, but sufficient snails were collected for habitat information.

Maximum shell length of snails was measured using a dissecting microscope with a calibrated ocular micrometer. Measurements were made with the aperture of the snail facing uppermost and the axis of the snail parallel to the stage of the microscope.

Snails were reared in small containers, ten cm. in diameter and four cm. deep, as well as in large (22-inch) enamel trays. Mud from a natural habitat of *L. humilis* was used. This mud was treated with hot water for at least four hours. No more than four adult *L. humilis* were placed in the small containers. A depression in which water could accumulate was made in a corner of both the small containers and the enamel trays. The remaining area of mud was kept moist by adding a few drops of water to it each day, thus simulating the natural habitat of *L. humilis* as closely as possible. Tap water which had been allowed to stand for at least 24 hours was always used. Snails were fed rat food (Purina), ground thoroughly in mortar and pestle, and sprinkled evenly over the mud surface. All aquaria were kept partially covered with glass to prevent moisture loss.

HABITATS

Areas for the present study were chosen because they represent three distinct habitats of *L. humilis*. These habitats are: a mud flat (Newburg, a river bank (Clinton) and a pond (Crane Pond).

NEWBURG HABITAT: The Newburg habitat consisted of an expansive mud flat which extended for approximately 150 feet along the edge of a small river. Located on the Raisin River at Newburg, in Lenawee County, Michigan, this flat has been built up slightly downstream from a fairly sharp bend in the stream bed. Opposite the elongate silty deposit which composed the flat habitat, the bank of the river was almost perpendicular and varied from two to four feet in height. There, the bank was being continuously eroded away by current action. The maximum width of the river in the vicinity (some 300 hundred yards up- and downstream from the mud flat) was 70 feet and in the immediate region varied from 30 to 40 feet throughout the year, depending on the level of the water.

Within ten feet of the eroded, opposite shore the current flowed at a moderate rate. There the water was deepest, varying from 100 to 170 cm. in depth throughout the year. From this deep portion to within about ten or 12 feet of the edge of the flat the river bed rose sharply so that the depth was only about 25 cm. In this shallow portion the direction of the current was indefinite. From this region of indefinite current direction to the water's edge, the water flowed gently upstream, decreasing in velocity toward shore. It was in this area of gentle upstream flow that silt was deposited, resulting in a continuous shorebuilding process which maintained the mud flat.

TABLE I

Records of the Water Levels, Widths of the Mud Flat, and Water and Air Temperatures for the Raisin River at Newburg, Michigan

Date	Water Level (cm.)*	Width of Flat (cm.)	Water Temp. °C.	Air Temp. °C.
Sept. 20 (1953)	4.4	365	19.0	22.0
Oct. 18	0	385	16.0	29.0
Nov. 3	11.5	280	12.0	17.0
Nov. 18	19.0	255	10.5	20.0
Dec. 19	12.0	300	3.0	5.3
Jan. 18 (1954)	19.0	100	3.0	10.0
Feb. 18	64.5	0	3.0	5.5
Mar. 19	39.0	10	5.5	6.0
Apr. 18	70.0	0	13.0	20.0
May 15	48.0	125	11.0	12.0
June 1	14.0	314	16.5	22.0
June 17	25.0	50	25.0	27.5
July 2	8.0	300	28.0	38.0
July 17	7.0	250	21.5	26.0
Aug. 6	8.0	150	24.5	30.0
Aug. 21	9.5	187	20.5	22.5

*Water level is expressed with reference to the lowest level recorded (October 18th, 1953).

The amount of exposed silty deposit depended upon the water level and the degree to which this deposit was encroached by marginal plants. This exposed flat was broadest in summer and autumn but during midwinter and early spring it was covered by ice or seasonally high water (Table I). Throughout the summer months this area was practically free of leafy debris but by late autumn it was moderately covered with leaf litter.

The mud habitat was on the east side of the river and was heavily shaded, mainly by willow. Centrally it was generally free of marginal plants. Grasses tended to invade the flat toward late summer, however, resulting in a gradual reduction of its size. Offshore, the river bed was devoid of rooted aquatic vegetation throughout the entire summer and autumn seasons. A sparse growth of filamentous algae was the only visible vegetation but this did not increase appreciably in abundance even by the end of summer. The river bottom was smooth and almost litter-free throughout the year except near the mud flat where willow leaves collected in autumn. Where the current was swift, near the opposite shore, the bottom consisted of water-deposited sand; where the current flowed gently upstream it consisted of silt alone, and in the region of indefinite flow the bottom was transitional, partly silt and partly sand.

The mud habitat supported a luxuriant growth of algae which formed visible mats. These algal patches attained a thickness of two or three mm. and were most extensive in late summer. Twenty genera of algae were identified.

ALGAL FLORA OF THE NEWBURG HABITAT

Chlorophyceae
- *Microspora* Thuret, 1850; emend., Lagerheim, 1888
- *Pediastrum* Meyen, 1829
- *Scenedesmus* Meyen, 1829
- *Spirogyra* Link, 1820
- *Cosmarium* Corda, 1834
- *Closterium* Nitzch, 1817

Euglenophyceae
- *Phacus* Dujardin, 1841

Bacillariophyceae
- *Melosira* Agardh.
- *Meridion* Agardh., 1824
- *Diatoma* DeCandolle, 1805

Bacillariophyceae
- *Cocconeis* Ehrenberg, 1838
- *Navicula* Bory, 1822
- *Pinnularia* Ehrenberg, 1840
- *Gyrosigma* Hassall, 1845; emend., Cleve, 1894
- *Cymbella* Agardh, 1830
- *Nitzschia* Hassall, 1845

Myxophyceae
- *Merismopedia* Meyen, 1839
- *Spirulina* Turpin, 1827
- *Oscillatoria* Vaucher, 1803
- *Phormidium* Kutzing, 1843

Phormidium was the most abundant alga and was considered responsible for the extensive mat formation. Smith (1950) states that this genus is primarily subaerial in habit and often grows in patches on moist rocks or damp soil. Diatoms composed the majority of the remaining genera and of these *Navicula* and *Nitzschia* occurred in the greatest numbers.

In number of species the molluscan fauna was poor. *L. humilis* was by far the most abundant species, and on the landward edge of the flat habitat where the soil was eroded, *Pomatiopsis cincinnatiensis* (Lea) was common. In the Raisin River itself the following molluscs were found: *Lampsilis siliquoidea* (Barnes), *Strophitus rugosus* (Swainson), *Campeloma decisum* Say, and *Physa gyrina* Say.

CLINTON LOCALITY: This locality was about four miles upstream from the Newburg habitat, one mile northwest of Clinton. The river was deeper in this section, and near shore the silt was 30 or more cm. deep, making it difficult to wade. The exposed muddy portion was between two and three feet wide, narrower than that at Newburg. The mud surface was pitted with many, small, rounded, depressions ten to 15 cm. in diameter. The floors of these depressions were invariably moist and supported visible algal patches similar to those at Newburg. Sometimes as many as 60 or 70 *L. humilis* were observed feeding in the depressions.

Marginal plants (mainly *Poa*) formed a distinct border along the river bank which was kept moist by seepage. *L. humilis* was not restricted to the open mud but was frequently found in large numbers among the marginal plants. Moisture from the seepage undoubtedly contributed to this extension of range. At Newburg, where the higher portions of the river bank were not as moist, *L. humilis* normally did not invade the region of marginal plants in any appreciable numbers except in spring when they were forced to do so by high water. Higher up the river bank, which was two or three feet high, *L. humilis* commonly overlapped the range of *P. cincinnatiensis*. This mingling of the two species was a rare occurrence at Newburg. The slope of the ground from the river's edge to the marginal plants was approximately 30 degrees at Clinton as contrasted with about three degrees for the mud flat habitat. Like Newburg, the river at Clinton was without rooted aquatic vegetation.

The following species of snails have been reported by van der Schalie and Dundee (1955) for the Clinton locality: *Lymnaea humilis* Say, *Stenotrema monodon* (Rackett), *Mesodon thyroidus* (Say), *Triodopsis multilineata* (Say), *Retinella indentata* (Say), *Zonitoides nitidus* (Müller), *Oxyloma retusa* (Lea), *Carychium exiguum* (Say), and *Pomatiopsis cincinnatiensis* (Lea).

CRANE POND: Crane pond is one of several on the George Reserve, 30 miles west of Ann Arbor. It is a permanent pond, divided into two portions which are joined by a narrow neck of water about 20 feet wide. The pond is about 300 feet in length. Although the water level varied seasonally, during the period of study which extended from 1952 to 1954, the two parts of this pond were always connected at the narrow portion by water at least 15 cm. deep. The border of the pond was almost devoid of trees. *L. humilis* were always present in this habitat but never in such large numbers as at Newburg, except occasionally during periods of low water when regions near the shore were exposed. Such an aggregation occurred in September, 1952 and the occasion emphasized how this snail concentrates on moist exposed surfaces. On the other hand, the pond habitat demonstrates how *L. humilis*, outside its preferred environment, is able to reproduce and maintain itself.

In contrast to the Raisin River habitats, Crane Pond abounded in rooted aquatic plants. Of these, species of *Potamogeton* were the most common. The most prominent alga was *Nostoc*, which collected on the surface of the water in large quantities by late summer. The bottom of the pond consisted mainly of autochthonous sediments. Zonation of the flora within the pond was ill-defined.

FLORA OF THE CRANE POND HABITAT

Myxophyceae
- *Nostoc* Vaucher, 1803

Rooted Aquatic Plants
- *Potamogeton natans* L.
- *P. vaginatus* Turcz.
- *P. amplifolius* Tuckerm
- *P. foliosus* Raf.
- *P. pectinatus* L.
- *Najas flexilis* (Willd.) Rostk. and Schmidt
- *Sagittaria latifolia* f. *gracilis* (Pursh) Robinson
- *Alisma Plantago-aquatica* L.
- *Polygonum natans* Eaton
- *Ceratophyllum demersum* L.
- *Nuphar advena* Ait.
- *Ranunculus longirostris* Godron.

Marginal Plants
- *Equisetum palustre* L.
- *Typha latifolia* L.
- *Poa compressa* L.
- *Eleocharis acicularis* (L.) R & S
- *Scirpus fluviatilis* (Torr.) Gray
- *Carex vulpinoidea* Michx.
- *Asclepias incarnata* L.

Typha latifolia was concentrated in a massive stand at the eastern end of the pond.

The molluscan fauna of a permanent pond contrasts clearly with that found in rivers. Although not especially rich in the number of species, those found were all commonly observed, and includes the following: *Sphaerium* Scopoli, *Lymnaea palustris* Müller, *Lymnaea humilis* Say, *Physa gyrina* Say, *Helisoma trivolvis* (Say), *Gyraulus deflectus* (Say), and *Ferrissia* Walker.

Behavior

When the Newburg locality was first visited the numbers of *L. humilis* present were so large that it was decided that this habitat should be studied quantitatively. On several of the mud flats in the vicinity the characteristic clicking sound caused by the movement of the foot of these molluscs over the mud could be clearly heard (Goodrich, 1932). In one area, the concentration of this snail on land was close to 400 per

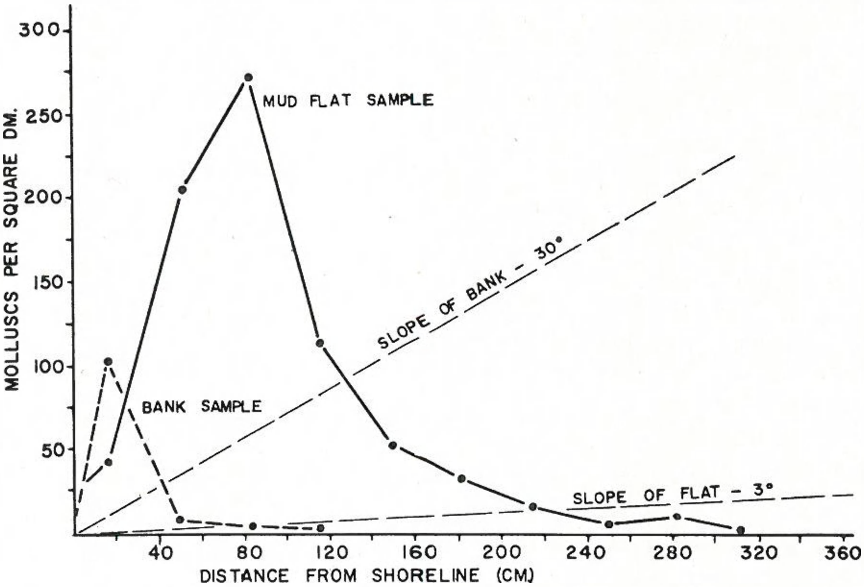

FIG. 1. The distribution of *Lymnaea humilis* on a mud flat and on a steep bank in relation to the distance from the edge of the water.

sq. dm. In water, although many snails were seen, they were not nearly as plentiful. It was evident that sufficient were present, however, to permit a statistical study both on land and in the river itself. Here, then, was an opportunity to study not only the comparative distribution of this snail but also the more precise land-water relations of this species

Opportunities to study the relative distribution of molluscs in a given locality do not occur frequently mainly because it is necessary for these animals to be present in a sufficiently high density upon a substrate for which some suitable sampling method can be devised. *Campeloma decisum* (Say), which inhabits waters with a silty or sandy bottom, occasionally occurs in large numbers and permits quantitative investigation. Bovbjerg (1952) sampled such a *C. decisum* population at 11 different transects in Dickerson Creek, in Montcalm County, Michigan. He used a metal frame, enclosing an area of one-fourth square meter and took five to nine such quadrats per transect. Using this method, Bovbjerg (*l.c.*) found the mean population density per transect to vary from six to 607 snails per quadrat. In an area studied by Prince (1952), who hand-picked all the snails on one square foot of substrate, no one sampling of

TABLE II

Summary of 24-Hour Quantitative Collections of *L. humilis* Taken on a Mud Flat of the Raisin River near Newburg, Michigan (October 17th and 18th, 1953). (The Number in Each Sample is also Expressed as a Percentage of the Total Number for Each Time Series. This Percentage is Shown in Parentheses).

Time Series	3 p.m.	7 p.m.	11 p.m.	3 a.m.	7 a.m.	11 a.m.	3 p.m.	7 p.m.
Distance From Edge of Water (cm.)								
At edge of water......	30 (5.2)	7 (1.3)	2 (0.5)	12 (2.9)	4 (0.9)	8 (1.7)	7 (1.3)	10 (0.2)
16	14 (2.4)	44 (8.5)	22 (5.6)	34 (8.3)	38 (8.4)	6 (1.3)	56 (12.2)	31 (5.5)
49	192 (33.1)	44 (8.5)	69 (17.4)	103 (25.1)	121 (26.9)	91 (19.4)	46 (10.0)	110 (19.6)
82	189 (32.6)	148 (28.6)	167 (42.2)	136 (33.2)	153 (34.0)	129 (27.6)	117 (25.4)	131 (23.4)
115	87 (15.0)	128 (24.7)	60 (15.2)	57 (13.9)	90 (20.0)	119 (25.4)	121 (26.3)	154 (27.5)
148	56 (9.7)	76 (14.7)	43 (10.9)	27 (6.6)	11 (2.4)	52 (11.1)	45 (9.8)	55 (9.8)
181	7 (1.2)	59 (11.4)	27 (6.8)	23 (5.6)	12 (2.7)	37 (7.9)	25 (5.4)	29 (5.2)
214	2 (0.3)	6 (1.2)	4 (1.0)	8 (2.0)	16 (3.6)	16 (3.4)	27 (5.9)	29 (5.2)
247	2 (0.3)	3 (0.6)	0 (0)	3 (0.7)	0 (0)	6 (1.3)	11 (2.4)	7 (1.3)
280	0 (0)	1 (0.2)	2 (0.5)	5 (1.2)	2 (0.4)	0 (0)	5 (1.1)	3 (0.5)
313	0 (0)	2 (0.4)	0 (0)	1 (0.2)	0 (0)	2 (0.4)	0 (0)	0 (0)
346	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.4)	0 (0)	1 (0.2)
Totals.....	579	518	396	410	447	468	460	560

Lymnaea humilis (*Fossaria parva*) (see Hubendick, *l.c.*) contained less than 220 snails and the largest contained 870. This accumulation represents a range of from 24 to 93 molluscs per sq. dm. In a pond studied by Strandine (1941), it was found that as the water level gradually receded, *Gyraulus parvus* (Say) concentrated in the central part and he reported a density of 122 living snails per sq. dm.

TERRESTRIAL DISTRIBUTION: Certain of the Lymnaeidae are wellknown for their ability to range from a few inches to several feet above the water's edge. The mud-flat zone was recognized as one of the habitats of the Lymnaeidae many years ago by F. C. Baker (*l.c.*). *Lymnaea caillaudi* Bourg., an intermediate snail host of liver fluke in east Africa is on occasion an amphibious organism and is often found out of water on mud or herbage (Porter, 1938; Van Someren, 1946). *Lymnaea truncatula* Müller is said to be even more terrestrial in habit. This species lives much of the time out of water on mud at the edge of streams or ditches and also in the slacks of sand dunes where it endures hot, dry conditions in summer (Boycott, 1936). *Lymnaea humilis* is very similar in its habits to *L. truncatula*, the European counterpart of the former species.

When first studying *L. humilis*, it was observed that this snail is not distributed evenly on land but exhibits a very definite zonation in relation to the shoreline. Along a mud flat whose slope with the surface of the water is approximately three degrees, the density was found to be lower within 20 or 30 cm. of the water's edge and beyond about 150 cm. from the shoreline, than in the zone between these two areas (Fig. 1). Expressed as the number of snails per sq. dm., the density was found to rise sharply to a maximum at about 80 cm. from shore and then to decrease rapidly. This was characteristically followed by a wide zone where the density was low and gradually decreased. Upon steeper surfaces the distribution of *L. humilis* was similar to that on more horizontal surfaces except that the maximum number present was lower and the range of the organism reduced. Quantitative samples taken at Newburg in a region of the river where the slope of the bank is 30 degrees showed that the highest density was only slightly over 100 per sq. dm., 16 cm. from shore along the bank surface, as contrasted with a maximum of nearly 275 per sq. dm. on the flat habitat (Fig. 1).

The occurrence of *L. humilis* in greatest numbers on land along a narrow zone a few centimeters from the shoreline is apparently related primarily to moisture and available food. In the zone nearest the water's edge, wave action and minor changes in water level probably are major factors in preventing large surface accumulations of algae which form the principal diet of *L. humilis* in the flat habitat. In fact, diatoms commonly were found both upon dissection and sectioning of the intestine of *L. humilis*. On the other hand, in the broad landward zone of low snail concentration the surface moisture as well as the snail population steadily decreases.

L. humilis is able to live on a variety of substrates which differ greatly in type and firmness as well as in the degree of incline. Van Cleave (1933) found colonies of *Fossaria modicella* (= *Lymnaea humilis*) (Hubendick, *l.c.*) in abundance upon vertical sandstone cliffs "barely moistened by the slight flow of water". The colonies were found at the head of a ravine more than one-hundred feet above the level of the nearest creek and at least one-hundred yards from it. According to Peters (1938) clay is the preferred substrate of the amphibious *L. truncatula*. In certain sections of northern Ontario *L. humilis* is found commonly in and around borders of shallow clay-bottomed pools. In these areas it is often difficult to detect the snail on clay surfaces until the sun has dried the fine clay deposit on the shell. Although *L. humilis* tolerates a wide range of substrates, it is rarely seen, if at all, on soft flocculent deposits. In a small body of water near Crane Pond on the George Reserve where *L. humilis* was present, the soft muck of this pond was apparently unfavorable as no specimens were found there. This reaction is evidently true among other amphibious lymnaeids (Walton and Wright, 1926; Van Someren, *l.c.*). Walton and Wright (*l.c.*) reported that *L. truncatula* will even leave a soft substratum for a firmer one.

In general, there is a greater percentage concentration of smaller snails near the water's edge than on the landward reaches of a mud flat (Fig. 2). This is generally true from month to month as shifts in the ranges of size-classes occur; however, when only larger snails are present,

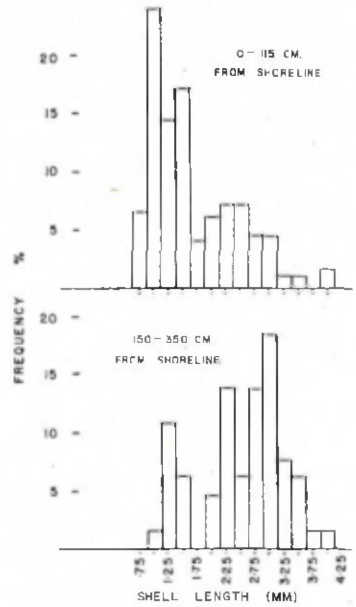

FIG. 2. The frequency per cent distribution of graded size classes of *Lymnaea humilis* on a mud flat in relation to the distance from the water's edge. (From a series taken along the Raisin River at Newburg, Michigan, September 26, 1953). The upper histogram represents the per cent distribution from a portion of mud flat ranging from 0 to 115 centimeters of the shoreline, and the lower histogram shows the per cent distribution from a 200 centimeter portion of mud flat from 150 to 350 centimeters of the shoreline.

this size distribution is not evident. When younger snails are present (1.00 to 1.50 mm. in length) they aggregate in greatest numbers along a strip about 100 cm. from the water (Fig. 2). This tendency is probably related to the egg-laying habits of *L. humilis*, which tend to oviposit near the land-water junction, both in and out of water, and possibly to the relatively limited range in the habits of juvenile snails. Van Cleave (1935) found that newly-hatched individuals show a more marked tendency toward an aquatic habit than older snails during periods of high water. Young *L. humilis* cultured in the laboratory avoided water but at the same time were more susceptible to desiccation than adults. There was no evidence in the field as to whether juvenile *L. humilis* actually selected this narrow portion of a mud flat. Undoubtedly, many juveniles wander to the drier reaches of the flat habitat and are unable to combat the increasing rate of moisture-loss, finally dying of desiccation. It seems probable that an optimum environment for developing *L. humilis* is provided by a narrow region extending from the shoreline, and that here maximum numbers of snails survive the period of development after hatching when moisture requirements are critical. This period extends over one or two weeks.

The literature contains conflicting reports on variation in the daily activity of gastropod molluscs. Binney (1885) stated that land snails generally did not range in the daytime except when the weather was damp and dull. On the other hand, Ingram (1941a) found that several common land snails were certainly active during the daylight hours. Among the ctenobranchiates, *Pomatiopsis lapidaria* (Say) is said to be more or less nocturnal (Ameel, 1938), so that on bright days the snails remain hidden under leaves and other cover but are exposed on dull days or on warm, humid evenings. Crowther (1896) maintained that *Lymnaea stagnalis* L. was more active in sunshine, both in aquaria and in the field. He believed that because the response was so immediate it must be due to light rather than to warmth. The importance of temperature and oxygen as well as of light on the diurnal activity of *L. caillaudi* is stressed by Van Someren (*l.c.*). This snail more often leaves the water when the water temperature approaches a maximum and is supersaturated with oxygen, and is most frequently found on mud in the hot noonday sun. It is certainly true that *L. humilis* is more active on a hot day than during cooler weather.

To determine whether there was any migratory behavior of *L. humilis* between night and daytime hours, quantitative samples were taken every four hours from 3:00 P.M. one day to 7:00 P.M. the following evening. This study was carried out on the mud flat habitat at Newburg, October 17th and 18th, 1953. No definite evidence of any migration was found (Fig. 3, Table II). It is significant to note, however, that the highest concentration of *L. humilis* was found in the same region of the mud flat throughout the 28-hour period. This massing occurred between the 49 and 115 cm. levels for each of the eight transects (Table II). The temperature data for this study are shown on Table III. Variation in both air and water temperature was great, showing a range of 25 degrees C. for air and six degrees C. for water. These extremes were recorded at 3:00 P.M. and 7:00 A.M. Both days on which the transects were taken were bright and sunny. The change from bright sun to darkness, and the great range in temperature, emphasize the extreme variation of the environment of *L. humilis* between day and night, but in spite of this, no significant change in the ranging habits of this snail was observed.

There is a considerable amount of information in the literature on the effect of drought on gastropods (Thomas, 1883; Cooke, 1913; H. B. Baker, 1914; Barlow, 1933; Van Cleve, 1931; Ingram, 1941; Strandine, *l.c.*; Kendall, 1949). Obviously, conditions which may be considered very dry for aquatic snails are not necessarily drought to amphibious forms. For example, Strandine (*l.c.*) encountered a dense population of *Gyaulus parvus* (Say) in a temporary pond that was completely dry from the first of August to almost the middle of November, except for short periods following heavy rains. A dry, dense algal mat covered the soil in the dried-out pond, but the soil itself was very damp and exhibited a moisture gradient from the edge to the deepest point in the pond. At the end of 66 days of drought 21 percent of the snails taken near shore were living and up to 90 percent in the deepest part, where the soil moisture was greatest. Although this environment was dry for *G. parvus*, these moisture conditions would probably fall very little short of a good environment for *L. humilis*.

TABLE III

Air Temperature, Maximum-Minimum Ground-Level Temperature, and Water Temperature for Twenty-Four-Hour Quantitative Collections of *Lymnaea humilis* Taken from a Mud Flat of the Raisin River at Newburg, Michigan (October 17th and 18th, 1953)

Time Series	3 p.m.	7 p.m.	11 p.m.	3 a.m.	7 a.m.	11 a.m.	3 p.m.	7 p.m.
Air Temperature °C..........	29.0	11.5	7.5	5.0	4.0	23.0	27.5	13.0
Maximum Ground-Level Temp. of Previous Interval °C..	——	33.3	——	10.0	8.3	17.2	27.2	25.5
Minimum Ground-Level Temp. of Previous Interval °C..	——	12.8	10.0	7.2	5.5	5.0	17.2	14.4
Water Temperature °C..........	16.0	15.0	13.5	11.5	1.00	13.0	16.0	15.5

Drought conditions for *L. humilis* are approached when the surface mud loses its minute film of water. In many instances, *L. humilis* lives on the threshold of drought conditions in the field. This is certainly true for those snails browsing upon the landward reaches of a mud flat. The relatively small numbers of snails found there attests to the unfavorableness of this environment (Fig. 1). When a handful of soil from this region of a mud flat is picked up, no water drips from it in contrast to regions near shore. In the laboratory *L. humilis* is very susceptible to drying. Four or five days on mud which has lost its visible moisture are sufficient to kill the snail. No precise data are available for the survival of *L. humilis* in the field. No doubt the survival time varies with individual snails and with age, as well as with the relative dryness from one microhabitat to another. A small algal mat will help retain moisture on the floor of a mud depression thus possibly permiting a colony of snails to survive. On the other hand, survival time is short on clay exposed to direct sunlight. In one area in northern Ontario, near North Bay, visited in June, 1949, a small clay-bottomed pool which had become dried and caked yielded considerable numbers of dead *L. humilis*. Those snails which remained at the bottom of deer tracks in the pool, evidently made before drying had taken place, however, were able to survive. Here they were protected from the sun and the rate of evaporation was decreased. It was found generally in the laboratory that delicate, younger snails were more susceptible to death from desiccation. It has already been shown that in nature the younger individuals are mostly confined to the more moist parts of a mud flat. It is evident that the chances of *L. humilis* to survive drought conditions depend upon the water-retaining properties of the soil, degree of exposure, age of snails and the amount of vegetation. Walton (1918) came to similar conclusions with *Lymnaea truncatula*, but he pointed out that the whole matter is a complex one.

That *L. truncatula* is able to survive rather long periods of drought is shown by the work of Kendall (*l.c.*). His observations have indicated that newly hatched snails, which had little if any opportunity of feeding in the interval between hatching and the onset of drought conditions, were able to survive at least two months of exposure on a hard mud surface in the dry atmospheric conditions of the laboratory. Larger snails (3–5 mm. in length) resisted drying for even longer periods; three snails of one group survived a year under experimental conditions. On the other hand, Walton (*l.c.*) found that in the field *L. truncatula* resisted drought only for a relatively short time. He stated that some snails will not recover when placed in water after two days' drying, if they have been subjected to continuous sun and wind in an exposed position. If the snails became buried in mud their chances of survival were greatly increased.

Cawston (1929) suggested that there was a relation between the width of the aperture of the shell and resistance to desiccation. It is unlikely that this is an important factor in the survival of *L. humilis* which remains with the mouth of the shell pressed closely to the ground when subjected to gradually drier conditions. As time passes the body withdraws further into the shell and remains there until the snail is placed in water or dies. Moreover, shells which are turned over are usually quite able to right themselves, so death from starvation or drying for that reason is unlikely. The ability to right itself is a necessity for a snail which lives much of the time away from the buoyant influence of water.

According to Walton (*l.c.*), *L. truncatula* does not attempt to follow retreating water as drought sets in. Likewise, in the laboratory *L. humilis* has been observed many times to die as a result of drying only a few centimeters from moisture and water. This behavior may be partly related, however, to certain peculiar conditions of laboratory culture. When first placed in an artificial mud habitat, the snails make persistent attempts to escape, even from large flat trays and even when mud from the original habitat is used. *L. humilis* seems to be more active during the first few days after being placed in laboratory habitats than in the field. The precise reasons for this behavior are obscure. In a few days, however, often after many have been lost, they spend more time on mud and relatively little in water. If the mud is allowed to dry gradually, some of the snails remain in more moist parts but many stay in the drying portions, eventually dying. Observations in the laboratory, therefore, indicate that the snails do not especially select more moist situations as artificial drought sets in, and their survival as a result of being in a more damp section of a mud-filled tray, is entirely fortuitious. During the present study no exact information was available on the behavior of *L. humilis* when confronted with gradually retreating water in nature.

DISTRIBUTION IN WATER: In the habitats studied, the numbers of *L. humilis* present in water were always found to be less than on land, both seasonally and throughout different times of the day. There was no variation of density in water throughout a 24-hour period in spite of a large variation in the water and air temperatures (Table III). A typical aquatic distribution of *L. humilis* is shown in Table IV. It is interesting to note that the snail was restricted primarily to regions of the stream bed where the substrate was transitional in type (partly sand and partly

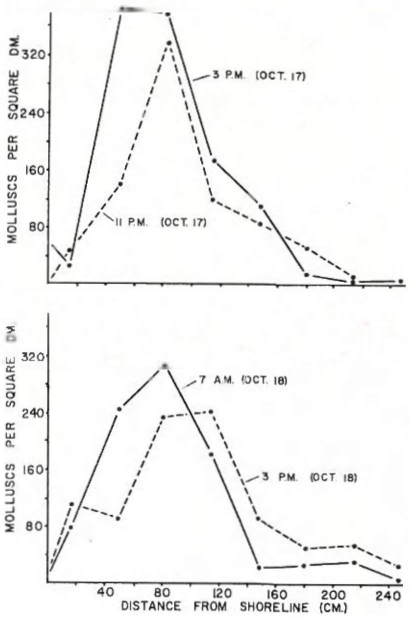

FIG. 3. The diurnal distribution of *Lymnaea humilis* on a mud flat. Quantitative series were taken at intervals of 25 centimeters perpendicular to the shoreline every four hours over a period of 28 hours. The results of four series are plotted (3 p.m., 11 p.m., 7 a.m., and 3 p.m.).

silt) or consisted of silt alone. Its absence on water-deposited sand, however, may also be related to the strength of the current in this part of the river as well as to the nature of the substrate. Within a few centimeters from shore the concentration of *L. humilis* rises slightly, but in a zone a few centimeters out of water the increase in numbers is several-fold.

Hoff (1936) found that a reduction of air temperature to less than 40 degrees F. (4.5 degrees C.) furnished a stimulus for the return of *Lymnaea humilis* (*Fossaria parva*) (See Hubendick, *l.c.*) to water. After cool nights the snails were seen in shallow water immediately under a layer of ice. As the ice melted during the day, the snails migrated from water, but returned again when the nocturnal temperature fell below 40 degrees F. This migration from water to land was often a daily occurrence during the last two weeks of March and most of April. In the present study, even during December and January when the water temperature was three degrees C. and the air temperatures were 5.3 and ten degrees C. respectively, there was no basic change in the land-water distribution of *L. humilis*.

As a check on temperature migration Hoff *l. c.*) placed snails (collected in Illinois and which had crawled up the sides of containers) into the refrigerator and found that they returned to water. *L. humilis* collected from the region of Ann Arbor and placed in a refrigerator, did not migrate from the sides of jars to the cooling water (which decreased to four degrees C.). Variation in certain characters of *Lymnaea palustris* Müller from the different localities have been reported by Forbes and Crampton (1942). This snail was shown to vary in fertility, size and longevity. In two local populations these differences persisted in successive generations reared in the uniformity of laboratory culture. That these different responses to temperature, by *L. humilis* collected from different regions, may constitute true geographic variation is open to question in the light of recent work by Hubendick (1951) who found that variation in certain characters of *Lymnaea peregra* (Müller) was without regional order.

When placed beneath the surface of water in which the temperature had decreased to five or six degrees C. in a refrigerator, *L. humilis* generally did not return to the surface or crawl up the sides of the container. At temperatures below this they soon became immobile. As the temperature rose, the snails became more active, and more and more snails inched their way up the walls of containers, until finally the majority of snails were out of water by the time the temperature reached 20 degrees C. The behavior of the snail in varying temperatures is undoubtedly directly related to the affect of this factor on activity and upon oxygen demand.

In the field a slight rise of the water level occasionally would cover 20 to 40 cm. of mud flat, immersing large numbers of *L. humilis*. If the level remained high, most of the snails eventually deserted the water for the exposed mud. The rate at which this occurred depended upon temperature but usually in one or two days the land-water distribution returned to normal.

Lymnaea humilis in Relation to Other Animals

One of the most important flukes transmitted by *Lymnaea humilis* (*Fossaria parva*) (see Hubendick, *l.c.*) is *Fascioloides magna* Bassi, a liver fluke which was first described by Bassi from deer enclosed in a national park in Turin, Italy (Swales, *l.c.*). Besides members of the Cervidae, the Bovidae are also susceptible (Swales, 1936). As one of the intermediate hosts of *F. magna*, it is quite possible that *L. humilis* will occupy the increasing attention of the wildlife specialist. *Fossaria modicella* (=*Lymnaea humilis*, Say of Hubendick, *l.c.*) also is an intermediate host for *Fasciola hepatica* L. (Krull, 1933). Although many *L. humilis* were dissected and sectioned no cercariae or sporocysts were seen in those snails from collection areas in Michigan. Moreover, no field-collected *L. humilis* shed cercariae while under observation in the laboratory.

Aquatic snails also are subject to predation (F. C. Baker, 1916; Boycott, 1936; Wild and Lawson, 1937). Boycott (*l.c.*) listed mammals, birds, fish, annelids, and carnivorous larvae of insects, especially larvae of aquatic beetles as enemies of aquatic snails. Taki (1931) found that the larva of the water beetle ***Hydrophilus acuminatus*** is the most formidable enemy of ***Lymnaea japonica*** Jay, attacking and crushing it with its powerful mandibles. Because *L.* ***humilis*** lives so much of the time out of water, it is undoubtedly exposed to a number of the same predators as terrestrial snails. There is no field evidence, however, that predation limits the population of *L.* ***humilis*** in any way. Boycott (1934) came to a similar conclusion in connection with land shells generally. Recently, Berg (1953) reported several sciomyzid (Diptera) larvae that feed upon

TABLE IV

The Distribution of *Lymnaea humilis* in Water, Showing the Concentration of Snails at 33 Centimeter Intervals (25 Centimeters between Each Sample) up to a Distance of Six Meters Perpendicular to the Shoreline. This Series Was Taken on October 18th, 1953 when the Population of *Lymnaea humilis* Was at its Maximum Density. (Raisin River, Newburg, Michigan)

Distance from Shore (cm.)	Depth (cm.)	Current Direction	Bottom	No. Snails In Sample	No. Snails per Suare dm.
610	60.5	Downstream	Water Deposited Sand	0	—
577	52.0	"	"	0	—
544	46.5	"	"	0	—
511	40.0	"	"	0	—
478	37.0	"	"	0	—
445	31.0	"	"	0	—
412	28.0	"	"	3	6
379	26.5	Indefinite	Transition	1	2
346	24.0	"	"	0	—
313	23.0	Upstream	"	0	—
280	21.0	" D	"	3	6
247	22.0	" E	Silt	2	4
214	21.0	" C	"	2	4
181	19.0	" R	"	0	—
148	17.0	" E	"	1	2
115	15.5	" A	"	1	2
82	9.0	" S	"	1	2
49	5.0	" I	"	2	4
16	1.0	" N	"	7	14
16*	—	– G	–	56	112

*Mud flat. Maximum depth of stream was 100 cm., at a distance of 750 cm. from shore.

living snails. Berg (*l.c.*) found that larvae of ***Dictya expansa*** Steyskal (Sciomyzidae), when exposed to ***Lymnaea obrussa*** = (***Lymnaea humilis***) (see Hubendick, *l.c.*), will kill and devour it. In the present study, predation of *L.* ***humilis*** by insect larvae was not observed; however, a systematic search for such predation was not made.

Pomatiopsis cincinnatiensis was a frequent associate with *L.* ***humilis*** at the Clinton habitat and was less commonly found with *L.* ***humilis*** at Newburg. Both snails occur in the same general habitat (van der Schalie and Dundee, *l.c.*) and, especially at Newburg, showed interesting ecological interrelations. As was pointed out in the recent paper of van der Schalie and Dundee (*l.c.*) *P. cincinatiensis* (Lea) is amphibious and confined to wet, marginal regions and is commonly found on muddy stream banks where it shows a uniform and somewhat linear distribution. It can withstand submergence in water during high-water periods, and like *L. humilis*, occurs in large numbers under optimum conditions. On the flat habitat (Newburg) it overlapped the range of *L. humilis* only at the periphery of the landward extent of this snail. Here, the concentration of *L. humilis* was usually less than four per square dm., whereas the concentration of *P. cincinnatiensis* was sometimes as high as 12 per square dm. The width of this common range of these two species of snails was narrow, only about 60 cm. wide, and was on the edge of or immediately within encroaching marginal plants, between 300 and 350 cm. from the edge of water. (The flat itself was free of marginal plants). In this common range the substrate was eroded and the moisture content of the soil visibly less than on the mud flat. No *P. cincinnatiensis* were found on the exposed flat. At the Clinton habitat *L. humilis* and *P. cincinnatiensis* shared the same range much more extensively than at Newburg. The sloping banks of the river abounded with marginal plants and the soil was more moist than on the mud flat habitat. As at Newburg, *P. cincinnatiensis* were not present in widely exposed areas where *L. humilis* were prevalent.

In comparing the behavior of these two species of snails, it is evident that they differ in their respective environmental preferences. Although *P. cincinnatiensis* inhabits places which are quite moist, it apparently is able to live in localities which contain less moisture than will support a maximum aggregation of *L. humilis*. The latter has a tendency to be somewhat more aquatic being more closely associated with water throughout the year than is *P. cincinnatiensis*. In autumn (October), *P. cincinnatiensis* disappears from wet and marginal mud surfaces and hibernates in grassy vegetation relatively high up on a river bank (van der Schalie and Dundee, *l.c.*). By early June, van der Schalie and Dundee (*l.c.*) have shown that *P. cincinnatiensis* begin to zone themselves along the edge of water again. As mentioned previously, *L. humilis* does not migrate seasonally but is found in the same habitat the year around. On the other hand, *L. humilis* is capable of living in broad exposed areas (and very frequently in maximum numbers), whereas *P. cincinnatiensis*, at least in habitats studied, generally avoided such areas. Finally, unlike *P. cincinnatiensis*, *L. humilis* does not show a linear distribution along a mud bank, but tends to show a graded aggregation which, on a flat habitat, is highest a few centimeters from the edge of water and then gradually declines away from the edge (Fig. 1). This graded aggregation may be obscured, however, by the presence of vegetational cover and modified soil moisture-content.

Discussion

L. humilis is able to live in a variety of habitats, including ponds, streams and rivers, both in and out of water. During this study, its relative abundance in water was always found to be less than on lan.d Although quantitative samples were not taken, observation indicated that the density of this snail under water in the pond habitat was sometimes greater than the density under water at either Newburg or Clinton. This was evidently related to the large quantity of aquatic vegetation upon which the snails could browse. The surfaces of the plants were covered with minute bubbles of oxygen. These factors may have been sufficient to enable the snails to remain under water longer than in the Raisin River habitats where no rooted aquatic vegetation was present.

There was always a much greater tendency for the snail to move from water to land rather than the reverse. At room temperature in the laboratory, a snail forced to remain under water by placing a screen below the surface died in about a day's time. On the other hand, *L. humilis* is able to survive longer under water at lower temperatures. Of a number of snails placed in the refrigerator (four to five degrees C.) in September, several were still alive the following February. This interval is a longer "winter" period than the snail would have to endure normally in the region of Ann Arbor, Michigan. In nature, undoubtedly many snails survive under water throughout the colder winter months.

Although laboratory studies indicate that *L. humilis* is unable to survive long under water at higher temperatures, observations in the field show that optimum conditions for its existence on mud deposits are present only along a narrow portion near the water's edge. Insufficient oxygen, or impairment of some physiological process unknown at the present time, evidently restrains the snail from living a completely aquatic mode of life. On the other hand, conservation of water is still a great enough problem for *L. humilis* to prevent it from leading the terrestrial existence followed by typical land snails. It is not well adapted to either a completely aquatic existence or to a truly terrestrial one. It is essential when assessing the suitability of a habitat that not only should the presence of the snail be taken into consideration but also its abundance in that habitat (Van Someren, *l.c.*). The tendency of *L. humilis* to aggregate in the transition zone between the aquatic and truly terrestrial habitats, as well as its tendency to move out of water, leads to the conclusion that it is, at the present time, an incipient land species.

Boycott (1936) stated that he knew of no reasons why in nature any species of snail has any direct relation to a particular plant. The specific associations seen in nature were thought by him to be due to the plant and the snail happening to flourish in the same kind of habitat. He believed that a good many molluscs in England are found with *Potamogeton crispus* L. because the environment is suitable for both, but that the snails can get along without the plants. Moreover, he thought that there was no essential biological connection with them. There is good evidence, however, that different types of plants have definite roles in the life of *L. humilis*. Algae were found to form the principal element in the diet of this snail. As mentioned earlier, rooted aquatic and other vegetation were considered important as a source of oxygen to snails browsing upon the vegetation under water. No definite species of plants are said to be associated with *Lymnaea caillaudi* (Van Someren, *l.c.*); a good habitat for this snail is characterized by a certain amount of macrophytic vegetation and a sufficient abundance of diatomaceous and chlorococcal algae for food. The evidence indicates that diatoms and desmids are food for *L. truncatula* since these algae are common in areas where this snail feeds (Walton, *l.c.*). L. *humilis* generally does not eat the green leaves of higher plants in the field probably because sufficient algal material is present on the surfaces of stems and leaves. In the laboratory they do feed on cultivated plants such as lettuce and even on ground-up rat feed.

Summary

1. A description of a characteristic mud flat habitat of *Lymnaea humilis* Say, is given. This habitat had the following features: (a) It was maintained and kept in a process of change by the actions of currents carrying silt. (b) Algae formed visible mats on the mud surface, especially extensive in late summer. Genera of Bacillariophyceae were especially prevalent. *Phormidium* was the most abundant alga. (c) Few species, but often a great number of the mollusc *L. humilis* were present.

2. A river bank as well as a pond habitat of *L. humilis* are described. This snail concentrated along the shore in both these habitats and was most prevalent in the pond locality during periods of low water.

3. The distribution of *L. humilis* on land exhibited a definite zonation in relation to the shoreline. The concentration on a mud flat was greatest about 80 cm. from shore. A similar zonation was present on steep river banks but was more attenuated than on the flat. This zonation on land was considered to be related to moisture and available food.

4. There generally was a greater concentration of smaller snails near the water's edge than on the landward reaches of a mud flat. This distribution is probably related to the egg-laying habits of adult snails and to the relatively limited range habits of juvenile snails. It is also concluded that an optimum environment for developing *L. humilis* is provided by a narrow region extending from the shoreline, and that here maximum numbers of snails survive the period of development after hatching when moisture requirements are critical. This period extends over one or two weeks.

5. *L. humilis* tolerates a wide range of substrates but rarely, if at all, is seen on soft flocculent deposits, at least in the region of Ann Arbor, Michigan.

6. Quantitative methods showed that *L. humilis* does not change its relative distribution during a 24-hour period, either on a mud flat or in water adjacent to a mud flat.

7. Drought conditions for this mollusc are approached when surface mud loses its film of water. *L. humilis* was very susceptible to drying under laboratory conditions but in the field often lives on the threshold of drought conditions. It was concluded that survival of drought by *L. humilis* depended on the water-retaining properties of the soil, the degree of exposure and the age of the snail.

8. Laboratory observations indicated that this snail does not select more moist situations as artificial drought sets in, and that its survival, as a result of being in a more damp section of a mud-filled tray, is entirely fortuitous.

9. *Lymnaea humilis* was always less abundant in water than on land, both seasonally and throughout different times of the day. The number of snails present in water, however, was found to increase slightly within a few centimeters of shore.

10. In the areas studied, there was no field evidence that *L. humilis* migrated to or from water as a result of a pronounced change in air or water temperature.

11. When placed beneath the surface of water in which the temperature was kept at five or six degrees C., *L. humilis* did not generally return to the surface. At temperatures below this, they soon become immobile.

As the temperature rose, the snails became more active and gradually inched their way up walls of containers. Snails were kept alive under water at four to five degrees C. for about six months.

12. If a rise in water level covered a portion of a mud flat, most of the snails immersed would desert the water and move to the exposed flat, establishing a typical zonation. This adjustment usually took one or two days.

13. When the behavior of *L. humilis* and *Pomatiopsis cincinnatiensis* was compared, it was found that the former species was somewhat more aquatic than the latter since *L. humilis* was more closely associated with water throughout the year. *L. humilis* was capable of living in exposed areas whereas *P. cincinnatiensis* tended to avoid these.

14. There was no evidence that predation limited a population of *L. humilis* in any way.

15. *Lymnaea humilis* is not well-adapted to either a completely aquatic existence or to a truly terrestrial one. At the present time it is considered an incipient land species.

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