Proceedings of the Iowa Academy of Science

Volume 92 | Number | Article 6

1985

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Proc. Iowa Acad. Sci. 92(2):67-69, 1985

Distribution, Dispersion, and Behavioral Ecology of the Land Snail *Oxyloma retusa* (Succineidae)

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Oxyloma retusa is a land snail found only along moist margins of freshwater wetlands and lakes. This study quantifies the dispersal pattern of *O. retusa* along permanent and temporary wetlands and considers the environmental factors to which this snail responds. On a lake shore, snail density peaked in the second or third meter from the water's edge but snails were present in decreasing numbers up to 7 meters inland. In field experiments, marked snails, initially distributed evenly along a shore transect, assumed a similar dispersion pattern within 72 hours. Two color morphs had overlapping but zonal dispersions, the amber morph farther inland than the dark. In drying ponds, snails followed the retreating shoreline. In reflooding of such ponds snails responded by crawling with the water's leading edge or ascending emergent vegetation. It is clear that *O. retusa* actively selects a precise microhabitat. This habitat selection appears dependent on a combination of physical and biotic factors acting separately and in combination.

INDEX DESCRIPTORS: *Oxyloma retusa;* Succineidae; color polymorphism; distribution; dispersion; behavioral ecology.

Oxyloma retusa (Lea) is a land snail species paradoxically bonded to water. Individuals avoid open water yet are found only along the moist margins of freshwater environments. A zonal distribution is well described for many marine intertidal gastropods (e.g. Bovbjerg, 1984; Garrity, 1984) but is less well documented in inland species. This paper analyzes such a zonation.

The freshwater habitats where *O. retusa* can be found are of two basic types. Permanent lakes have relatively stable margins and constant habitats for this species. Seasonal and semipermanent marshes and ponds tend to dry as summer progresses and *O. retusa* surrounding these shores face a gradually receding habitat. Mid- and late-summer rains can then refill these basins within hours. For *O. retusa* to survive around shallow wetlands, individuals must respond to not only seasonal lowering of water levels, but also to rapid refilling of these basins following rains.

We had several objectives in this study: (1) to document the distribution of *O. retusa* on a variety of shorelines, (2) to quantify the dispersion of the population within the zone occupied, and (3) to consider some of the environmental factors to which these snails respond that result in this dispersion pattern.

Our work was done at The Iowa Lakeside Laboratory and vicinity (43°23'N, 95°11'W), located on the southern border of the Prairie Pothole Region (Weller 1981: Fig. 1). We surveyed shores of 22 lakes, ponds, marshes, wet roadside ditches, and the banks of the Little Sioux River. We found *O. retusa* at every site, frequently in high densities. This is a very characteristic land snail of this lake and wetland region of Iowa.

SYSTEMATICS AND NATURAL HISTORY

Oxyloma retusa is a member of the primitive, morphologically diverse land snail family Succineidae. Patterson (1975) recognizes twelve genera in this cosmopolitan family. The genus *Oxyloma* occurs in the Americas, Europe, and South Africa (Patterson 1971). *O. retusa* is widespread across North America (Pilsbry 1948; La Roque 1953).

O. retusa life history has not been well studied. It is known that this is a hermaphroditic species. We have observed egg laying throughout the summer in Iowa; gelatinous egg masses, containing around one dozen eggs, are loosely adherent to moist soil detritus. Strandine (1941) found that *Succinea ovalis* may live a little over a year; we suspect the same for *O. retusa*. Hibernating snails survived over winter under refrigeration in our laboratory.

While most succineids are found in moist habitats (Hyman 1967), *O. retusa* is extreme and regarded as the most hygrophilic of succineids (e.g. Baker 1939; Miles 1958; Leonard 1959; Schrader 1972). Any inhabitant of temporary waters must survive periods of drought. When exposed to desiccating conditions, *O. retusa,* like land snails in general, produce a mucous ephiphragm across their aperture and estivate. However, this offers only temporary refuge for these snails. Hyman (1967) reports survival times of ten days for desiccated *Succinea*. We have observed that *O. retusa* can survive up to two weeks of desiccation in the laboratory. Estivation seems to allow succineids to handle daily (i.e., afternoon) dry conditions. Shimek (1935) noted succineids are active ". . . during the early morning hours in drier periods, but close up promptly as soon as dry conditions return." Our own observations corroborate this, but we have repeatedly seen snails remain active on marsh vegetation throughout moist days (i.e., 100% relative humidity).

The diet of *O. retusa* includes both living and dead plant material, fungi, algae, and pollen (Schrader 1972). Our own observations confirm this. The shell of these snails is thin and delicate which makes them vulnerable to predators. Avian predation on succineids has been known for many years from research in parasitology; snails are intermediate hosts for the trematode *Neoleucochloridium* sp. (Woodhead 1935; Ingram and Hewitt 1943). Our laboratory observations showed that crayfish (*Orconectes immunis*) also will eat these snails. This crayfish leaves ponds at night and forages on the shore.

ZONATION AROUND PERMANENT BODIES OF WATER

To determine the dispersion of *O. retusa* populations along stable shores of a lake, ten 1-m wide transects perpendicular to the shore of Lake West Okoboji (surface area 1558 ha) were sampled. Shore gradients were between 3° and 5° for these ten transects. Transects were divided into 1-m increments allowing us to sample consecutive 1-m^2 quadrats. Collecting began on emergent vegetation in open water and continued inland. All living vegetation (e.g. *Rumex* sp. and *Typha* sp.) and detritus were removed and examined for snails. Sampling ceased when snails were no longer found. In three of these transects, snail color (dark or amber) was recorded.

A total of 3,280 snails was collected. Density peaked in the second or third meter from the water's edge and decreased to zero 5 to 7 m inland (Fig. 1a). The two color morphs exhibited overlapping but zonal dispersion (Fig. 1b). Dark snails were closer to the water's edge (peak density at 1.5 m) and associated with the mud shoreline; amber snails were proportionately more numerous farther inland (peak density at 3.5 m) and associated with thick detritus and vegetation.

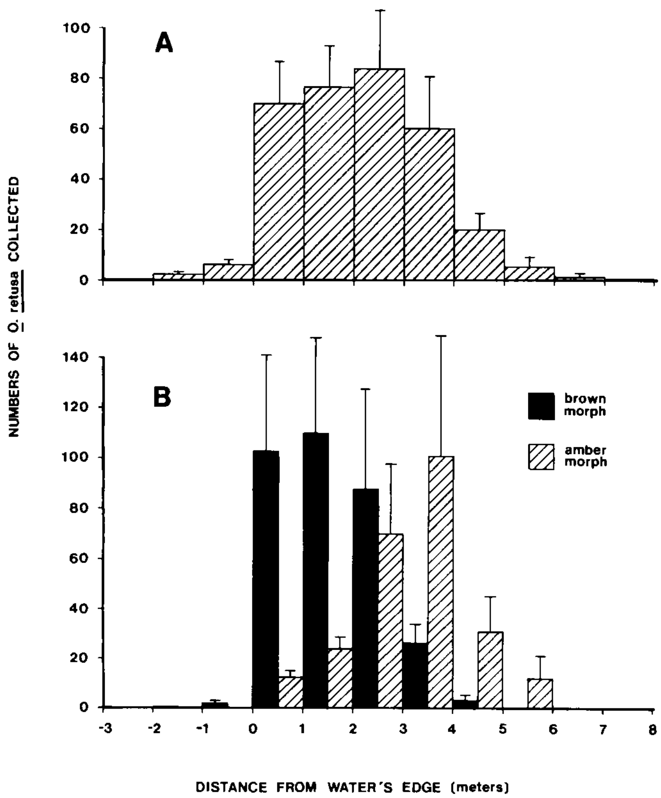

Figure 1. Field density of snails on a lake shore. A. Mean density (snails/m²) of 10 transects from shoreline to 8 m inland on the shore of an embayment on Lake West Okoboji. B. Mean density of 3 transects identifying brown and amber color morphs. Standard error indicated.

Habitat selection experiments were done in the field. Two groups of 100 snails were marked with fingernail lacquer and placed uniformly in sheet-metal enclosures 1 m wide and 10 m long. These enclosures were perpendicular to the shoreline and bracketed the limits of snails as measured in the field. Before snails were placed in the enclosures, all other snails were removed. The enclosures were covered with screens to prevent avian predation. After 72 hours the snails were removed and recorded by 1/2 m quadrats. In both enclosures, densities peaked in the second or third meter from the water's edge (Fig. 2). This is essentially identical to their natural dispersion on the lakeshore and suggests active habitat selection. High mortality (25%) was probably due to the disturbed and exposed experimental environment.

ZONATION AROUND TEMPORARY BODIES OF WATER

When temporary ponds and marshes are filled with water, the dispersion of *O. retusa* is similar to that around lakes. However, when ponds dry, *O. retusa* can migrate with the receding waters or they can remain behind in the basin anywhere there is sufficient moisture. We have seen both responses.

A marsh in the last stage of drying was sampled for *O. retusa* in 42 1-m² quadrats (Fig. 3). Sampling was random throughout most of the basin, but additional sampling was done near the drier basin edge and the moister basin center. Snails were found throughout the basin, but by far the greatest density was in a central depression where the bottom was still very wet. They had apparently followed the receding water.

On several occasions, after rains had reflooded portions of ponds, we sampled 1-m² quadrats for snails. Many snails apparently moved peripherally with the rising waters and a ring of snails around the pond resulted. Large numbers of snails also were left behind, having ascended emergent vegetation. We recorded the heights above water of 900 snails on newly flooded cattails. Some had climbed up to a meter though most were in the first one half meter above water. We also saw many dead snails in the water that had failed to retreat successfully either vertically or horizontally as the basin flooded.

We made careful observations of the response to flooding. As water covered the snails, many twisted their foot 180° on an anterior-posterior axis so that instead of crawling on the flooded pond bottom they crawled on the undersurface film of the water. Crawling continued until snails encountered emergent vegetation, which they then ascended. Snails on emergent vegetation were not trapped. They often voluntarily left the stem and crawled on the undersurface film until they came upon another stem, which they again ascended. Some snails drowned while submerged and some reached the shore.

DISCUSSION

It is clear that *Oxyloma retusa* actively selects a precise microhabitat. This results in a unimodal, bounded dispersion pattern along the shores of all bodies of water in the area. It is also clear that this snail responds to environmental changes in the several adaptive behaviors that result in zonation. What is unclear is which of the potential environmental factors are acting and to what extent. We have not examined the physiological mechanisms of perception and response.

In general, unimodal dispersion patterns, such as that exhibited by *Oxyloma,* are the result of proximal factors acting separately or in

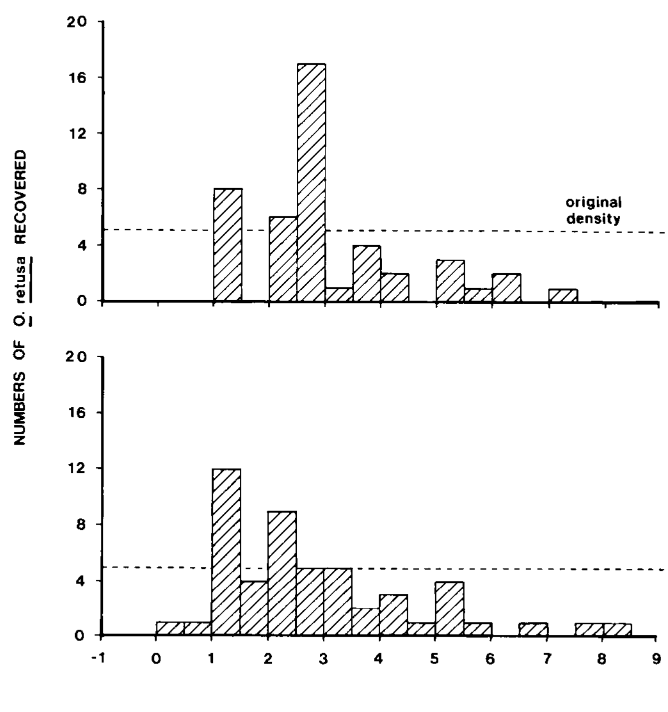

Figure 2. Experimental habitat selection. Density of snails in two 10-m transects on a lake shore 72 hours after release in uniform density throughout an experimental enclosure. Original density indicated by dashed line. N = 100 marked snails in each experiment.

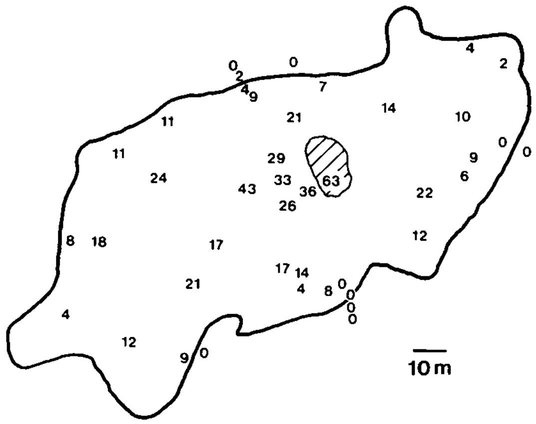

Figure 3. Snail migrations following receding water of a drying marsh. Numbers are densities of snails/m^2 in a marsh at the Iowa Lakeside Laboratory. The entire marsh basin had a moist substratum but the central patch (hatched) was still very wet.

combination. Animals may avoid environmental extremes or they may be attracted to optimal conditions (*sensu* Thorpe 1963; Sale 1969). It is probably also the case that these snails are responding to more than one environmental factor, as has been demonstrated in pond snails (Bovbjerg 1975). There are sharp gradients in such physical factors as water depth, light, temperature, wind and humidity. Potential biotic factors would include food, competition, cover, and predation.

It is clear these snails avoid open water. In the laboratory, snails invariably ascend the sides of their containers when placed in water. In the field, snails respond to basin reflooding by ascending emergent vegetation or retreating shoreward. However, *O. retusa* will voluntarily enter the water when trapped on emergent vegetation.

On the shore the physical factors of light, temperature, and wind decrease sharply inland as vegetative cover increases. Singly, these factors are probably unimportant — snails are active in bright sunshine, cold and warm, and windy or quiet — if the humidity is 100%. In combination, however, these factors are closely related to humidity and humidity appears to be the primary factor determining *O. retusa* dispersion. These snails are found in microhabitats which have high humidities and are only active when relative humidities approach or exceed 100%. To the best of our knowledge the question of how *O. retusa* monitors humidity — whether from specific sensors or their general skin surface — has not been investigated.

Of the potential biotic factors acting here, food and competition seem less important than predation. Food for these detritivores is abundant relative to snail density and food does not vary in a gradient. A potential competitor, *Succinea ovalis*, is found throughout the region but occupies a zone distinctly higher on the shore. Birds prey heavily on this species. The low snail density at the immediate shoreline may reflect this predation or reflect an adaptive response to cover. The association of brown morphs with mud substrates and amber morphs with detritus may reflect such selection pressures.

Left dangling in this discussion has been the presence of dark and amber color morphs and their separate but overlapping zonation. These are morphs of the same species. Baker (1939) observed seasonal changes from dark in the spring to amber in the summer. We found a temporal overlap and in fact found that snails brought into the laboratory could change color (usually to intermediate shades) within a few days. Our data show that color is related to moisture, the amber morph apparently more tolerant of desiccation. We have no explanation. Nor can we ascribe cause to color or color change. Causes could include degree of exposure to light, diet differences, or a visually-mediated response matching snail color to background color. This dimorphism offers exciting potential for future study.

ACKNOWLEDGEMENTS

Charles Abraham assisted in data collecting. MJL was aided by a Thomas H. Macbride scholarship to Lakeside Lab. K. Nishikawa and R. Wassersug made several suggestions which improved this manuscript.

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