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Cepaea nemoralis (Gastropoda, Helicidae): The Invited Invader

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ABSTRACT

Marauding snails may not immediately come to mind when considering invasive species, but many non-native snails have successfully colonized the U.S. The wood snail, *Cepaea nemoralis* (L.), is one of the most striking of these introductions, due in part to its attractive shell coloration. This is one of the few snails that people have purposely introduced into their gardens. Several populations are now established in Kentucky, including a newly discovered population in Kenton County. The bright, striped or solid, yellow, pink, and brown shells of this species have long caught the eyes of natural historians and biologists. Populations of these snails are classic model systems for ecological genetics studies. While introduced populations of wood snails seem to have had only minor impact as agricultural pests, they may have the potential to competitively exclude some native species of snails.

INTRODUCTION

Though snails may not be the speediest of beasts, several species have launched successful invasions of the U.S. (Cowie and Robinson 2001; Dundee 1974; Mead 1971). Perhaps the most glamorous of these invaders is the wood snail, *Cepaea nemoralis* (L.). While many gastropods rely on stealth and interstate shipping to fuel their spread, wood snails have another weapon in their arsenals: charm. Their colorful shells (see Figure 1) are nearly irresistible to small children, nostalgic malacologists, and many an evolutionary biologist.

TAXONOMY

The wood snail belongs to the family Helicidae, which includes the bulk of the European edible snails. It is a Linnaean species described in 1758 and was originally *Helix nemoralis,* until Held established the genus *Cepaea* in 1837 (Abbott 1989). Currently, four species are included in the genus, of which *C. nemoralis* is the type. The specific epithet means 'of the woods' or 'inhabiting woods/groves' (Pilsbry 1939; Reeve 1863; Rimmer 1907).

Cepaea hortensis, the white-lipped grove snail, is considered the sister species of *C. nemoralis* (Jones et al. 1977). Historically, taxonomists often treated *C. hortensis* as a variant of *C. nemoralis* (Step 1901). The two species are primarily differentiated by lip color of the shells, which seems a minor feature in light of the fact that *C. nemoralis* is the most variably colored species in its genus and perhaps even among European land snails. However, Rimmer (1907) argued in support of recognizing *C. hortensis,* having observed several mixed populations and noting that of the many snails seen paired on tree trunks, he saw no "matrimonial alliances between these two forms." Current taxonomists also take this view, and the occasional hybrids produced by these species are sterile (Jones et al. 1977). Both taxa occur in the U.S., and though wood snails are known to be introduced, there is disagreement on whether *C. hortensis* is native or was also introduced from Europe (Burch 1962; Dundee 1974; Jones et al. 1977; Mead 1971).

LIFE HISTORY AND NATIVE RANGE

Native to central and western Europe, wood snails are widespread in disturbed habitats, from woodlands to fields and yards, but are also found on chalk cliffs and even coastal dunes (Reeve 1863). They are known by a variety of common names, the English ones including banded grove snail, banded wood snail, brown-lipped snail, and girdled snail (Abbott 1989; Reed 1964; Step 1901; Turton 1857). This species has been widely introduced and now has a nearly worldwide distribution (Abbott 1989).

Wood snails are obligately outcrossing hermaphrodites, with both individuals exchanging sperm during mating, and both individuals able to lay eggs afterward (Stine 1989). Like other members of the Helicidae, *Cepaea* snails have a bizarre courtship behavior in which the courting pair stabs each other with sharp, calcareous structures, aptly named darts, before mating (Abbott 1989; Pilsbry 1939). Wood

Figure 1. Shells of *Cepaea nemoralis* (L.), the wood snail, showing solid pink (left), solid yellow (top), and striped morphs. Note the brown lip characteristic of this species. These European snails have been introduced throughout the northeastern U.S. and occur in at least three counties of Kentucky.

snails often mate multiple times prior to egg laying and can store sperm for up to 15 months (Murray 1964). It is not unusual for one clutch of eggs to include offspring from two different fathers (Murray 1964). Eggs are buried in moist soil, hatching after about 3 weeks (Abbott 1989). The snails reach maturity in 4 years and may live as long as 5–9 years (Abbott 1989; Jones et al. 1977).

Like those of most land snails, wood snail shells are dextral (spiraling to the right), though rare sinistral individuals are sometimes seen (Rimmer 1907; Turton 1857). Mature individuals of *C. nemoralis* reach 2–2.5 cm in diameter and have five whorls to the shell (Pilsbry 1939). When the snail reaches full size and ceases to grow, a reflexed lip forms around the aperture of the shell. The dark brown coloration of this lip differentiates *C. nemoralis* from the similar *C. hortensis*. Shell color varies from yellow, to pinkish, brown, or occasionally even white (Step 1901; Turton 1857). Shells are also generally augmented with 1–5 dark brown bands, though unstriped shells are seen as well (Figure 2). Multiple color variants are commonly found within the same population.

Wood snails, feeding primarily at night, eat a variety of plants, though they often prefer dead plant material to living, and may even forage on dead organisms such as worms or other snails (Thompson 1996; Turton 1857). Among living plant materials, they prefer broad-leaved plants over the tougher grasses

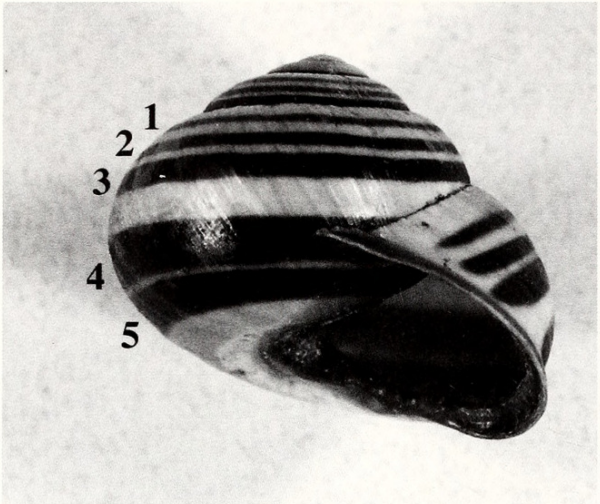

Figure 2. Typical five-striped wood snail morph. There is such great variation in shell striping for this species that a coding system has been developed to catalogue it (Howe 1898; Jones et al. 1977). Stripes are numbered from top to bottom. This shell would be coded 12345. A shell with only the third stripe present (Figure 3) would be 00300. When partial or total fusion of bands is taken into account, there are hundreds of possible variants.

which are common in their habitats, and avoid species with high concentrations of secondary compounds or physical defenses against herbivory such as hairs (Grime et al. 1968; Thompson 1996). Oddly enough, they are said to particularly favor the leaves of stinging nettles (Step 1901). They are adaptable in the lab or under cultivation and happily eat lettuce, carrots, fruit, pure cellulose filter paper, and even (occasionally) mutton (Grime 1968; Judd 1953; Murray 1964; Sowerby 1825; Thompson 1996).

Though these snails lack operculums which would allow them to close their shells, they have a relatively high drought tolerance due to their ability to aestivate. After feeding, they generally crawl up onto the plant or a nearby shrub or stone wall, stick themselves down with a dab of slime, and remain inactive until the next moist evening. During dry spells, these organisms can remain dormant for long periods of time until conditions improve. (Aestivation in many species of snails can last for months, and even for years in some [Abbott 1989].) For the winter months, the snails bury into the soil and remain dormant until spring (Lovell 1884).

In Great Britain, song thrushes can be a major predator of adult wood snails, crushing their shells on stones to get at the soft snail within. Other birds, including chickens, will sometimes eat wood snails (Howe 1898). Several snail predators are invertebrate organisms, including certain beetles, glowworm larvae (related to fireflies), and even predatory snails (Jones et al. 1977; Woodward 1913). Small mammals such as shrews, moles, and hedgehogs also enjoy these slow-moving morsels (Dees 1970; Reed 1964; Woodward 1913).

SPREAD IN THE U.S.

Since the arrival of Europeans, many species of molluscs have been both purposely and accidentally introduced into the U.S. In recent years, the number one pathway for the introduction of new land snail species seems to be via infested horticultural materials (Cowie and Robinson 2001). Eggs and small individuals such as juveniles can be difficult to see when intermixed with soil, mulch, or other plant material (Cowie and Robinson 2001). Many snail species can also self-fertilize or store sperm for up to a year after mating, so one overlooked adult may be all it takes to pioneer an invasion (Cowie and Robinson 2001; Thompson 1996). Wood snails specifically have also been found by the USDA stuck to vehicles and military cargo (Dundee 1974).

The helicid snails, which include *C. nemoralis,* have a somewhat more colorful history of introduction, as many of these were purposely established in new habitats (Dees 1970; Mead 1971). Helicids, such as *Helix pomatia,* the French escargot, are often prized as choice comestibles. Many helicid introductions can be traced back to the kitchen gardens of European immigrants desiring a renewable source of snails (Mead 1971).

As a small and unusually colorful species, *C. nemoralis* has the distinction of being more often introduced for ornament than for food. The earliest U.S. introduction of this species was made by malacologist William Binney in 1857 (Pilsbry 1939). Binney collected snails in Sheffield, England, returned to the U.S. and then released them in his Burlington, NJ, garden, where they proceeded to flourish (Binney and Bland 1869).

The U.S. populations of *C. nemoralis* originate from multiple sources, however. A Lexington, VA, population was attributed either to an introduction of Italian snails in packing ma-

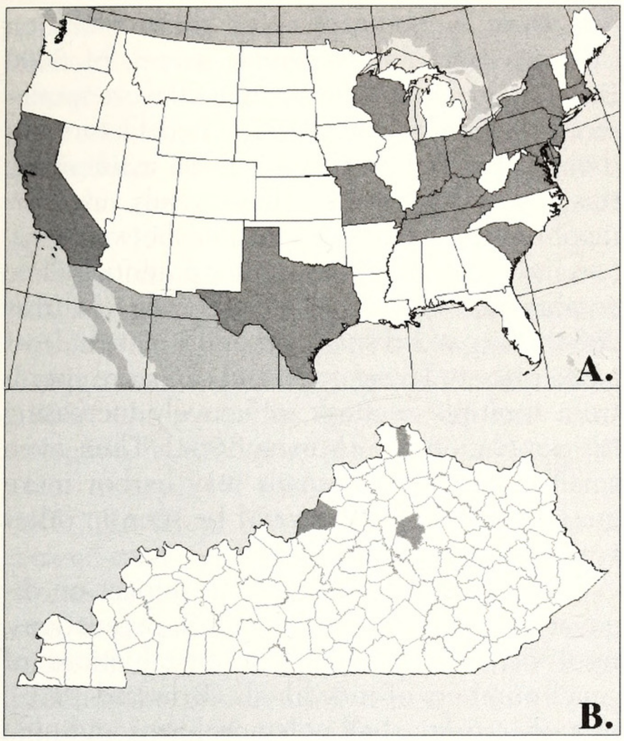

Figure 3. A. The wood snail has successfully colonized most of the northeastern U.S. and has also been found in some western states, including California and Texas (Abbott 1950; Burch 1962; Dundee 1974; Reed 1964). B. In Kentucky, populations of the wood snail have been found in Fayette, Jefferson, and Kenton Counties. (Maps courtesy of the online National Atlas of the United States [2005].)

terials or of British snails in imported ivy (Barber 1918; Howe 1898). After the turn of the century, imported shrubs from the Netherlands and Ireland were probably the source of other snail populations discovered in Virginia and Massachusetts, respectively (Reed 1964). By 1974, populations of wood snails had been documented in at least 15 states and throughout the northeastern U.S. (Figure 3A).

KENTUCKY POPULATIONS

Documentation of land snail diversity and distributions in Kentucky is scanty, but scattered populations of *C. nemoralis* are reported from the state (Figure 3B). Reed (1964) cited a specimen found in Ohio River drift at Louisville, and at least three Lexington collections have been recorded (Branson and Batch 1969; FNMH 2005). Specimens have also been noted from Cincinnati, Ohio (Reed 1964; FMNH 2005), so it is not surprising that a large population of *C. nemoralis* was recently found in northern Kentucky near Ft. Mitchell, Kenton County (pers. obs.; see Figure 4). Surveys of snail fauna from Mammoth Cave National Park in Edmonson County and the Doe Run Creek Area of Meade County did not list *C. nemoralis* among the species found, perhaps because these are less disturbed areas than those noted above (Hubricht 1968; Kaplan and Minckley 1960).

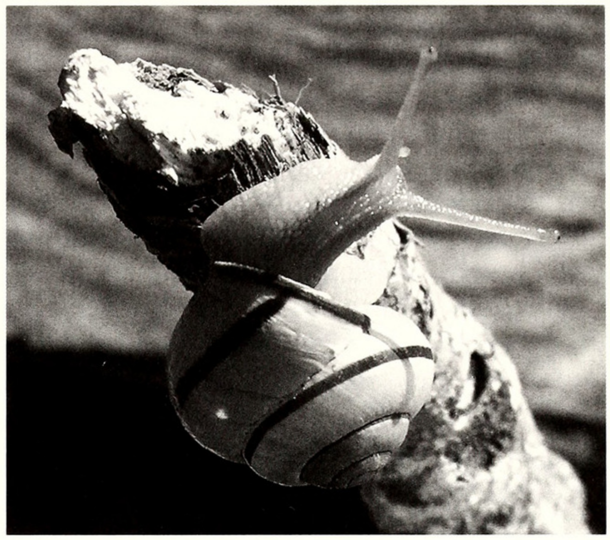

Figure 4. Living wood snail from Kenton County, Kentucky. These snails have four pairs of tentacles, with the eyes located at the tips of the retractable upper pair. A shorter pair of sensory tentacles bracket the snail's mouth.

ECONOMIC IMPORTANCE

While considered one of the European edible snails, its small size, and the belief that species with striped shells are inferior in flavor have limited the popularity of *C. nemoralis* among gastronomes (Lovell 1884). None the less, the relative hardiness of this species compared to larger species of escargot, the ease of culture, and the nearly worldwide availability has kept them on the lists of species with potential for cultivation (Dees 1970; Thompson 1996).

Though wood snails eat a variety of plant materials, their apparent preference for dead material has limited their impact as agricultural pests (Dees 1970; Thompson 1996). Occasional note has been made of the fact that even in areas with many snails, they appear to do little damage to the flora (Abbott 1950; Brooke 1897; Judd 1953). However, in high enough densities, they have the potential to damage landscaping or crops. For example, one Virginia population ranged from 50–100 snails per square meter, with an estimated total of 2500–5000 individuals (Stine 1989).

Wood snail shells are carried by some shell dealers, but generally tropical landshells and marine shells are more popular with collectors. At least one U.S. population may have been introduced to serve as a shell source (Cowie and Robinson 2001).

Wood snails also make easy to care for, if unusual, pets. However, most land snails are considered potential pest species by the USDA, and there are restrictions even on state-to-state transport of living snails (Dees 1970; Thompson 1996), dashing the hopes of those in the exotic pet industry hoping to spark a nationwide snail craze.

ECOLOGICAL AND GENETIC STUDIES

The variety of shell colors seen among banded wood snails has long fascinated naturalists, and many papers catalogue diversity within populations (Brooke 1897; Howe 1898; Johnson 1928; Judd 1953). The genetics of most color variations have been determined via crossing studies (Cain et al. 1968). At least five shell color loci are linked into a "supergene" (Jones et al. 1977). These control the shell's base color and four banding features: presence or absence, intensity of band and lip color, whether bands are continuous or dotted, and their spread (Jones et al. 1977). Four other unlinked loci also affect banding, with the number of bands controlled by two, one controlling darkening along the length of the bands, and one determining whether bands are black or orange (Cain et al. 1968; Jones et al. 1977). Epistasis between some loci also plays a role (Jones et al. 1977). Considering that there are no fewer than six alleles for base color of the shell, and that banding is affected by at least eight loci and 18 alleles (Jones et al. 1977), it is not surprising that early workers enumerated hundreds of shell varieties (Howe 1898).

Researchers have wondered how such high levels of variation are maintained. With long distance gene flow often limited by the slow spread of individuals, and many populations founded by small numbers of snails, one would expect to commonly see fixation of shell morphs through loss of alleles. However, fixed populations are rare. For example, a survey of 1000 French populations revealed only two that were monomorphic for shell coloration (Murray 1964). In a similar survey of 3000 British populations, fewer than 20 were monomorphic (Jones et al. 1977). Two factors are thought to play a crucial role in maintaining this diversity. Because these snails are hermaphrodites, mating is possible between any two individuals, increasing the potential allele combinations available to offspring (Murray 1964). Also, wood snails generally mate at least twice prior to laying eggs, and can store sperm from multiple matings, effectively increasing the population size (Murray 1964). Thus, even small populations of snails may harbor more genetic diversity than would be seen in other types of organisms.

Founder effects do have an impact on diversity, though, especially in U.S. populations, most of which arose from introductions of small numbers of individuals (Brussard 1975). A study scoring shell polymorphisms and nine isozyme loci showed that the major differences between U.S. populations seemed to be based on which part of Europe the snails had been introduced from, rather than the environment they were currently in (Brussard 1975). Later isozyme studies have also supported the founder effect as having a major impact on the genetic variation within U.S. populations (Selander and Foltz 1981).

Climate also has great influence on the diversity of shell colors. Wood snails, commonly found in cool temperate climates, are sensitive to overheating (Arnold 1969; Jones et al. 1977). One study of populations on sand dunes found a disproportionate number of brown and pink shelled individuals dying from heat shock (Jones et al. 1977). Climatic selection is thought to play a major role in large-scale patterns of shell color, with pale shells being selected for in hotter climates (Jones et al. 1977). Indeed, there is a cline for shell color across Europe, and in the hottest parts of their European range, yellow shelled wood snails are the most common type (Jones et al. 1977). Additionally, observation of shells dug from archaeological sites in England shows that, historically, brown shells were more common during periods with colder climates (Jones et al. 1977). However, interpretation of the interplay between climate and color is complicated by the fact that small scale environmental conditions may also have an effect

(Arnold 1968, 1969; Jones et al. 1977). For example, even in regions with generally warm climates, brown shells may be favored in certain cool, shady microhabitats, because brown individuals absorb heat faster than pale individuals and can thus become active more quickly (Jones et al. 1977).

Early workers observed that wood snails had a tendency to "mimic" their backgrounds, with the shell colors that best blended into the background being the most common (Howe 1898). Later workers have shown that visual selection by predators can produce this effect (Currey et al. 1964; Davison 2002; Jones et al. 1977). In Great Britain, song thrushes are efficient snail predators, crushing the shells on stones to get to the snail. Birds see in color, and in areas where song thrushes are common, shells which contrast with their backgrounds are preferentially eaten (Currey et al. 1964; Jones et al. 1977). Other predators such as mammals and glowworms have also been shown to prefer certain shell morphs over others (Jones et al. 1977).

With such a wealth of information on the genetic control of shell color, diversity of natural populations, and factors influencing shell morphs, wood snails have become wonderful model systems for study of evolutionary mechanisms and ecological genetics (Davison 2002). These organisms have the added advantage of being common and easy to work with in both the field and the lab.

ECOLOGICAL IMPACT

Some authors have expressed concern about the potential impact of non-native snails upon populations of our native species (Cowie and Robinson 2001; Mead 1971). Several years ago, wood snails were introduced to the Stone Lab area of Gibraltar Island (Ohio) via landscaping activities, and Dr. Michael Hoggarth of Otterbein College has since noted an apparent decrease in the numbers of native snails seen there (pers. comm.). This is an issue that calls for further study.

CONCLUSION

While recent surveys of *C. nemoralis* populations in the U.S. are limited, it is obvious that this species has become widely established. Several populations from Kentucky have been noted, and further searching would undoubtedly uncover more. Though the species is apparently not a major agricultural pest, the potential impact of these very successful aliens on our native snail populations should be of concern. However, now that the wood snail has come to stay, its potential for use in the classroom or for ecological genetics studies is an opportunity not to be overlooked.

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