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DISPERSAL ECOLOGY AND CONTROL OF THE INVASIVE LAND SNAIL CEPAEA NEMORALIS (L. 1758), FROM INGHAM COUNTY, MICHIGAN

presented by

MERRITT GALE GILLILLAND III

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IGHAM COUNTY, MICHIGAN

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DISPERSAL ECOLOGY AND CONTROL OF THE INVASIVE LAND SNAIL CEPAEA NEMORALIS (L. 1758), FROM INGHAM COUNTY, MICHIGAN

By

Merritt Gale Gillilland III

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology Program in Ecology, Evolutionary Biology, and Behavior 2006

ABSTRACT

DISPERSAL ECOLOGY AND CONTROL OF THE INVASIVE LAND SNAIL CEPAEA NEMORALIS (L. 1758), FROM INGHAM COUNTY, MICHIGAN

By

Merritt Gale Gillilland III

Cepaea nemoralis is an exotic and invasive species of land snail in North America. To understand how this species could potentially spread it was necessary to determine its short-distance dispersal capabilities. Harmonic radar was used to track the daily and weekly dispersal of this land snail species in two distinct habitat types from 2003 — 2005. The first habitat type was woodland with both biotic and abiotic conditions suitable for this species. The second habitat was grassland and was not considered a suitable type for this species. Cepaea nemoralis dispersed further distances in the woodland habitat (2.1 m/day) than in the grassland habitat (0.39 m/day). Snail dispersal was closely related to the abiotic (temperature and relative humidity) conditions of the environment. The woodland habitat was significantly cooler and more humid than the grassland habitat. Snail activity was greatest when the temperature ranged from between $19 - 20$ °C and the relative humidity was above 80%. This population of C. *nemoralis* was comprised mostly of 5 banded individuals and was dominated (85.1%) by juveniles. A commercially manufactured molluscicide was evaluated for its effectiveness at controlling C. nemoralis. It was determined that snail mortality was significantly higher in areas treated with the molluscicide than in areas treated with no molluscicide or sham molluscicide. The snail mortality also increased during successive treatments with the molluscicide. The efficacy of using harmonic radar to track the daily and weekly dispersal of C. nemoralis was evaluated. Harmonic radar is a useful tool that can be used to determine the dispersal of land snails. In this study the with daily tracking success rates ranged from 74% to 100% and weekly tracking success rates ranged from 40% to 52%.

DEDICATION

^I would like to dedicate this dissertation to my wife, Carolyn and my son, Brennan. You both make life so very interesting.

ACKNOWLEDGMENTS

To start, ^I would like to thank my advisor, Dr. James W. Atkinson, for all of his help and continued guidance over the years and for the intriguing and long discussions about science, philosophy, politics and sports. ^I am in debt to my guidance committee, Dr. Doug Landis, Dr. Jim Smith and Dr. Richard Snider for their constructive criticism throughout this project and for their help in the design and execution of the experiment. Special thanks are owed to the private landowners, Brad and Anna Stockwell, for allowing me access to their land, and most importantly, the snails for ³ years. ^I want to also acknowledge Dr. Doug Landis and the Invasive Species Ecology and Biological Control Lab for allowing me to use the RECCO Detector and thermohygrometer in the field. ^I would also like to graciously thank those who helped me in the field on one or more occasions, my father, Mr. M. Gale Gillilland Jr., Ms. Bridget Kruger, Dr. James Atkinson, Dr. Jim Smith, and Ms. Alicia Bray. Soil chemistry analyses were paid for by the MSU Invasive Species Initiative.

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CHAPTER 1: INVASIVE SPECIES

INTRODUCTION

Invasive Species: Examples of Selected Taxa

It has been suggested that exotic species are now the number one threat to biodiversity (Cohen, 2002). Once established in a new area these invading organisms can devour native species, compete with native species, alter existing habitats, hybridize with native species, and possibly infect them (Simberloff et al., 2005). Many factors are important for an invading organism to possess in order for that organism to successfully establish in a new habitat: (1) ability to readily adapt to a new or changing environment; (2) to out-compete native species within the same niche; (3) to have a wide tolerance to biotic and abiotic factors; (4) to have very few predators in the newly colonized area; (5) to be a generalist; (6) to grow quickly with high reproductive rates; (7) have longdistance and short-distance dispersal of offspring; and (8) to live at high population densities.

Examples of the introduction, establishment, spread, ecological damage, and economic cost an invading organism can have are numerous. The zebra mussel, Dreissena polymorpha (Pallas, 1771), was first detected in the Great Lakes in 1988 (Garton et al., 1993). It is believed that this invader was accidentally introduced via release of ballast water from ships used for maritime commerce. Infested ships came from parts of Europe where *D. polymorpha* is native. This species is now being spread from one inland lake to another in the U.S. primarily through recreational boating. It is estimated that $D.$ polymorpha control costs the U.S. \$100 million annually. This species can plug water intake and discharge pipes of water systems used by industries and

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municipalities. Industries and municipalities that use the Great Lakes as a water supply pay ~\$360,000/year to control this invading aquatic mollusc (Glassner-Shwayder, 1998). It has been estimated that between the years 1989-1994 D. polymorpha cost Great Lake companies and municipalities over \$120 million. Further, the nationwide cost to US. industries is over \$1 billion annually.

The ecological impact of D. polymorpha is even greater than the economic impact. In Europe it was reported that these mussels can live at densities of $10,000/m²$ (Garton et al., 1993). Dreissena polymorpha also has free-swimming planktonic larva which provides for long- and short-distance dispersal in the aquatic environment (Ackerman et al., 1994). An individual female can release as many as 300,000 eggs in one season (Garton et al., 1993). In Lake Eric D. polymorpha was responsible for increasing water clarity by decreasing phytoplankton numbers found in the water column, detrimentally altering pelagic and benthic food webs (Garton et al., 1993). Native North American unionid clams are also negatively affected by *D. polymorpha*. They will attach to any hard surface, including native unionid shells.

Purple loosestrife, Lythrum salicaria (L.), was introduced to the east coast over 200 years ago and since has spread throughout most of the US. It has been reported in 40 of the 48 continental states (Glassner-Shwayder, 1998). It has had significant economic impacts costing the US. \$45 million annually (Pimentel et al., 2000). This plant is a good example of a species that can dominate communities. Lythrum salicaria will out-compete native plants, especially cattail, *Typha* spp., forming a monoculture. A mature plant can produce over 2.7 million seeds annually and remain viable for up to 5 years (WSDE, 2004). Seeds are small, light and disperse via wind, water, and animals

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(e.g. birds); it can also spread vegetatively via a spreading rootstock (WSDE, 2004). This plant is a threat to biodiversity; not only to other plant species, but to those organisms that use the native plant species as resources.

More recent introductions into the U.S. include the emerald ash borer, Agrilus plam'penm's Fairrnaire 1888, which was discovered in Michigan in 2002 (MacFarlane and Meyer, 2005). This destructive insect has killed millions of ash trees, *Fraxinus* sp. The green macroalga, Caulerpa spp. "killer alga" is currently becoming established in the US. This species is widely bought and sold by the aquarium trade (Walters et al., 2006). Highly invasive, its sale via the intemet is mostly unregulated. The northern snakehead fish, Channa argus (Cantor, 1842), was first reported in 2003 from Maryland (Simberloff et al., 2005). Brought to this country via ethnic markets to be sold as food, it has since spread into American waterways (Odenkirk and Owens, 2005). It is feared that the species will damage native fisheries and have major economic and ecological impacts.

At least 20 different mammal species have been introduced into the U.S. (Pimentel et al., 2000). Many of these species (European rat, Rattus rattus (Linnaeus, 1758), and the Asiatic rat, R. norvegicus (Berkenhout, 1769)) have established themselves as terrible pest species throughout much of the US. The Indian mongoose, Herpestes auropunctatus (Hodgson, 1836), was introduced to Hawaii as a biological control for rats. Since its introduction it has eaten many of the native ground-nesting birds (Pimentel et al., 2000). At least 53 species of reptiles and amphibians have been introduced into the Continental U.S. and its territories. Among them is the brown tree snake, Boiga irregularis (Merrem, 1801), of Australia which was transported to the island of Guam via military airplanes during World War II (Pimentel et al., 2000). This

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snake has now consumed much of the islands native mammals, birds and lizards.

The examples mentioned above are but a few of the tens of thousands of exotic animals and plants introduced into the US. Pimentel et al. (2000) estimated that 50,000 new animal and plant species have been introduced at a cost of \$137 billion per year to manage, control, and eradicate. These numbers are expected to continue to increase with no foreseeable decrease. Human activity is the primary cause of these new animal and plant introductions around the world. Global economy and world trade are major influences that promote spread of invasive species. A much more recent world phenomenon (e-commerce and the intemet) is also playing a major role in spreading exotic species with the simple click of a computer mouse (Walters et al., 2005). Much of the e-commerce trading in exotic species goes on unregulated and invasive species move quietly around the U.S. and the world via the U.S. Postal service and other private shipping companies (Walters et al, 2005). Detrimental human activity that can also promote spread of exotic animals includes modification of natural landscapes. Habitat fragmentation can produce an ideal situation for invasives by creating new habitats that can benefit spreading of biological invaders (Harris and Silva-Lopez, 1992).

Invasive Terrestrial Gastropods

Invading gastropods have many routes to gain entry into a new area. The introductions can be deliberate or accidental and the majority of times the introduction has been anthropogenic. Cowie (2005) reviewed several modes that can lead to introduction of gastropods and lists six routes that can be used for deliberate introduction of land and aquatic gastropods to new areas: (1) aquarium industry to be sold as pets, (2) food industry to consume as a food source, (3) medicinal purposes, (4) as a biological

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control for other snail species, (5) for aesthetics and their remarkable appearances, and (6) for biological research and experimentation. Cowie (2005) also lists many routes for the accidental introduction of land gastropods to new areas, as hitchhiker's on agricultural products, horticultural products, commercial and domestic shipments, military shipments, soil, aquarium industry, aquaculture, ships and boats, and airplanes. It is not known what effect many of these land gastropods have had once they are introduced to new areas because they frequently go unnoticed for great lengths of time, there are not enough trained malacologists studying them and land gastropods can be misidentified leading to confusion which retards any control strategies that could be implemented (Robinson and Slapcinsky, 2005). Preventing introduction is also crucial in stopping invaders from becoming established. Cowie (2005) called for better quarantine strategies, pre-entry regulations and screening, and establishing a rapid response to eradicate new populations of invading land snails as a way to prevent establishment and spread of an invader.

Over 80 species of land gastropods have been introduced to the continental U.S. and Canada including seven recent introductions of serious land gastropod pests (Robinson and Slapcinsky, 2005). Seven recently introduced non-native snails by site of introduction are: (1) Beckianum beckianum Pfeiffer, 1846 (Broward County, Florida); (2) Paropeas achatinaceum Pfeiffer, 1846 (Palm Beach County, Florida); (3) Bulimulus tenuissimus pueIlaris (Orbigny, 1835) (New Hanover County, North Carolina); (4) Ovachlamysfulgens (Gude, 1900) (Broward County, Florida); (5) Monacha cartusiana (Muller, 1774) (Newcastle County, Delaware); (6) Monacha syriaca (Ehrenberg, 1831) (Brunswick County, North Carolina); and (7) Xerolenta obvia (Menke, 1828) (Detroit,

Michigan). These species came from Southern Europe, Central and South America and were most likely brought in accidentally by shipping containers (Robinson and Slapcinsky, 2005).

Some introduced gastropods can have impact beyond the environment, posing serious health risks to humans as the intermediate hosts to infectious agents. The giant African land snail, Achatina fulica (Bowdich, 1822), is native to Kenya and since the $18th$ Century it has spread around the globe (Smith, 2005). This species is an intermediate host to the rat lungworm, *Angiostrongylus cantonensis* (Chen, 1935), which can cause a serious disease (eosinophilic meningoencephalitis) in humans if raw and undercooked snails are eaten (Waugh et al., 2005). Achatina fulica also carries the bacterium, Aeromonas hydrophila (Chester, 1901), which can cause osteomyelitis, septic arthritis, tonsillitis and meningitis in humans (Smith, 2005). Achatina fulica was deliberately introduced into Florida in 1966 by a young boy returning from Hawaii where it was also an invader. The Florida population was eradicated in 1975, but at a cost of \$700,000 and seven years of eradication work (Smith, 2005).

Aside from being an intermediate host for infectious agents A. fulica is also a serious pest species. It has been documented that A . fulica will eat over 500 different plant species (USDA-APHIS, 2005). Achatina fulica was introduced to Hawaii in 1936, becoming established, and consuming indigenous plant species (Cowie, 2005). In an attempt to control and eradicate A . fulica in Hawaii many carnivorous land snails were introduced to eat this snail species. Of the carnivores introduced Euglandina rosea (Ferussac, 1821) became established and is now consuming the native and threatened Hawaiian tree snails, Achatinella spp., instead of the target organism, A. fulica (Hadfield

et al., 1993).

Management of introduced gastropods includes eradication and control strategies (Barker, 2002; and Cowie, 2005). If an introduced exotic species is detected early enough, it may be possible to eradicate them before they become established. For example, a population of *Achatina fulica* was discovered in California in the 1940's and because it had not yet established as population, it was successfully eradicated from that area (USDA-APHIS, 2005).

Achatina fulica has been reported in 9 states throughout the Midwest and eastern United States, but no populations have become established and all introductions have been eradicated (USDA-APHIS, 2005). *Achatina fulica* was sold in the U.S. as a pet and for biological research. The USDA began controlling A. fulica in 2004, and the last cohort was found and removed from Michigan by the USDA on September 28, 2004 (USDA-APHIS, 2005). It is now illegal to own or possess Λ . fulica in the U.S. without a government issued permit. The story of A. fulica demonstrates what can go wrong when a new invasive species is introduced and little is known about its natural history.

It is not currently known what impact the exotic invader Cepaea nemoralis (Linnaeus, 1758), is having in North America because no research has yet been performed. It has been ignored as a pest by the USDA-PPQ and is considered established in the US. (Sullivan et al., 2004). Dr. W. G. Binney, an English malacologist, first introduced C . *nemoralis* into the U.S. in 1857, at his home in Burlington, New Jersey (Reed, 1964). Dr. Binney imported the snails from England to release in his private garden for reasons that were purely aesthetic. It is interesting to note that Binney himself declared "The whole town is full of them now", only eight years afier their introduction

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(Reed, 1964). Twenty-two years later a second population of C. nemoralis was found in Lexington, Virginia, and was reported by Pilsbry in 1889 (Reed, 1964). This second population of Cepaea was introduced from Italy for unknown reasons. Since its introduction it has spread throughout the United States and Canada.

The most complete list describing the occurrence of C. *nemoralis* in North America was complied by Reed (1964), which reported the snail in 17 states (California, Colorado, Indiana, Kentucky, Maryland, Massachusetts, Missouri, New Jersey, New Hampshire, New York, Ohio, Pennsylvania, Rhode Island, South Carolina, Tennessee, Virginia, and Wisconsin) and from Ontario and Quebec, Canada. As of 1964, C. nemoralis had not been reported in Michigan, it is not known when this species was first reported in this state. To date, C. nemoralis, in Michigan, has only been officially reported from Ingham, Lapeer and Sanilac Counties (MSU-1PM, 2001). Anecdotal reports have also placed this organism in Presque Isle, Gratiot, Oakland and Wayne Counties Michigan.

In Germany C. *nemoralis* has been reported as a pest species from agricultural areas and grasslands (i.e. beets, spring grain, clover, and lucem), gardens and greenhouses (i.e. kidney bean, chicory, cucumber, pumpkin, and spinach), viticultures and omamentals (i.e. black currant, apple, pear, grapevine, monks hood, and jimson weed), and by forest managers on trees (i.e. beech, alder, larch, and poplar) (Godan, 1983). Cepaea nemoralis has been reported as a pest in raspberries and black currant in England (Godan, 1983). Other countries that recognize C. *nemoralis* as a pest species are Belgium, Canada, France, Portugal, Russia, Spain, Sweden, and the United States (Godan, 1983, USDA, 1959).

Martinson (1999), reported C. nemoralis as a vineyard pest in Ontario, Canada. It was found during this study that the snail fed superficially upon grapevines and seemed to use them as a daytime roost. The snail became a problem when it was picked accidentally with grapes and fouled the product being produced (wine). Martinson also indicated that California citrus producers easily control C . *nemoralis* by girdling trees with copper foil, which creates a barrier the snail seems unable to traverse. In Michigan, C. nemoralis has been reported as a pest species in a private flower/vegetable garden and hay field in Lapeer and Sanilac Counties (MSU-1PM, 2001).

Ehrlich (1986) listed eight characteristics which are important for invasion of a novel habitat by a terrestrial, exotic species, and they are: (l) numerous and abundant in original range; (2) polyphagous diet; (3) short generation times; (4) high degree of genetic variation; (5) females are able to colonize after fertilization; (6) physically larger than other related species; (7) human association; and (8) wide tolerance for different environments. *Cepaea nemoralis* is (1) numerous and abundant in Western Europe; (2) has a polyphagous diet; (3) fertile individuals (snails are hermaphroditic) are able to colonize new areas; (4) has a high fecundity and can mate multiple times during the spring and summer seasons; (5) has a high degree of genetic variation; (6) is larger than most other snail species; and (7) is associated with humans. Ehrlich (1986) suggested that a species possessing one or more of these characteristics would be a candidate to become a 'good' biological invader. *Cepaea nemoralis* possesses seven of these eight characteristics making it a good candidate for an invasive species. This snail species also has a propensity to survive at high population densities. In summary, all of these natural history traits make C. nemoralis an ideal invasive species and it should be subjected to

further investigation here in Michigan and elsewhere.

Terrestrial gastropods face challenges to dispersal that other animal taxa are often better at overcoming. These challenges are closely tied to the physical conditions of the environment (temperature and humidity). Because of this, very little attention is often paid to their short-distance dispersal. Terrestrial gastropods are thought to have poor dispersal capabilities because they are stereotyped as being very slow and not capable of traversing great distances on their own. In contrast, animals that are considered to have good dispersal capabilities are mammals, birds, reptiles, amphibians, fish, insects, and plants. Animals that can run, walk, hop, crawl, fly, swim or release seeds to be transported by wind or water they are usually considered as having greater dispersal capabilities than an animal that glides over a trail of mucus. Human mediated longdistance dispersal of gastropods is very important for their dispersal.

Shigesada and Kawasaki (2002) suggested that it is imperative to collect detailed statistical data on dispersal and natural history of the invader to understand how it will spread. No attempt has ever been made to quantify the spread of or dispersal capabilities of C. nemoralis in North America. The most likely means of C. nemoralis long-distance dispersal is anthropogenic and passive making its association with humans a very important characteristic. It is vital to understand how this species will disperse naturally. Since it is very likely that the presence of C . *nemoralis* will remain unnoticed in many areas within the US. it is important to have data on its short-distance dispersal so when populations are found managers can determine how it will spread. Being ignored could allow C. nemoralis to slowly spread over large areas becoming further established and more difficult to eradicate. If managers remain complacent towards C. nemoralis this

species could become the proverbial time-bomb and explode as a pest species.

Once invading gastropods become established they can have serious impact on the environment, human health, and cost millions to control and manage. While there are no current dollar estimates for the impact these invading gastropods have had, the overall impact of non-native Species has been staggering. This species should still be treated more seriously as an invasive species and its spread should be controlled through eradication programs.

CHAPTER 2: NATURAL HISTORY OF CEPAEA NEMORALIS

INTRODUCTION

The banded wood snail, *Cepaea nemoralis*, is a pulmonate land snail and can be found in a wide range of terrestrial habitats. It currently has a Palaearctic and Nearctic distribution and native to Western Europe. Cepaea nemoralis was introduced to North America in 1857 (Reed, 1964). This species is highly polymorphic and perhaps best known from field studies of natural selection by Arthur Cain and Philip Sheppard, at Oxford University, in the 1950's (Cain and Sheppard, 1954). Cain and Sheppard attempted to explain the selective force(s) responsible for maintaining a balanced polymorphism of banded and non-banded shells within European populations of C. nemoralis. Cepaea nemoralis has also been regarded as one of the most damaging pest land snail species known. In Europe, C. *nemoralis* is responsible for causing much damage to the plants commonly associated with greenhouses, gardens, viticultures, omamentals, grasslands, forests, and in agriculture (Godan, 1983). In North America it has been reported as ^a pest from the vineyards of Ontario, Canada and Upstate New York, and from the citrus producers of California.

Description

Cepaea nemoralis is placed in the Family Helicidae, a group of medium to large size snails. The shell of C. nemoralis is known to have several different background colors (yellow, red, pink and olive). As the name implies, the shell will usually have dark brown or black bands. However, in some individuals these bands may be absent, if present they can vary in number from between one and five. Adult snails have a reflected lip around the shell aperture which is also dark brown in color. Shell shape is sub-

globose, imperforate, with aperture ovate-lunate. The adult shell will usually consists of 5 whorls and ranges from 18 — 24 millimeters in diameter (Backeljau et al., 2001; Burch, 1962; and Goodhart, 1962).

Reproduction

Cepaea nemoralis is simultaneously hermaphroditic with cross-fertilization. Mating between conspecifics is random, and multiple mating between different individuals has been observed in a single mating season (Heller, 2001; and Murray, 1964). Cain and Currey (1968) reported that juvenile snails usually require two years to reach reproductive maturity which is indicated by the reflected lip of the adult shell. In the United Kingdom, C. nemoralis will lay eggs in early June with hatching in late June and early July (Cain and Currey, 1963). Cepaea nemoralis is known to store sperm for very long periods and any clutch of eggs produced could be the product of many matings with different individuals (Murray, 1964). Eggs are laid in clutches, numbering up to 90, and are buried just below the soil surface (Baur and Baur, $1993a$). It may take up to 36 hours for an individual to produce one clutch (Wolda, 1967). These eggs can develop and hatch within $2 - 3$ weeks depending on environmental conditions. Eggs are oval and measure 3.2 x 2.7 mm (Baur and Baur, 1993a). In Michigan, C. nemoralis has been observed copulating and laying eggs as early as May and has been seen to mate at least twice per year (pers. obs.). *Cepaea nemoralis* can live up to 7 years in the wild (B. Baur, pers. comm), possibly producing 900 eggs or more in their lifetime.

Habitat. Diet and Food Preference

Cepaea nemoralis is common in numerous habitat types, ranging from softwood forests, sand dunes, grasslands, meadows, hedgerows, gardens, nettle patches, orchards,

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and vineyards (Cain and Currey, 1968; Chang, 1991; Godan, 1983; Goodhart, 1962; and Richardson, 1975). In Europe it was reported that this species is crepuscular, foraging and feeding is generally nocturnal, while movement is limited during diurnal periods (Cain and Currey, 1968; Martinson, 1999; and Speiser, 2001).

Williamson and Cameron (1976) reported that C. nemoralis, in the United Kingdom, will feed on most plant material, however, it seems to prefer dead and senescent herbs. Dead plants become softer and more palatable, while living plant tissue had a harder external surface and an unfavorable taste (Williamson and Cameron, 1976). These authors also found that herbs were preferred over grasses. They showed that herbs compared to grasses contained more calcium and other essential minerals when compared to grasses. These nutrient rich herbs would be important for shell maintenance and growth. Richardson (1975), and Wolda et al. (1971), in Europe, indicated that C. nemoralis preferred dead and senescent plant material to living plants. It is interesting that Richardson (1975) reported that C. nemoralis, from sand dunes, were not selective with regards to herbs and grasses.

Chang (1991), in North America, reported C. nemoralis were very selective when choosing food. This author reported that of the twenty plant species, collected from habitats where C. nemoralis was found, ten (50%) were rejected when offered to individuals within the laboratory, interestingly these ten plant species were the most abundant. Chang (1991) also found that grasses were not accepted as food, and herbs were preferred, which is similar to the finding of Williamson and Cameron (1976). Shell Polymorphism

Cepaea nemoralis is perhaps best known for its highly polymorphic Shell patterns.

In fact, the majority of studies published on this snail species explore the environmental and genetic nature of this balanced polymorphism within and between populations of C. nemoralis in both North America and Europe (Arnold, 1969; Brooks and Brooks, 1934; Brussard, 1975; Brussard and McCracken, 1974; Cain and Currey, 1963a, 1963b and 1968; Cain et al., 1990; Cain and Sheppard, 1950 and 1954; Cameron, 1992; Clarke and Murray, 1962; Cook, 1998; Cook et al., 1999; Currey et al., 1964; Davison, 1999; Davison and Clarke, 2000; Diver, 1939; Goodhart, 1962; Heath, 1975; and Ozgo, 2005a).

Interpopulation variation is commonplace, in regards to color morphology and number of bands present with C. *nemoralis* (Backeljau, 2001; Cain and Sheppard, 1954; Currey et al., 1964; and Goodhart, 1962). Many different theories have been proposed to explain the variation that occurs in wild populations. It was originally theorized that the interpopulation variation that occured within small populations of C. nemoralis was caused by genetic drift of non-adaptive genes 'Sewall Wright effect', thus, demonstrating that selection was not involved (Diver, 1939). It was later theorized that visual selection of a predator caused interpopulation variation (Cain and Sheppard, 1954). More specifically, that the primary selection pressures are the song thrush, Turdus ericetorum Turton, 1807, and missel thrush, T. viscivorus (Linnaeus, 1758) (Cain and Currey, 1968; Cain and Sheppard, 1950 and 1954; and Currey et al., 1964). Cain and Currey (1963) later proposed that visual selection alone could not explain this variation. These authors further suggested that 'area effects' or strong environmental forces, that were then unknown, were involved. Climate, and its ability to change topography, has also been implicated as a selection force (Arnold, 1969; Cameron, 1992; and Heath, 1975).

The current theory is that habitat is responsible for inter- and intrapopulation

variation (Ozgo, $2005a$ and $2005b$). Ozgo was able to identify some of these 'area effects' that eluded Cain and Currey in 1963. Ozgo, in Poland, demonstrated that habitat type is the definitive selection force, and that banded C . *nemoralis* are found more often in woodland habitats and that non-banded C. nemoralis are found in grassland and more open habitats. The theory is that banded individuals are more susceptible to over heating in grassland habitats where the radiant energy is greater and the dark bands cause the shell to absorb more solar radiation. Further, non-banded individuals are less likely to overheat in grassland habitats due to the absence of dark shell pigmentation and lighter overall shell color. In general open habitats are less humid and have higher temperatures while shaded habitats are more humid and have lower temperatures (Ozgo, $2005a$ and $2005b$).

The current study quantified the dispersal capabilities of C. *nemoralis* in two very different habitats. One habitat was considered to be 'high quality' and was the epicenter of this established C. nemoralis population. The other habitat was considered 'low quality' and was adjacent to the high quality patch. If this population of C. *nemoralis* was to spread naturally to the south and west individuals would have to traverse across this sub-optimal patch. Control of C. *nemoralis* may become necessary if it were to spread; therefore ^a control method was also tested. A commercially available molluscicide (Sluggo® - iron phosphate) was used to test its usefulness at controlling a large, established population of C. *nemoralis*. The molluscicide, iron phosphate, was chosen because it is environmentally friendly and it is not a broad spectrum poison and targets only molluscs (USEPA, 2005). This study also evaluated the efficacy of using harmonic radar as a method to track terrestrial snails. Along with population dynamics

and distribution data this research is intended to provide insight into the natural dispersal, spread, and control of an exotic, invasive, and pest land snail species.

CHAPTER 3: USING HARMONIC RADAR TO TRACK CEPAEA NEMORALIS **INTRODUCTION**

Harmonic radar (HR) was developed in Switzerland and was first introduced in 1983 as a tool designed for detection of persons caught in an avalanche (www.recco.com). An individual person carries a 'reflector' or transponder which is integrated into their clothing or safety equipment. If an avalanche event occurs then it is possible for rescue workers to locate victims buried under snow using an HR transmitter/receiver. Range of detection is contingent upon transponder size (diode and antenna length). Transponders used for rescue purposes can be detected from a distance of several miles.

HR technology is ideal for tracking invertebrates due to the small size transponders that can be built. In comparison, using a radio transmitter is not practical with most invertebrates because transmitters are too large and heavy. It is possible, however, to construct very small and lightweight HR transponders ($\sim 10^{-3}$ g) that can be attached to almost any macroinvertebrate. Mascanzoni and Wallin (1986) were the first to use HR technology for the tracking and detection of invertebrates (e.g. ground beetles). HR technology has been used to track bumble bees, butterflies, caddis flies, honey bees, land snails, moths, various dipterans, various ground beetles, and weevils (Carreck et al., 1999; Brazee et al., 2004; Lovei et al., 1997 and 2003; O'Neal et al., 2004; Riley et al., ¹⁹⁹⁸ & 1999; and Roland et al., 1996). Lovei et a1. (1997) were the first to use HR to track the movements of a land snail, Paryphanta busbyi watti Powell, 1946, in New Zealand. What makes HR ideal for tracking otherwise cryptic invertebrates in their natural environment is that it affords a high degree of tracking success with little

disturbance to their habitat.

Traditionally, 'mark and recapture' (MR) techniques have been employed to track invertebrates. MR is ^a visual survey that requires going into the animals' environment for prolonged periods in order to relocate marked individuals and potentially disrupting the habitat. MR is useful for determining population size and estimating the rate of immigration and emigration in an animal population. The most commonly used method for determining dispersal in land snails has been by using MR. The usual MR snail method is conducted by marking individuals with nail polish, paints or dyes and releasing them at a given starting point or at the place of capture, finding and recapturing them at a later time, and then measuring the distances moved from that point over a period of time (Cameron and Williamson, 1977; and Baur and Baur, 1993b) These MR methods, while useful, do have limitations: (1) low recapture rates; (2) intrusive human movement in and out of the snails natural environment; and (3) repeated sampling done over longer time intervals can give a false idea of how snails actually move in their environment. As ^a result the traditional MR methods are not very useful for determining dispersal.

HR is ^a tracking technique that allows the user to accurately track an organism in their natural environment with minimal disturbance. Direct measurement of dispersal can be done on a daily, weekly or seasonally. The current study is the first attempt to measure land snail dispersal on a daily and weekly basis using harmonic radar. The objective of this study were to calculate tracking success using HR techniques and compare these findings to other studies that have used traditional method of mark and recapture to relocate terrestrial snails, and to determine HR limitations.

MATERIALS AND METHODS

The study site was located in Ingham County, Michigan (42°36.790'N 84 \degree 27.460'W) and is privately owned. Tracking of C. nemoralis was performed in a favorable habitat (Snail Central) and in an unfavorable habitat (South Field). For a complete description of these habitats please refer to Chapter 4 Materials and Methods. Harmonic Radar

HR employs the use of ^a hand-held RECCO transmitter/receiver (RECCO Rescue Systems, Lindingo, Sweden, www.recco.com) that transmits microwaves with a frequency of ⁹¹⁷ MHz. Two different types of HR tags (transponders) were used in this study. The monopole (single wire) transponder was composed of two parts: (1) a Schottky barrier diode (weight = 0.0046 g); and (2) a Teflon coated aluminum or iron wire (Omega Engineering Inc., www.0mega.com) of 0.10 mm (aluminum) or 0.25 mm (iron) diameter and ⁸ cm in length. The dipole (double wire) transponder used the same diode, mentioned above, but consisted of ² wires (0.25 mm diameter), both ⁴ cm in length, with the diode attached between them. The transponder receives power from the microwave signal transmitted by the RECCO unit, the diode in turn doubles the frequency of the signal to that of the harmonic $(1,834 \text{ MHz})$ which is then sent back to the RECCO unit and converted to an audible beeping sound. The exact location of HR tagged snails is determined by the intensity and direction of the audible signal.

In 2003 a total of 17 (15 adult and 2 juvenile) C. nemoralis were collected from the study site. In 2004 and 2005 a total of 40 adult (20 in 2004, and 20 in 2005) C. nemoralis were also collected from the study site and taken to Michigan State University for HR tag attachment. The shells of collected snails were cleaned with ^a cotton swab dipped in isopropyl alcohol and then wiped dry. HR tags were then glued to the surface

of the cleaned shell using superglue (Loctite Precision Super Glue®) and a small bead of hot glue was then placed over the diode to help water proof and protect the diode from damage. Nail polish was used to give each snail a unique identification code. To test the usefulness of different style transponders one snail (in 2003) and eight snails (in 2004) were tagged with dipole HR transponders. Snails were returned to the field the following day and placed at the same location they were captured in 2003 or placed in either SC or SF in 2004 and 2005. At the time of tracking the RECCO unit was held in hand and turned clockwise and counter clockwise while sweeping it up and down and from left to right in front of the user. This method maximized the detection ability of the RECCO unit because the transponder will only work when receiving microwaves that are parallel to the wire antenna.

Daily dispersal was tracked over a 14 day period from May 18-31st, 2003 in the SC, and from June 5-18th, 2004 and June 8-21st, 2005 in the SC and SF. Weekly and biweekly dispersal was tracked from May — September 2003 and June — September 2004. If snails were found dead they were removed from the study area. The tracking success rate indicates the percent of C. nemoralis that were successfully tracked and found on subsequent days and weekly collecting intervals. Therefore a tracking success rate of 75% would indicate that 75% of the snails tracked were recovered.

RESULTS

Pilot Study 2003

Seventeen C. nemoralis were tracked daily from May $18-31st$ and then weekly and bi-weekly from May — September 2003. The daily tracking success rate was 74.6%. Of the individual snails a total of 5 individuals were tracked 100% of the time, and ³ were

tracked successfully 93% of the time. The weekly tracking success rate was 40.2%. The ^l snail tagged with ^a dipole HR transponder had ^a daily tracking success rate of 100%. During this period ^a total of ² snails had dropped their HR tags and ⁴ had been killed presumably by predators because the shells were either crushed or broken; a common indication of a predator.

2004

Twenty C. nemoralis (10 SC (Snail Central) and 10 SF (South Field)) were tracked daily from June 5 -18th and then weekly and bi-weekly from June – September 2004. The tracking success rates in the SC and SF were 77.1% and 91.5%, respectively. Of the individual snails in SC a total of ⁵ individuals were tracked 100% of the time and in SF a total of 9 individuals were tracked 100% of the time. The weekly tracking success rates for SC and SF in 2004 were 43.6% and 51.8%. In SC a total of 5 snails were tagged with dipole HR transponders and they had daily tracking success rates of 100%. In SF ^a total of ³ snails were tagged with dipole HR transponders and they had ^a daily tracking success rate of 100%. During this study 3 snails died in SC and ¹ snail died in SF.

2005

Twenty C. nemoralis (10 SC and 10 SF) were tracked daily from June 8-21st, 2005. The daily tracking success rates in SC and SF were 89.8% and 100%, respectively. Of the individual snails in SC a total of 4 were successfully tracked 100% of the time and in SF a total of 10 were successfully tracked 100% of the time. During this study ¹ snail died in SC and 5 snails died in SF.

Radar signals from dipole HR tagged snails could be detected from as far away as
¹⁰ m; monopole HR tagged snails could be detected up to ² m. In ²⁰⁰³ and 2004 the individual snails fitted with the dipole transponders were much easier to relocate and had individual recapture rates of 100% during the daily recapture studies. Snails could be located if they were buried $2 - 3$ centimeters in the soil. Several HR transponders were found in following years still attached to a broken shell and buried in the soil. In some cases it was found that if the wire antenna became bent or crimped the detection distance was greatly reduced to less than ¹ meter. Some animals became hung up on vegetation if they were tagged with a dipole transponder. It seems that the diode hanging off of the animal free in space can catch on vegetation. This finding however was rare. In earlier work done in 2003 hot glue was used to join the diode to the shell and in all cases this failed and the transponders fell off within $1 - 2$ days. Super glue was found to work much better at joining the HR tags to the shell and in no cases did an HR tag ever fall off using super glue.

At times no signal could be found for some of the snails even after a thorough search of the study site. In most cases the snail was relocated the following day within a few meters from where it had been located previously. It was concluded that many of these snails were climbing into the tree canopy and became undetectable using HR. If these snails climbed high into the tree canopy they would be nearing the limit of detection for the HR and in essence disappear from the study area. Even when transponders were placed in trees several meters off the ground it was very difficult to get any type of positive signal. This may be due to the angle at which the user is to the transponder. It is essential for the HR user to become parallel to the transponder in order to obtain ^a strong signal from the HR tag.

DISCUSSION

The tracking success in this study was much higher than the recapture rates reported from studies on other land snail dispersal. Goodhart (1962) captured and released 200 adult C. nemoralis, in England. Snails were then recaptured after 4 weeks, ¹³ weeks, and ¹ year. This author calculated his recapture rates to be 66.5%, 54% and 41.5% after 4 weeks, 13 weeks, and ¹ year, respectively. Lamotte (1951) worked with C. nemoralis, in France, from two different habitat types, garden and herb meadow. In the garden habitat 20 C. nemoralis were marked, released at a central point, and recaptured after 2 years. In the herb meadow 200 C. nemoralis were marked, and recaptured after ⁵ months. The garden and herb meadow the recapture rates were 4%, and 15%, respectively. Schnetter (1951) performed a mark-recapture study on C. nemoralis, in Germany, from two different habitat types, uncultivated meadow and scattered brushes. In the uncultivated meadow 100 snails were marked, released at a central point, and recaptured after 6 months. In the scattered brushes 100 snails were marked, and recaptured after 2 years. The recapture rates of snails, for both habitat types, were 13%.

Baur and Baur (1990) tracked the movement of 807 marked Arianta arbustorum (Linnaeus, 1758), in Switzerland, after one month and 3 months. They reported recapture rates after one month and three months as 29.4% and 28.1%, respectively. Further, Baur and Baur (1993b) tracked the daily movements of A. arbustorum in a clearing for 16 consecutive days, and in a vegetative belt 10 months after release, they reported recapture rates of 47.5%, and 42%, respectively.

The snail tracking success rates of C. *nemoralis* in this study are the highest ever reported. In this study the daily tracking success rates ranged from 74.6% - 100%. In most scenarios all the snails could be found within ² hours, demonstrating that HR is ^a very good method by which to track terrestrial snails. Very little time was spent in the animal's habitat and thus little damage was done.

Harmonic radar does appear to have some limitations. In the rain it was difficult to obtain a true positive signal and much of the 'noise' heard by the user was a falsepositive signal. A fair amount of noise was added because of the falling rain drops, which are reflecting the radar signals and sending ^a false signal back to the receiver. HR was not of much use if it was raining at the time of tracking. It was difficult to obtain a signal from snails that had climbed into the tree canopy. This was probably the result of the dense leaf canopy which impeded the HR signal, snails moving beyond the range which the receiver could obtain a signal from the transponder, and the HR user not being able to get in a parallel position to the transponder.

It was reported that HR was not very useful for tracking carabid beetles because of several problems (O'Neal et al., 2004). O'Neal reported that beetles ofien became hung up on vegetation and seemed to lack the physical strength needed to remove themselves from the obstructions. Also, these authors had problems with HR tags falling off the beetle elytra. This may be due to the use of hot glue and not super glue to join the HR tag to the animal's surface. In this study when hot glue was used to join the HR tags to the shell, all of them fell off within $1 - 2$ days. However, when super glue was used, the HR tags no longer fell off. Similar to what was found in this study O'Neal reported that when the wire became bent the detection distance was greatly reduced. In 2005 all HR tags were built with ^a much thicker (0.25 mm) wire and this seemed to reduce wire bending because it was much more rigid. O'Neal reported less success with a thicker

inflexible wire, but this was not the case when tracking snails in this study.

Even though harmonic radar has some minor limitations it offers a very effective method to track daily and weekly dispersal of land snails in a very detailed manner. This method permitted the precise measuring of land snail movement with minimum disturbance to their natural environment. Cameron and Williamson (1977) reported that direct measurement of snails within their natural environment is difficult because it requires continuous detailed mapping and frequent sampling. While the frequency of sampling may not decrease with HR, the amount of time spent in the environment does. Precision of relocation, with minimum disturbance, made it possible to correlate movements of land snails to a range of biotic and abiotic factors at the level of microhabitat. HR will also prove useful for obtaining accurate dispersal distances achieved by land snails, which could potentially impact how we control and manage invasive land snail Species as well as conserve habitat for threatened and endangered species.

CHAPTER 4: DISPERSAL, POPULATION DENSITY AND DISTRIBUTION OF CEPAEA NEMORALIS

INTRODUCTION

To become a successful invader, an organism must (1) move to a new location; (2) establish a viable population; and (3) disperse from that locality (Mack, 2000; and Shea and Chesson, 2002). How an organism spreads is ^a function of its dispersal capabilities. Whether it establishes a viable population in a new area is a function of how it responds to niche opportunities. The niche opportunities found in a new area are greatly influenced by resource availability, natural enemies, and the physical environment (Shea and Chesson, 2002). These three factors will also affect the invaders ability to disperse beyond its established new location.

Dispersal is the capacity of an individual animal to move from the place of its origin to new areas or away from centers of population density (Stiling, 1996). This is an ecological process and selection tends to favor those individuals that move away from their birthplace, and away from parents and siblings and thus utilize resources with less competition from conspecifics. There are two types of dispersal; (l) long-distance, and (2) short-distance. In their review of dispersal Shigesada and Kawasaki (2002) describe the two types and introduce a useful terminology. Long-distance dispersal can be thought of as rare, stochastic, and mediated by passive transport. Passive transport is facilitated by naturally occurring phenomenon such as storms, water flow, rafting, and wind, as well as agents such as other animals and humans (i.e. husbandry, cultivation, modification of natural barriers, building of corridors, fragmentation, and commerce (Cohen, 2002; Glassner-Shwayder, 1998; Harris and Silva-Lopez, 1992; and Mack et al., 2000)). Shortdistance dispersal occurs when offspring leave the area where they were born. This form of dispersal depends upon the organisms own ability to move (i.e. walking, flying, gliding, swimming, hopping, creeping, etc.). Land snails are often thought to have poor short-distance dispersal capabilities (Heller, 2001). This long standing viewpoint of land snail dispersal may be a reflection of the methodology used to determine snail dispersal. It may also reflect stereotypes that snails are slow moving animals randomly wandering through an environment.

It is essential to understand dispersal and life history of an exotic and invasive animal if one wants to understand the rate at which it could potentially spread (Shigesada and Kawasaki, 2002). Everything that is known about C. nemoralis dispersal has come from a few published reports in Europe (Cain and Currey, 1968; Cameron and Wilson, 1977; Goodhart, 1962; Greenwood, 1974; Lamotte (1951); and Schnetter (1951)). Interestingly, the dispersal of C. nemoralis has never been reported in North America where this species is an exotic invader. While these European reports are useful, they may seriously underestimate the dispersal capabilities of C. *nemoralis*. The mark and recapture methods by which the dispersal was estimated in these studies are not accurate because of low recapture rates. In addition, the time intervals between recapture events are often very long, even exceeding one to two years. To truly understand dispersal of C. nemoralis it is necessary to track this organism over shorter time intervals (one day) to reveal the subtle movements that are overlooked when snails are recaptured monthly or yearly.

The population of C. *nemoralis*, established in Ingham County, Michigan, is growing and most certainly viable. This population appears to have vast resources available with regards to food and Shelter. Also, the physical environment (temperature and humidity) which plays a vital role in affecting niche opportunities for this population are also ideal. All land gastropods glide on a layer of mucus in order to move. It is also very costly for the gastropod to produce mucus. Mucus is approximately 96 — 97% water and the more mucus a land gastropod produces the more water it will lose (Baur and Baur, 1990; and Denny (1980)). Williamson and Cameron (1976) found that C. nemoralis will use 15% of the energy it acquires from food to produce mucus. When physical conditions are not ideal C. nemoralis will become inactive and cease movement so they can preserve valuable resources otherwise lost in mucus production (Cameron, 1970). This physiological dilemma could influence use of niche opportunities available to C. nemoralis and decrease its rate of dispersal.

Baur and Baur (1993b) defined dispersal for a land snail to be "the distance traveled by a snail in its daily activity during periods longer than one day". Cepaea nemoralis, and land snails in general, maintain a very intimate relationship with the temperature, humidity, and habitats through which they move. To date no research has been conducted using C. *nemoralis* to investigate the relationship among dispersal, temperature, humidity and habitat on a daily basis. One explanation for this lack of research has been that technology has never offered a means to track land snails accurately and consistently. Currently a new method, harmonic radar (HR), is being used and developed to track land snails and other invertebrates (Carreck et al., 1999; Brazee et al., 2004; Lovei et al., ¹⁹⁹⁷ and 2003; O'Neal et al., 2004; Riley et al., ¹⁹⁹⁸ & 1999; and Roland et al., 1996) (For ^a complete review of HR please see Chapter 3).

The objectives of the study are to (1) use HR to track the dispersal of C.

nemoralis in two distinct habitats and to investigate the relationship between dispersal, temperature and humidity within each habitat; (2) measure the population density and demographics to determine if this population is expanding; and (3) survey outlying areas for C. nemoralis to ascertain its spread from the source population.

MATERIALSAND METHODS

The Study Site and Habitat

The study site was located in Ingham County, Michigan (42°36.790'N 84° 27.460'W) and is privately owned. The site was ten acres in size and was subdivided into five distinct habitats designated as Snail Central, Blue Spruce, South Field, North Field, and Homestead. These designations were based primarily upon vegetation (Appendix A) and the mowing patterns of the homeowner (Figure 4.1). The total area $(m²)$ of each patch was approximated using aerial images obtained from the Michigan Department of Natural Resources (www.mdnr.gov) and analyzed with Geo Express Viewer with Mr. Sid® (www.1andsystems.com). The study area was formerly owned by a commercial plant nursery.

The habitat called Snail Central (SC) was located on the southeast portion of the site and was approximately 2,404 m^2 in area. A total of 25 plant species were identified in the SC (Appendix A). The SC had a closed canopy and the most abundant tree species was green ash, *Fraxinus pennsylvanica*; the most abundant herbaceous plant and ground cover was poison ivy, Rhus radicans. The SC is considered the source of this established population of C. nemoralis and is considered the 'high quality' habitat because of the dense vegetation in the herbaceous layer. This dense layer maintains high humidity levels at the surface of the ground which is favorable for land snail activity. The majority

of the soil surfaces in the SC receive no direct sunlight and most of the radiant energy of the sun is filtered by the tree canopy and dense herbaceous layer.

The habitat called Blue Spruce (BSp) was adjacent to and west of the SC and was approximately 4,882 m^2 in area. A total of 22 plant species were identified in BSp (Appendix A). The BSp had primarily an open canopy and the most abundant tree species was blue spruce, *Picea pungens*, and the most abundant ground cover was a mix of R. radicans and various grasses (Poaceae).

The habitat called South Field (SF) was on the southwest portion of the site and adjacent to the BSp and was approximately 23,734 $m²$ in area. A total of 20 plant species were identified from the SF (Appendix A). The SF had no canopy and the only tree present was F. pennsylvanica less than 2 meter in height. The ground cover of SF was primarily a mix of various grasses, herbaceous, and woody plants. The SF is considered the 'low quality' habitat because it lacks a tree canopy and does not have a dense herbaceous layer. It is also deemed low quality because of the population density survey of 2003. This type of habitat has the tendency to dry out during the day. Much of the soil surface is directly exposed to the radiant energy of the sun.

The habitat called North Field (NF) was on the northwest portion of the site and was adjacent to and north of SF and was approximately $4,851 \text{ m}^2$ in area. A total of 15 plant species were identified from the NF (Appendix A). The NF had no canopy and no trees were present, the ground cover of NF was primarily ^a mix of various grasses and herbaceous plants.

The habitat called Homestead (HS) was on the northeast portion of the site and was adjacent to and north of SC and BSp and was approximately $3,757 \text{ m}^2$ in area. A

total of 6 plant species were identified from the HS (Appendix A). The HS was comprised of a maintained lawn around the homeowner's house and had a partially closed canopy comprised of silver maple, Acer saccharinum. The yard was a mix of grasses.

Dispersal

Harmonic radar (HR) was used to track daily and weekly dispersal (in meters) of C. nemoralis over ^a ³ year period (For ^a complete review of HR and habitat types, see Chapter 3). The year 2003 was considered a 'pilot study' and was used to develop a methodology and to determine the efficacy of tracking land snails with HR. The years 2004 — 2005 were considered the definitive portion of the research which compared the dispersal of C. nemoralis in two different types of habitat called Snail Central (SC); and South Field (SF) - SC was considered to be 'high quality' habitat and SF was considered to be 'low quality' habitat.

In 2003 at total of 17 (15 adult and 2 juvenile) C. nemoralis were collected in SC. In 2004 and 2005 a total of 40 adult (20 in 2004, and 20 in 2005) C. nemoralis were collected in SC. Adult snails were chosen as the focus of this research because the shell is thick and the studies in Europe also examined the dispersal of adult snails. Juvenile C. nemoralis have very thin shells, especially in the early spring, and those Shells broke when the transponder was glued to the shell. All C. *nemoralis* were captured by hand and taken to Michigan State University for HR tag attachment. The shells of collected snails were cleaned with a cotton swab dipped in isopropyl alcohol and then wiped dry with tissue paper. HR tags were then glued to the surface of the cleaned shell using superglue (LOCTITE Precision Super Glue®). A small bead of hot glue was then placed over the

diode to help water proof and protect the diode from damage. Nail polish was used to give each snail a unique identification code.

HR tagged snails were placed at the location of initial collection in ²⁰⁰³ from SC. In 2004 — 2005 they were placed in either SC or SF at random starting positions; all starting positions were marked with a flag that corresponded to the unique ID on individual snails. Daily dispersal was tracked over a 14 day period from May $18-31st$, 2003 in SC, and from June 5-18'", 2004 and June 8-21", 2005 in SC and SF. Weekly and bi-weekly dispersal was tracked from May — September 2003 and June — September 2004. If HR tagged snails were found dead they were removed from the study area. When tracked snails were located the new position of the snail was marked with a flag and the distance (in meters) in a straight line from the previous day's location, and direction moved (compass degrees) between the initial collection point and the recapture point was determined. The percentage of time that C. nemoralis spent inactive (not moving) from one day to the next or from week to week was calculated for the dispersal studies in 2003 — 2005 in SC and SF. For the directionality data an individual snail could move north (between compass points $315^{\circ} - 45^{\circ}$); east (46^o – 134^o); south (135^o – 224^o); or west $(225^{\circ} - 314^{\circ})$ (Appendix B).

In 2003 the air temperature $({}^{\circ}C)$, taken approximately one meter above the ground, and the surface temperature, taken at the soil surface, were determined at the time of snail recovery using ^a hand-held thermometer. In 2004 — ²⁰⁰⁵ HOBO Dataloggers® were placed approximately 10 cm above the soil surface in SC and SF for the entire sampling season to collect temperature (°C) and relative humidity (%) at 2 hour intervals. The 'daytime' temperature and humidity was determined from the hours

between 7am and 7pm. The 'nighttime' temperature and humidity was determined from the hours between 9pm and 5am. The 'time of collection' temperature and humidity was determined from the 11am hour; a time when most tracking was conducted.

Population Density

During the late spring and early summer of 2003 the population density (number of snails/ $m²$) of C. nemoralis was determined for each habitat. At the time of sampling an individual habitat, a ball was randomly thrown over the shoulder, and at the location where the ball landed ^a hula hoop (WHAM-O®) was placed. The inside area of the hula hoop was determined to be 0.5 m^2 . All C. *nemoralis* within the hula hoop area were removed, placed into a plastic container, counted, and returned to the hula hoop area when sampling was completed. The entire area within the hula hoop (litter layer, herb layer, and shrub layer) was searched; trees were excluded. A total of 20 $m²$ (40 tosses of the hula hoop) was sampled within SC, SF, Bsp, NF, and HS.

This sampling method was also used to sample the population density of C. nemoralis again in the spring of 2005 for SC and SF only. In 2005 snails were identified as either an adult (presence of peristome lip) or as juvenile (peristome lip absent), the shell diameter was measured (mm), body color was noted (brown or yellow) and the number of brown bands $(1 - 5)$ on the shell were counted. Sampled snails were placed into 4 size categories based upon the shell diameter: (1) Adult ($>$ 20 mm); (2) large juvenile (15 – 19 mm); (3) medium juvenile (10 – 14 mm); and small juvenile (< 9 mm). Soil Chemistry

Soil samples were collected, using the protocol of the M.S.U. Soil and Plant Nutrient Laboratory (SPNL), in SC and SF for comparative purposes. Samples were

submitted to the M.S.U. SPNL for analysis of soil pH , calcium (Ca), phosphorous (P), potassium (K), magnesium (Mg), and nitrate-N.

Distribution

To determine the distribution of C. nemoralis in areas that surrounded the study site a survey of outlying areas was performed during the summers of 2003 - 2005. Roadway verges, public land and private property in the vicinity of the study area were surveyed. Surveyed areas usually were composed of habitat suitable for C. nemoralis and areas that could serve as ^a corridor for dispersal were also surveyed. A hunt-andpick method was used to survey for snails on the ground as well as looking for any sign of the snails on vegetation (fecal deposits), or empty and broken shells. The latitude/longitude or township/range information was recorded for all sites surveyed. Latitude and longitude was recorded using a hand-held GPS manufactured by Garmin®. When referencing the township/range a method was used to denote the 40 acre parcel of each section that was sampled. Each section denoted on a plat map is 640 acres. For this study each section was subsequently divided into four 160 acre quadrants, and each quadrant was divided into four 40 acre sub-quadrants. Therefore a notion such as 'Section 29 SW/SE' would indicate that the sample was taken in the southwest subquadrant of the southeast quadrant of section 29.

Statistics

For the data collected in 2004 — 2005, a general linear model (GLM) was used to find a relationship between dispersal (response variable - Y) and the temperature (predictor variable $- X_1$) and relative humidity (predictor variable $- X_2$) at the time of collection. The general a priori hypothesis for the GLM was $Y \sim X_1 + X_2$. A GLM was also used to examine the relationship between dispersal and temperature and to examine the relationship between dispersal and relative humidity. A Student's t-test was used to evaluate differences in the dispersal, temperature (daytime, nighttime and time of collection), and relative humidity (daytime, nighttime and time of collection) between SC and SF. Chi-square (χ^2) test of Independence was used to determine if snails moved in a particular direction within the SC and SF. The dispersal (meter), temperature (°C), and humidity (%) are expressed as a mean ± 1 standard error (SE). Statistical analyses were conducted using R v. 1.9.1 \mathbb{R} , Systat 11 \mathbb{R} , and EZ-Stat \mathbb{R} for Windows.

RESULTS

Dispersal

2003 Pilot Study:

A total of ¹⁷ (15 adult and ² juvenile) C. nemoralis were tracked from May — September 2003 in the SC (Appendix C). The mean $(\pm 1 \text{ SE})$ daily air and soil temperatures (°C) were 10.5 ± 1.1 and 13.0 ± 0.85 (Figure 4.2). The mean daily dispersal (meters) was 1.09 ± 0.085 (Figure 4.3). The maximum and minimum dispersal by an individual *C. nemoralis* in one day was 3.78 and 0.05 meter, respectively. The mean weekly air and soil temperatures were 23.4 ± 0.86 and 21.2 ± 0.93 (Figure 4.4). The mean weekly dispersal was 4.07 ± 0.99 (Figure 4.5). The maximum and minimum dispersal by an individual C. nemoralis in one week was 24.9 and 0.07 meter, respectively. During the 14 day trial C. nemoralis was found to disperse in a northerly and easterly direction in the SC (χ^2 = 13.341, d.f. = 3, p = 0.00395). Cepaea nemoralis did not disperse in a preferred direction during the weekly trial (χ^2 = 5.247, d.f. = 3, p = 0.1545). Two individual C. nemoralis crossed from SC into BSp during the weekly

trials.

14 Day Temperature, Relative Humidity and Dispersal in the SC and SF 2004:

A total of ²⁰ adult (IO/SC and 10/SF) C. nemoralis were tracked from June ⁵ — 18, 2004 in the SC and SF (Appendix D). The temperature (°C) and relative humidity (%) data have been summarized in Table 4.1 and Table 4.2, respectively. The mean daytime temperatures in SC (20.5) and SF (23.5) were significantly different ($p <$ 0.0312). The mean daytime relative humidity (%) in SC (92.7) and SF (85.8) was significantly different ($p < 0.001$). The mean nighttime temperatures in SC (17.8) and SF (16.0) were significantly different ($p < 0.001$). The mean nighttime relative humidity in the SC (95.8) and SF (98.1) was significantly different ($p < 0.001$). The mean temperatures at the time of collection in SC (20.2) and SF (25.3), Figure 4.6, were significantly different ($p < 0.008$). The mean relative humidity at the time of collection in SC (94.3) and SF (83.0), Figure 4.7, was significantly different ($p = 0.009$).

The mean daily dispersal in SC (2.1) and SF (0.71) was significantly different (p) < 0.001), Figure 4.3; Table 4.7. Maximum and minimum daily dispersal by an individual C. nemoralis in SC were (7.13 and 0.02 meter) and SF (4.59 and 0.02 meter). In SF there was a relationship between dispersal and temperature and relative humidity at the time of collection (GLM, $F = 5.99_{13,114}$, $r^2 = 0.1362$, $p = 0.0007$). Further regression analysis revealed that dispersal was related to humidity (GLM, $F = 10.92_{1,116}$, $r^2 = 0.086$, $p =$ 0.0012) but not to temperature (GLM, $F = 2.304_{1,116}$, $r^2 = 0.019$, $p = 0.1318$) Figures 4.8 and 4.9. The slope of the regression line for dispersal and humidity was positive in SF (Figure 4.8), however the slope of the regression line for dispersal and temperature was negative (Figure 4.9). There was no relationship between dispersal and temperature and

relative humidity at the time of collection in SC (GLM, $F = 1.249_{3,103}$, $r^2 = 0.0351$, $p =$ 0.295). Further regression analysis revealed that dispersal was not related to humidity (GLM, F = 0.025_{1,105}, r^2 = 0.0002, p = 0.8735) or temperature (GLM, F = 0.8613_{1,105}, r^2 = 0.008, $p = 0.3555$) Figures 4.10 and 4.11. The slope of the regression line for dispersal and humidity, and dispersal and temperature was positive in SC (Figures 4.10 and 4.11). Frequency histograms of dispersal can be found in Appendix G. The percentage of time that C. nemoralis spent not moving in SC was 3.6% and in SF was 14.0%. Cepaea *nemoralis* was found to disperse in a westerly direction in the SC (χ^2 = 25.98, d.f. = 3, p < 0.0001). In SF C. nemoralis did not disperse in any preferred direction (χ^2 = 0.4266, d.f. $= 3$, p = 0.9346). The percentage of tracked *C. nemoralis* that died before the study was completed in SC and SF were both 10% (1/10). Daily dispersal figures for snails from SC in 2004 and 2005 can be found in Appendix 1.

Weekly Temperature, Relative Humidity and Dispersal in the SC and SF 2004:

A total of 20 adult (IO/SC and 10/SF) C. nemoralis were tracked from June — September 2004 in SC and SF (Appendix D). Temperature (°C) and relative humidity (%) data have been summarized in Table 4.3 and Table 4.4, respectively. The mean weekly daytime temperatures in SC (20.6) and SF (22.0) were significantly different ($p <$ 0.0005). The mean daytime relative humidity in SC (88.1) and SF (84.9) was significantly different ($p < 0.0005$). The mean nighttime temperatures in SC (16.7) and SF (14.3) were significantly different ($p < 0.001$). The mean nighttime relative humidity in SC (97.1) and SF (99.1) was significantly different ($p < 0.001$). The mean temperatures at the time of collection in SC (20.0) and SF (22.0) were not significantly different ($p = .2016$). The mean relative humidity at the time of collection in SC (86.6)

and SF (87.0) were not significantly different ($p = 0.944$).

The mean weekly dispersal in SC (4.98) and SF (3.06) were not significantly different ($p = 0.127$), Figure 4.5; Table 4.7. The maximum and minimum weekly dispersal by an individual C. nemoralis in SC were (17.32 and 0.66 meter) and SF (37.49 and 0.15 meter). There was no relationship between the dispersal and the temperature and relative humidity in SC and SF (GLM, $r^2 = 0.0828$, p = 0.298 and $r^2 = 0.0578$, p = 0.3127, respectively). Frequency histograms of dispersal can be found in Appendix G. During the weekly trial in SC C. nemoralis did not disperse in a preferred direction (χ^2 = 1.505, d.f. = 3, $p = 0.68103$). However, during the weekly trial in SF C. nemoralis did move in a westerly and southerly direction (χ^2 = 8.533, d.f. = 3, p = 0.03618). The percentage of time that C. nemoralis spent not moving in SC was 0.0% and in SF was 2.5%. The percentage of C. nemoralis that died before the study was completed in SC was 22% (2/9) and in SF was 0.0%. One individual C. nemoralis crossed from SC into BSp during the weekly trials.

14 Day Temperature, Relative Humidity and Dispersal in the SC and SF 2005:

A total of 20 adult (10/SC and 10/SF) C. nemoralis were tracked from June $8 -$ 21, 2005 in SC and SF (Appendix E). The temperature (°C) and relative humidity (%) data have been summarized in Table 4.5 and Table 4.6, respectively. The mean daytime temperatures in SC (20.9) and SF (25.7) were significantly different ($p < 0.001$). The mean daytime relative humidity in SC (96.6) and SF (72.6) was significantly different (p < 0.001). The mean nighttime temperatures in SC (17.6) and SF (15.2) were significantly different ($p < 0.001$). The mean nighttime relative humidity in SC (97.8) and SF (99.1) was not significantly different ($p = 0.3806$). The mean temperatures at the time of

collection in SC (21.3) and SF (29.0) were significantly different ($p < 0.001$). The mean relative humidity at the time of collection in SC (97.3) and SF (62.2) was significantly different ($p < 0.001$).

The mean daily dispersal in SC (1.134) and SF (0.359) were significantly different ($p < 0.001$), Figure 4.2; Table 4.7. The maximum and minimum daily dispersal by an individual C. nemoralis in SC were (4.7 and 0.1 meter) and SF (1.83 and 0.0 meter). In SC there was a relationship between dispersal and temperature and relative humidity at the time of collection (GLM, $F = 4.515_{3,111}$, $r^2 = 0.1028$, $p = 0.0023$). Further regression analysis revealed that dispersal was related to humidity (GLM, $F = 4.867_{1.113}$, $r^2 = 0.0412$, p = 0.0294) but not to temperature (GLM, F = 2.58_{1,113}, $r^2 = 0.022$, p = 0.111) Figures 4.16 and 4.17. The slope of the regression line for dispersal and humidity was positive in SC (Figure 4.16), however the slope of the regression line for dispersal and temperature was negative (Figure 4.17). There was no relationship between dispersal and temperature and relative humidity at the time of collection in SF (GLM, $F =$ 1.986₃₉₄, r^2 = 0.0596, p = 0.1213). Further regression analysis revealed that dispersal was not related to humidity (GLM, $F = 1.402_{1.96}$, $r^2 = 0.014$, $p = 0.2394$) or temperature (GLM, $F = 1.332_{1.96}$, $r^2 = 0.0136$, $p = 0.2513$) Figures 4.18 and 4.19. The slope of the regression line for dispersal and humidity was positive in SF (Figure 4.18), however the slope of the regression line for dispersal and temperature was negative (Figure 4.19). Frequency histograms of dispersal can be found in Appendix G. Cepaea nemoralis was found to disperse in a westerly direction in SC (χ^2 = 7.455, d.f. = 3, p < 0.058). In SF C. *nemoralis* did not disperse in any preferred direction (χ^2 = 4.262, d.f. = 3, p = 0.2344). The percentage of time that C. nemoralis spent not moving in SC was 0.0% and in SF

was 27.5%. The percentage of C. nemoralis that died before the study was completed in SC was 10% (1/10) and in SF was 50% (5/10). Daily dispersal figures for snails from SC in 2004 and 2005 can be found in Appendix H.

Population Density and Demographics

The population density of C, nemoralis in 2003 for all patches was: SC (11.6/m²); BSp $(8.1/m^2)$; SF $(0.05/m^2)$; NF $(1.1/m^2)$; and HS $(0.65/m^2)$ – Figure 4.20. In 2005 the population density for SC and SF were 12.1 m^2 and 0.0 m^2 , respectively. Cepaea nemoralis in SC were found to have 5 different shell morphologies based upon the number of bands present. Of the C. nemoralis identified in SC 86.3% had 5 bands; 10.8% had 4 bands; 2.1% had 3 bands; 0.4% had 2 bands; and 0.4% had ¹ band (Figure 4.21). Two distinct body colors were also identified (brown or yellow) and 71.7% were brown and 28.2% were yellow. The mean shell diameter for C. nemoralis in SC was 15.2 mm, a size within the juvenile range. The smallest adult and largest juvenile snail identified in SC had ^a shell diameter of ¹⁸ mm and ²² mm, respectively. The age distribution of C. nemoralis in SC was 85.1% juvenile and 14.9% adult (Figure 4.22). The most abundant size class in SC for 2003 was the medium juvenile ($10 - 14$ mm) C. nemoralis (Figure 4.23). The most abundant size class in SC for 2005 was the large juvenile $(15 - 19$ mm) C. nemoralis (Figure 4.24). A large number of snails died off before reaching adult size and the numbers of small juveniles were underrepresented in the population sampling (Figures 4.15 and 4.16).

Distribution

A total of ³³ sites were surveyed outside the boundary of the study site for the presence of C. nemoralis (Appendix F). Of these survey sites only one (Hunt's Verge)

was found to have C. nemoralis. Hunt's Verge was directly across the road (Hagadom Rd.) from SC. Numerous times the broken shells of C. nemoralis were found along the east and west verges of Hagadom Rd. in direct proximity to SC.

DISCUSSION

Cepaea nemoralis individuals have greater daily dispersal capabilities in the high quality habitat (SC) than in the low quality habitat (SF). During the daily 'daytime' hours of 2004 and 2005 SC had significantly higher relative humidity than did SF. Cameron (1970) demonstrated that C. nemoralis become much less active when the relative humidity is low (65%). In SF where the mean 'daytime' humidity ranged from 72.6 (2005) — 87% (2004), C. nemoralis would spend less time moving and more time closed down with an epiphragm. Cameron (1970) suggested that C. nemoralis would remain inactive at low humidity levels once the epiphragm had been laid. However, in SC, where the mean 'daytime' humidity ranged from 88.1 (2004) – 96.6% (2005), C. nemoralis were more active, dispersed greater distances and rarely produced an epiphragm.

The importance of moisture is more evident in 2005 than in 2004. The year 2004 had more rain events than did the year 2005. For much of the daily tracking, in 2004, it was either raining at the time of collection or had rained the previous night. In the year 2005 it was warmer and drier with fewer rain events. Rain events in 2004 helped keep the mean 'daytime' humidity levels in SF at or above 85% while in 2005 the mean humidity level in SF never exceeded 72.6%. Dispersal of C. nemoralis was greater in 2004 than in 2005 from both SC and SF.

In Europe it was reported that C. nemoralis have a preferred temperature range

 $(19 - 20 \degree C)$ in which they remain active (Godan, 1980). In SC the mean 'daytime' temperature never exceeded 20.9 °C over a three year period at the soil surface and dispersal was higher. However, in SF the mean 'daytime' temperature was as high as 25.7 °C in 2005. This showed the importance of temperature in the dispersal of this snail species. When snails were under favorable conditions (low temperature and high humidity) they tend to disperse greater distances and remain active longer. This was true for both SC and SF, in 2004, a high rain event year. In 2004 the mean 'daytime' temperature in SF ranged from $22 - 23.5$ °C, temperatures above the preferred range for C. nemoralis, however this cohort of snails remained active throughout the year and dispersal was not significantly different from SC during the weekly assessment. This was most likely due to the mean daytime relative humidity being as high as 85.8%. Cameron (1970) has shown that during times of high humidity C. *nemoralis* will remain active even if the temperature is high. In comparison, SF in 2005 had a mean 'daytime' temperature of 25.7 °C and a mean 'daytime' humidity of 72.6% and C. nemoralis was much less active and dispersed over shorter distances.

In 2005, the hot, dry year, there was a strong relationship between C. nemoralis dispersal and temperature and humidity in SC. In the SC the mean 'time of collection' temperature (21.3 °C) and humidity (97.8%) were high in comparison to SF where no relationship of dispersal to temperature (29.0 °C) and humidity (62.2%) was found. In 2004, the wet and rainy year, there was a strong relationship between C. *nemoralis* daily dispersal and the temperature and humidity in SF. Even though the mean 'time of collection' temperature (25.3 °C) was high the humidity was also high (83.0%) in SF. No relationship was found in SC where the mean 'time of collection' temperature (20.2 °C)

was ideal and the humidity was high (94.3%). Finding no relationship in SC demonstrates that C. *nemoralis* will disperse actively when conditions were ideal (low temperature and high relative humidity). When temperature was high (above the ideal) and humidity was high there is a correlation between dispersal and temperature and humidity (2005 SC and 2004 SF).

In all years for both SC and SF increases in dispersal were associated with increases in humidity (Figures 4.25, 4.27, 4.29 and 4.31) and decreases in dispersal were associated with increases in temperature (Figures 4.26, 4.28, 4.30 and 4.32). In SF 2004 and SC and SF in 2005 the slopes of the regression lines were negative for dispersal and temperature (Figures 4.9, 4.17 and 4.19). Temperature negatively effects dispersal especially if the temperatures were high and above the ideal range. In SC and SF 2004 and in SC and SF 2005 the slopes of the regression lines were positive for dispersal and humidity (Figures 4.8, 4.10, 4.16 and 4.18). Humidity was a very important factor driving the dispersal of this species. High humidity often could offset the negative effects of high temperature. Even under conditions when the temperature was high snails would still disperse if the humidity was also high (Figures 4.27 and 4.28). Dispersal activity was greater in SC than in SF because the humidity levels were higher in SC and temperatures were usually higher and humidity lower in SF. Many more snails remained active and were dispersing in SC while snails were inactive and dispersed less (Appendix G).

These results support the finding that C. *nemoralis* do have an optimum temperature range (19 – 20 °C) in which they are active. If the temperature is ideal and the humidity is high then C . *nemoralis* will disperse. It is clear that C . *nemoralis*

dispersal is closely linked to environmental temperature and humidity and that these two parameters are greatly influenced by the structure of that environment (vegetation). Cepaea nemoralis will disperse more often when the humidity is above 83% even if the temperature is high, and this is evident from the daily results in 2004 from SF. If the temperature is ideal and the humidity is above 86% then C. nemoralis are very active and disperse greater distances and this is evident from weekly results from 2004 in SC and SF.

Snail Central, in all 3 years of this study, produced the ideal physical conditions required for C. nemoralis dispersal. Conversely, SF only produced ideal physical conditions during times of frequent rain events. Therefore, SF was a barrier to C. nemoralis dispersal and would only become a viable corridor if the conditions were right and rain was frequent.

It has often been cited in the literature that C. nemoralis are primarily nocturnal with little diurnal activity (Cain and Currey, 1968; Martinson, 1999; and Speiser, 2001); however in the present study it was found to have diurnal activity. If C. nemoralis activity was a function of temperature and humidity than it seemed nocturnal activity would have been greater in SF rather than SC. At night SF became significantly cooler and more humid than SC in 2004 and 2005. If activity of C. *nemoralis* was primarily nocturnal then one would expect the activity to be greater in SF than in SC where at night the conditions are more optimal (low temperature and high humidity). However, in both habitats mean 'nighttime' temperature was below the established ideal range of $19 - 20$ °C. The mean 'nighttime' temperature in SF ranged from $14.3 - 16$ °C during 2004 and 2005. In SC, the mean 'nighttime' temperature ranged from 16.7 — 17.8 °C during 2004

and 2005. It seemed the lower, and the higher the temperature was from the 'ideal' range the less active C. *nemoralis* became regardless of humidity levels. These results and field observations would suggest that C. nemoralis may not be nocturnal, and that diurnal activity does take place. If C. nemoralis were dependent upon optimum ranges of temperature and humidity than the 'ideal' conditions are present more often during the day than at night in SC and SF. These physical characteristics of SC and SF would then promote diurnal activity.

It has been reported that brown shelled and banded C. nemoralis are found more often in wooded and shaded habitats than their yellow shelled and non-banded morphological counterpart which were found in grassy and open habitats (Jones et al., (1977); Ozgo (2005 a and 2005 b). Cain and Curry (1968) reported that dark brown morphs were much more frequent in nettle patches than in grassland habitats. These authors reported that yellow and pink shelled C. nemoralis were more common in the grasslands. Brown shelled and banded individuals are more susceptible to over heating in grassland habitats where the radiant energy is greater and the darker color causes the shell to absorb more solar radiation. Further, yellow and non-banded individuals are less likely to overheat in grassland habitats due to the absence of dark shell pigmentation and a lighter overall shell color (Ozgo, 2005a and 2005b).

In the present study 97.1% of C. nemoralis identified in the SC had either ⁵ bands or 4 bands and 71.7% had brown bodies. This is suggestive of a morph that would be common to woodland areas possessing shade. The SC is wooded, shaded, and has a dense herbaceous layer while SF is an open habitat with very little shade. Only one C. nemoralis was ever found in SF during the population density sampling of 2003 and

2005. All SF C. nemoralis used in this dispersal study came from SC.

If C. nemoralis morphology did play a role in activity then it is plausible that individuals tracked in SF overheated at the higher temperatures and therefore had decreased activity levels. The phenomenon of overheating is more evident from SF in 2005 where 50% of C. nemoralis being tracked died within the first week. The daily temperature during the day in 2005 from SF often exceeded 40 °C. Ozgo (2005b) showed that yellow shelled C. nemoralis were more active at low (70%) humidity levels and that brown shelled C. nemoralis are active when humidity levels are high. This polymorphic banded dilemma of C. nemoralis population found in SC may also have acted as a barrier to further dispersal beyond that area.

What made SC an ideal habitat for C. nemoralis was the dense herbaceous layer, primarily composed of poison ivy, Rhus radicans. This author feels that the dense layer of vegetation was important in keeping the moisture levels high at the surface of the ground by keeping moisture trapped there and slowing down evaporation. The SC also had a tree canopy which shades a major portion of that habitat. According to Ozgo (2005a), adequate shade decreased the amount of solar radiation reaching the ground and reduced overheating. In stark comparison SF was comprised of various grasses and shade was almost nonexistent. The type of vegetation in SF was not conducive to maintaining high moisture levels at the soil surface thus contributing to the dryness of SF during the day. Banded C. nemoralis in this type of habitat would absorb much more solar radiation and overheat as a result of exposure. The niche opportunities for C. nemoralis were decreased in SF due to the physical conditions of that habitat. Therefore, C. nemoralis dispersal was greatly reduced outside SC because of poor physical

characteristics (low humidity and high temperature).

Several soil nutrients (Ca, Mg, P, N, K) and soil pH are important factors that shape gastropod communities (Burch, 1955, Lozek, 1962). Areas depauperate in these soil nutrients are usually void of gastropods. Calcium carbonate is an essential soil nutrient and has been correlated to the presence of gastropods in the environment (Lozek, 1962). Soil nutrients varied only slightly between SC and SF (Table 4.8); therefore soil nutrients and pH were not used as variables to differentiate SC and SF. Both habitats were considered of suitable quality for C. nemoralis based upon these soil nutrients and soil pH.

Goodhart (1962) attempted to determine the population density and dispersal of C. nemoralis from the Hundred Foot Bank in England. Two-hundred individuals were captured, marked and released, and then recaptured after four weeks, 13 weeks, and one year, and the distances moved were calculated. This author found that snails moved on average 0.18 m (4 weeks), 1.1 m (13 weeks), and 3.02 m (1 year). Goodhart considered this ^a low rate of natural dispersion. From these calculations he estimated that only 3% of adult C. nemoralis would disperse 10.97 m in ⁴ years. Also, it was determined that the density of C. nemoralis was $3.5/m^2$. Recapture rates were 66.5%, 54% and 41.5% after four weeks, 13 weeks, and one year, respectively.

Lamotte (1951) worked with C. nemoralis in France from two different habitat types, garden and herb meadow. In the garden habitat 20 C. nemoralis were marked, released at a central point, and recaptured after two years; the snails moved an average 9.7 m. In the herb meadow 200 individuals were marked, and recaptured after 5 months; the snails moved an average 8.1 meter. In the garden, and herb meadow snail recapture

rates were 4%, and 15%, respectively.

Schnetter (1951) performed a mark-recapture study on C. *nemoralis* in Germany. Two different habitat types were studied: uncultivated meadow and scattered brushes. In the uncultivated meadow 100 snails were marked, released at a central point, and recaptured after six months; the snails moved an average 23.8 m. In the scattered brushes 100 snails were marked, and recaptured after 2 years; the snails moved an average of 32.1 m. The recapture rates of snails, for both habitat types, was 13%.

Cain and Currey (1968) reported migration rates of C. nemoralis within a quartered testing plot comprised of various grassland species. These plots also had nettle patches between the boundaries of the four quadrants. These authors found that the emigration from nettle patches to the surrounding grassy areas was low $(2.9 - 8.6\%)$, even though population densities in nettle patches were high. Conversely, emigration from grassy areas to nettle patches was high $(5.6 - 35.2\%)$, even though the population densities in grassy areas were low. Cain and Currey (1968) suggested that perhaps nettle patches were more suitable habitats because predators (birds) could be avoided. Cameron and Williamson (1977), in England, estimated the migration rates of C. *nemoralis* from a grassland habitat. These authors reported that $26 - 56\%$ of C. nemoralis migrated, however they did not directly measure the dispersal distances achieved.

The dispersal rates of C. nemoralis, at the study site in Michigan, were the highest ever reported. For example, Goodhart (1962) estimated that adult C. nemoralis, in England, would not disperse more than 12 yards in 4 years. The results of the present study are drastically different from that reported by Goodhart. In SC adult C. nemoralis

were found to have a mean dispersal of 4.98 m/week (2004) and 2.1 m/day (2004). Individual snails were also found to disperse great distances over the course of a single day. In SC an individual C. *nemoralis* moved 7.13 meters in a single day. The snail moving the greatest distance between collecting periods was from SF. In SF an individual C. nemoralis moved 37.49 meter in ¹¹ days! While this distance was impressive, at least from the standpoint of a snail, it is possible that this individual was carried by a predator or moved by a bird. However, it rained for many of days between tracking events and had rained the night before this snail was recovered.

It may be that the dispersal capabilities of C. nemoralis in Europe are reportedly so low because the techniques used were not sufficient for estimating dispersal. Goodhart (1962), Lamotte (1951) and Schnetter (1951) all utilized mark and recapture techniques to estimate dispersal. Mark and recapture is useful for determining immigration and emigration as well as population density based upon the proportions of marked snails to unmarked snails. It is not, however, effective for determining dispersal. Lamotte (1951) reported that C. nemoralis would disperse 9.1 m/2 years and concluded this by a recapture rate of 4%. Lamotte (1951) also reported C. nemoralis would disperse 8.1 m/5 months and concluded this with a recapture rate of 15%. Schnetter (1951) reported C. nemoralis dispersal to be 23.8 m/6 months and 32.1 m/2 years both estimates were based upon a recapture rate of 13%. The work of Goodhart (1962) was based on recapture rates that ranged from $41.5 - 66.5\%$. The daily tracking success (habitat and year) in the present study was 74.6% (SC 2003), 77.1% (SC 2004), 91.5% (SF 2004), 89.8% (SC 2005), and 100% (SF 2005).

Cepaea nemoralis in SC are a source population. No other populations of C.

nemoralis were found in surrounding areas (Appendix F). It is not known how this population was introduced. It has been suggested that perhaps this population was brought to this location by a local nursery. At one time a local nursery owned and operated part of its business at this location and was responsible for planting the trees in SC. The trees were planted some time in the late 1980's to early 1990's. The property was sold to the current landowner's in 1994. So it is feasible that this population of C. nemoralis was introduced to SC when trees were planted over a decade ago.

If C. nemoralis were to spread naturally beyond SC it would encounter many barriers. For the population to spread to the East it would have to cross an adjacent road (Hagadom Rd). It is not impossible for C. nemoralis to cross this type of obstacle and two adult individuals were found in the verge on the opposite side of the road. However, this verge is one meter in width and beyond it is a mowed lawn. No individuals were ever found East beyond the verge directly across the road from SC. If C. nemoralis were to spread to the North and South they would encounter well maintained and mowed lawns. No C. nemoralis were ever found to the South of SC and only a few were found to the North in the homestead (HS) habitat. Individual C. nemoralis found in HS were most likely moved there via human activity because the children that lived at this private home often played with the snails. If C. *nemoralis* was to spread to the West it would have to move through the blue spruce (BSp) habitat and then traverse across SF for several hundred meters before encountering a woodland habitat. Even though some C. nemoralis have been found in SF and the north field (NF) to the west of SC no individuals were been found in the woodland area beyond. During 2004 C. nemoralis did disperse over 3m/year in SF the conditions required to obtain these dispersal distances were frequent rain storms. It was concluded that SF was a sink and any C. nemoralis that venture there would most likely die before ever reaching the woodland area beyond.

This population has failed to spread beyond SC for 2 reasons: (1) surrounding habitats are not optimal (i.e. grassland) and even hazardous to C . *nemoralis* (i.e. manicured lawns and roads); and (2) there is a morphological barrier (i.e. being banded and having dark pigmentation in the body) that this population is currently unable to overcome. The selective advantage of being banded and dark in color would be to survive in shaded habitats. The SC was an ideal habitat for this particular C. *nemoralis* morph to survive, reproduce and multiply. But, SC is land locked and is essentially an island for this population of C. *nemoralis*. In three years of tracking in SC only 3 snails ever crossed over into BSp which is adjacent to SC and separated by approximately 2 meters of mowed grass.

Baur and Baur (1992) reported that once land snails reached the edge of a habitat they are unwilling to travel into the sub-optimal area beyond. Instead snails either travel along the edge or turn back into the original habitat. *Cepaea nemoralis* seem to do both (edge follow and turn back) when they encountered the border of SC. This phenomenon can be likened to 'ping-pong' in that when C. nemoralis reach the margin of SC they bounce back towards the interior or travel along the edge rather than pass into the habitat beyond. In SC C. nemoralis encountered a mowed path to the west which if crossed would lead to BSp. To the North and South were mowed lawns and to the East is an area of tall grasses approximately 5 meters in width which lead to the adjacent road (Figure 4.1). All outside areas surrounding the perimeter of SC were considered sub-optimal to SC and therefore C. *nemoralis* would be unlikely to move into that area unless conditions were very good at the time of dispersal (e.g. raining). Currently, no corridor exists that would link SC to the adequate habitats beyond. This was due primarily to human activity, however if this activity were to change corridors could be created allowing a route by which C. nemoralis could spread beyond SC.

Table 4.1. The mean $(\pm SE)$ daily daytime, nighttime, and time of collection

temperature (°C) for Snail Central and South Field 2004 taken at the height of 10 Table 4.1. The mean (± SE) daily daytime, nighttime, and time of collection
temperature (°C) for Snail Central and South Field 2004 taken at the height of 10
cm using a HOBO datalogger. Table 4.1. The mean (± SE) daily daytime, nighttime, and time of collection
temperature (°C) for Snail Central and South Field 2004 taken at the height of 10
cm using a HOBO datalogger.
2004 Snail Central Mean temperature cm using ^a HOBO datalogger.

[†] Significantly different (Student's t-test, $t = 3.152$, d.f. = 204, p < 0.001).

¹ Significantly different (Student's t-test, t = -2.855, d.f. = 26, p < 0.008).

Table 4.2. The mean $(\pm S E)$ daily daytime, nighttime, and time of collection

relative humidity (%) for Snail Central and South Field 2004 taken at the height of Table 4.2. The mean $(\pm \text{ SE})$ daily daytime, nighttime, and time of collection
relative humidity (%) for Snail Central and South Field 2004 taken at the height of
10 cm using a HOBO datalogger.

¹⁰ cm using ^a HOBO datalogger.

1 Significantly different (Student's t-test, $t = -2.788$, d.f. = 26, $p = 0.009$).

Table 4.3. The mean $(\pm SE)$ weekly daytime, nighttime, and time of collection

temperature (°C) for Snail Central and South Field 2004 taken at the height of 10 Table 4.3. The mean $(\pm \text{ SE})$ weekly daytime, nighttime, and time of collection
temperature (°C) for Snail Central and South Field 2004 taken at the height of 10
cm using a HOBO datalogger.

cm using ^a HOBO datalogger.

[†] Significantly different (Student's t-test, $t = 9.861$, d.f. = 827, p < 0.001).

1 Not significantly different (Student's t-test, $t = -1.331$, d.f. = 16, $p = 0.2016$).

Table 4.4. The mean $(\pm SE)$ weekly daytime, nighttime, and time of collection

relative humidity (%) for Snail Central and South Field 2004 taken at the height of Table 4.4. The mean $(\pm \text{ SE})$ weekly daytime, nighttime, and time of collection
relative humidity (%) for Snail Central and South Field 2004 taken at the height of
10 cm using a HOBO datalogger.

¹⁰ cm using ^a HOBO datalogger.

I Not significantly different (Student's t-test, $t = -0.0705$, d.f. = 16, $p = 0.944$).

Table 4.5. The mean $(\pm S E)$ daily daytime, nighttime, and time of collection

temperature (°C) for Snail Central and South Field 2005 taken at the height of 10 Table 4.5. The mean (± SE) daily daytime, nighttime, and time of collection
temperature (°C) for Snail Central and South Field 2005 taken at the height of 10
cm using a HOBO datalogger.

cm using ^a HOBO datalogger.

1 Significantly different (Student's t-test, $t = -4.677$, d.f. = 26, $p < 0.001$).
Table 4.6. The mean $(\pm SE)$ daily daytime, nighttime, and time of collection

relative humidity (%) for Snail Central and South Field 2005 taken at the height of Table 4.6. The mean $(\pm \text{ SE})$ daily daytime, nighttime, and time of collection
relative humidity (%) for Snail Central and South Field 2005 taken at the height of
10 cm using a HOBO datalogger.

¹⁰ cm using ^a HOBO datalogger.

[†] Not significantly different (Student's t-test, $t = -0.879$, d.f. = 138, $p = 0.3806$).

^{\ddagger} Significantly different (Student's t-test, t = 8.577, d.f. = 26, p < 0.001).

Table 4.7. The mean $(\pm S E)$ daily and weekly dispersal (meter) of C. nemoralis Table 4.7. The mean $(\pm \text{ SE})$ daily and weekly dispersal (meter) of *C. nemoralis*
from SC in 2003 and from SC and SF in 2004 and 2005.

* Significantly different (Student's t-test, $t = 7.861$, d.f. = 223, $p < 0.001$).

¹ Significantly different (Student's t-test, $t = 6.736$, d.f. = 211, $p < 0.001$).

^{\uparrow} Not significantly different (Student's t-test, t = 1.543, d.f. = 71, p = 0.1271).

Table 4.8. Soil nutrients and pH from SC and SF 2005.		
Soil Nutrient	Snail Central	South Field
Calcium	1,167 ppm	1,082 ppm
Magnesium Potassium	176 ppm	172 ppm
Phosphorous	118 ppm 28 ppm	293 ppm 55 ppm
Nitrate-N		
Soil pH Lime Index	0.9 ppm 6.0 68	2.5 ppm 6.4 70

Table 4.8. Soil nutrients and pH from SC and SF 2005. Table 4.8. Soil nutrients and pH from SC and SF 2005.

Figure 4.1. Map outlining the 5 distinct patches (snail central, blue spruce, south field, north field, and homestead) within the study area in Ingham County, Michigan.

Figure 42. Air and soil temperature (Celsius) taken over a 14 day period (5/18/2003 - 5/31/2003) in the SC.

Figure 4.3. The mean daily dispersal $(\pm 1 \text{ SE})$ of C. nemoralis from SC in 2003 and the SC and SF in 2004 and 2005.

Figure 4.4. Weekly air and soil temperature (Celsius) taken from 6/11/2003 -9/26/2003 in the SC.

Figure 4.5. The mean weekly dispersal $(\pm 1 \text{ SE})$ of C. nemoralis from SC in 2003 and the SC and SF in 2004.

Figure 4.6. Temperature (Celsius) taken at ground level over a 14 day period (6/05/2004 - 6/18/2004) in the SC and SF.

Figure 4.7. Relative Humidity (%) taken at ground level over a 14 day period (6/05/2004 - 6/18/2004) in the SC and SF.

Figure 4.8. Regression analysis of C. nemoralis daily dispersal and relative humidity (%) from SF in 2004.

Figure 4.9. Regression analysis of C. nemoralis daily dispersal and temperature (celsius) from SF in 2004.

Figure 4.10. Regression analysis of C. nemoralis daily dispersal and relative humidity (%) from SC in 2004.

Figure 4.11. Regression analysis of C. nemoralis daily dispersal and temperature (celsius) from SC in 2004.

Figure 4.12. Weekly temperature (Celsius) taken at ground level from 6/25/2004 -9/15/2004 in the SC and SF.

Figure 4.13. Weekly relative humidity (%) taken at ground level from 6/25/2004 -9/15/2004 in the SC and SF.

Figure 4.14. Temperature (Celsius) taken at ground level over a 14 day period (6/08/2005 - 6/21/2005) in the SC and SF.

Figure 4.15. Relative Humidity (%) taken at ground level over a 14 day period (6/08/2005 - 6/21/2005) in the SC and SF.

Figure 4.16. Regression analysis of C. nemoralis daily dispersal and relative humidity (%) from SC in 2005.

Figure 4.17. Regression analysis of C. nemoralis daily dispersal and temperature (celsius) from SC in 2005.

Figure 4.18. Regression analysis of C. nemoralis daily dispersal and relative humidity (%) from SF in 2005.

Figure 4.19. Regression analysis of C. nemoralis daily dispersal and temperature (celsius) from SF in 2005.

Figure 4.20. Specific patch and population density (snails/ m^2) of C. nemoralis in 2003.

Figure 4.21. The number of bands present (percentage of population) in C. nemoralis from the SC in 2005.

Figure 4.22. The percentage of juvenile and adult C. nemoralis from the SC in 2005.

Figure 4.23. The distribution of C . nemoralis by size class (adult, large juvenile, medium juvenile and small juvenile) from the SC in 2003.

Figure 4.24. The distribution of C. nemoralis by size class (adult, large juvenile, medium juvenile and small juvenile) from the SC in 2005.

Figure 4.25. The mean daily dispersal (meters) of C. nemoralis and relative humidity (%) from SC in 2004.

Figure 4.26. The mean daily dispersal (meters) of C. nemoralis and temperature (celsius) from SC in 2004.

Figure 4.27. The mean daily dispersal (meters) of C. nemoralis and relative humidity (%) from SF in 2004.

Figure 4.28. The mean daily dispersal (meters) of C. nemoralis and temperature (celsius) from SF in 2004.

Figure 4.29. The mean daily dispersal (meters) of C. nemoralis and relative humidity (%) from the SC in 2005.

Figure 4.30. The mean daily dispersal (meters) of C. nemoralis and temperature (celsius) from the SC in 2005.

Figure 4.31. The mean daily dispersal (meters) of C . nemoralis and relative humidity (%) from SF in 2005.

Figure 4.32. The mean daily dispersal (meters) of C . nemoralis and temperature (celsius) from SF in 2005.

CHAPTER 5: CONTROL OF CEPAEA NEMORALIS

INTRODUCTION

Control of Pest Gastropods

Because of their recognized pest status around the world in greenhouses, gardens, viticultures, grasslands, forests, and in agriculture many control strategies for land gastropods have been designed using a wide variety of chemicals, physical barriers, traps, and biological controls (Godan, 1983; Barker, 2002; and UCIPM, 2006). Some of the more common molluscicides used to control land gastropods are metaldehyde ((CH₃- $CHO₄$) – derived from polymerization of acetaldehyde), isolan (1-isopropyl-3-methyl-5pyrazolyl dimethylcarbamate), cloethocarb ((2-(2-chloro-lmethyloxyethoxy)phenyl methylcarbamate)), and methiocarb (4-methylthio-3,5-xylyl-N-methylcarbamate). These toxins can be applied as either sprays, baits, or broadcast upon the ground, and enter the snail's body by ingestion or through dermal contact (Henderson and Triebskom, 2002). Once these chemicals contact the land gastropod they act as irritants and desiccants, and if ingested they inhibit metabolism and have neurotoxic effects.

Molluscicide toxins are broad spectrum and can affect a wide range of vertebrates and invertebrates. For example, carbarnates (isolan, cloethocarb, methiocarb) are cholinesterase inhibitors and allow accumulation of acetylcholine causing loss of muscle tonus in the intoxicated animal (Henderson and Triebskorn, 2002). Any animal that uses acetylcholine as a neurotransmitter can be effected by this toxin. Metaldehyde can cause the release of the neurotransmitter gamma-aminobutyric acid (GABA) which is an inhibitory neurotransmitter. GABA is produced to block the signals sent from one cell to another in the central nervous system. In gastropods metaldehyde causes convulsions or

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seizures. Metaldehyde is also an irritant to the gastropod and causes the animal to produce large amounts of mucus. Increasing mucus production is a defense against the irritant, but at the same time it will cause desiccation through water loss.

Other strategies have been developed to control land gastropods. Citrus growers in California are using copper sheathing to girdle the bases of trees (Martinson, 1999; Sakovich, 2002). *Cepaea nemoralis*, and land snails in general, seem unable to traverse across a barrier made of copper. It is thought that the mucus trail left by the gastropod reacts with the copper to produce a small electrical charge (UCIPM, 2006). This method is a deterrent and does not harm the snail but it can prevent them from reaching the tree canopy and fruit. Traps have been used such as boards placed upon the ground and attract land gastropods which are subsequently crushed and destroyed. Also, traps containing beer are useful in attracting and killing snails within small gardens. However, most traps are not very effective in controlling large populations and require a high degree of maintenance.

Carnivorous snail species like Rumina decollate (Linnaeus, 1758) and Euglandina rosea (Ferussac, 1821) have been used as a biological control to eat pest Cantareus aspersus (Mueller, 1774) in California and Achatina fulica (Achatinidae) in Hawaii (Hadfield et al., 1993 and Sakovich, 2002). The parasitic nematode, Phasmarhabditis hermaphrodita (Schneider, 1859), has also been used to control pest gastropods. Biological controls that have been used for several African land snail species, include predaceous flatworms (Geoplana septemlineata Hymen, 1939, and Platydemus manokwari de Beauchamp, 1962), carnivorous snails (*Edentulina affinis* Boettger, 1913, Gonaxis quadrilateralis Preston, 1910, and Streptaxis kibweziensis Smith, 1894), hermit

crabs (Coenobita sp. and Birgus sp.), and rats (Rattus spp.) (USDA-APHIS, 2005). Parasitoids such as sarcophagid flies, Sarcophaga spp. have been used to control white snails, Theba pisana (Muller, 1774) and Cernuella virgata (de Costa, 1778), and conical snails, Cochlicella spp., in southern Australia (Baker, 2002). Other predators of land gastropods include Coleoptera (Carabidae and Lampyridae) and Hymenoptera (Formicidae) (Raut and Barker, 2002).

California citrus growers have implemented a program of integrated pest management (IPM) that utilizes several methods to control for pest snails in orchards. This IPM calls for the (1) spraying of a commercial molluscicide in infested areas; (2) citrus trees are skirt pruned removing those branches that contact the ground; (3) copper barriers are installed around tree bases; and (4) introduction of R. decollata after molluscicide break down to eat any pest snails lefi within the treated area (Sakovich, 2002). This approach is having positive results in the orchards of California.

Martinson (1999), reported C. *nemoralis* as a pest of vineyards in Ontario, Canada. This author reported that C. nemoralis was easily controlled by using Prozap® 2% Metaldehyde in the grape canopy. In most cases applying large quantities of ^a molluscicide can have positive effects on controlling pest populations. What makes most molluscicides undesirable to use is the impact they can have on non-target species including hmnans. These toxins can kill indiscriminately and have long lasting effects on non-target wildlife. Increasing awareness of pesticide contamination and its environmental impact is forcing ^a search for less harmful means of pest control. New molluscicides such as iron phosphate have recently been developed which are less toxic to wildlife.

Iron Phosphate

Because iron phosphate is a less toxic molluscicide it was chosen for a short-term experimental trial to determine the efficacy of this bait/molluscicide to kill and eradicate C . nemoralis. The SC was used because of its high population density of C . nemoralis (For more information on habitat description and population density please see Chapter 4). A bait containing 1% iron phosphate (FePO4) was chosen because of its recognized toxicity to molluscs and that it has no observable effect on wildlife (mammals, birds, fish, non-target insects, and aquatic invertebrates) while generally regarded as safe for food use and non-toxic to humans (USEPA, 2005). Iron phosphate is naturally occurring in nature as a solid, and will not readily dissolve in water. When consumed by the gastropod iron phosphate inhibits calcium absorption in the gut and will quickly halt the feeding process. Intoxicated gastropods usually die within $3 - 6$ days post-consumption (USEPA, 2005).

Iron phosphate was approved for use by the E.P.A. in 1997 (E.P.A. Reg. No. 67702-3-54705) and commercially produced by W. Neudorff GmbH KG, Germany, and distributed in the United States by Lawn and Garden Products, Inc. It is known by the trade name Sluggo® and commonly sold at garden and home improvement centers. It is known to control both slugs and snails (Deroceras reticulatum, D. laeve, Arion subfuscus, A. circumscriptus, A. hortensis, A. rufus, A. ater, Limax flavus, L. tenellus, Ariolimax columbianus, Helix spp., Helicella spp., and Cepaea spp.). The purpose of this study was to test the efficacy of iron phosphate as a chemical control agent for a large, established population of pest C. nemoralis.

MATERIALS AND METHODS

Study Design

In 2005 the 2,404 m^2 site (SC) was divided into 15 equal size plots of 10 X 10 meters (Appendix I). Within each 10 X 10 plot a smaller 3 X 3 meters (9 m²) sub-plot was established and designated as the treatment zone. Flags of two different colors were used to designate plot and sub-plot boundaries. Plots were then grouped into five blocks $(A, B, C, D, E - Appendix I)$ each containing three of the 10 X 10 meter plots. The 3 X 3 meter sub-plot was used as the area for treatment application. Each plot within a block was assigned a treatment (bait, no bait, and sham bait) by using a random number generator. Bait and sham bait was applied to each treatment zone at the manufacturers recommended amount of 1 lb./1,000 ft² (= 48.4 gram/9 m²). A total of 0.45 Kg Sluggo® was purchased from a local nursery at a cost of $\sim 17 U.S. A total of 500 grams of sham bait was obtained from the manufacturers of Sluggo®. Sham bait contained the attractants of the bait, but was missing the active ingredient iron phosphate. The manufacturer provided enough sham bait for two treatments.

A pre-application population density survey was performed within each of the ¹⁵ 3 X 3 meter sub-plots to get baseline information on the number of C. *nemoralis* present in each area. Each time the population density was sampled ^a hula hoop (WHAM-O®) was randomly tossed within each ³ X ³ meter sub-plots for ^a total of ³ times. The inside area of the hula hoop was determined to be 0.5 m^2 . All live and dead snails within the area of the hula-hoop were counted. All dead snails were removed from the ³ X ³ meter sub-plots. Bait and sham bait was applied to each treatment zone every week for two weeks. One week after the first treatment applications were applied the population density of C. nemoralis was again assessed from within the ³ X ³ meter sub-plots, and

the following day bait and sham bait were re-applied. After the second week the population density of C. nemoralis was again determined. At the time of sampling a thermohygrometer was used to measure the temperature $({}^{\circ}C)$ and relative humidity $({}^{\circ}C)$ at the soil surface from within each ³ X ³ meter sub-plot.

Symptoms of Intoxication

To study symptoms of intoxication by iron phosphate 20 (7 adult and 13 juvenile) C. nemoralis were exposed to iron phosphate in a small laboratory experiment. C. nemoralis were collected from SC and placed into a plastic container and starved for 7 days. After starvation five snails were placed into a plastic container with approximately 2.5 cm of moist soil and bait pellets. Enough pellets were placed in the container to cover most of the surface area to ensure immediate contact with the snails. Snails were allowed to feed for one hour and then they were removed and placed into another container with only moist soil. Behavior of intoxicated snails was observed for up to an hour and then checked every day for seven days to determine when death had occurred. **Statistics**

A general linear model (GLM) 2-way Blocking ANOVA was used to evaluate blocking effect and differences in the number of live snails and the number of dead snails among treatments. Further evaluation between treatments was done using a l-way ANOVA and Tukey's post-hoc test. One-way ANOVA and Tukey's post-hoc test was used to evaluate differences in the temperature and relative humidity among the blocks. χ^2 Test of Independence was used to determine if there was an increase in the number of dead snails found in each treatment between week one and week two. Statistical analyses were conducted using R v. 1.9.l® and Systat 11® for Windows.

RESULTS

Post-Application (One Week)

The number of live and dead C. nemoralis recovered from each treatment zone has been summarized in Table 5.1. The number of pre-treatment live snails was not significantly different among blocks (GLM, $F = 0.424_{2,12}$, $p = 0.664$), Figure 5.1. There is no evidence for differences in the number of living C. nemoralis among blocks (GLM 2-way ANOVA, $F = 2.811_{3,11}$, $p = 0.2094$). There is no evidence for differences in the number of living C. nemoralis among treatments (GLM 2-way ANOVA, $F = 2.811_{3,11}$, $p =$ 0.0888). There is no evidence for differences in the number of dead C. *nemoralis* among blocks (GLM 2-way ANOVA, $F = 2.73_{3,11}$, $p = 0.9083$), but there is evidence for the differences in the number of dead snails between treatments. Significantly more C. *nemoralis* were found dead in the bait treatment than in the sham bait treatment ($p =$ 0.042, Tukey's test). Just under half (41.8%) of all C. nemoralis surveyed in the bait treatment was found to be dead (Table 5.1). The physical parameters (temperature and humidity) among the blocks were not different except for Block A which was significantly warmer than the other 4 blocks ($p < 0.05$; Table 5.2).

Post-Application (Two Weeks)

There is no evidence for the differences in the number of living C. nemoralis among blocks (GLM 2-way ANOVA, $F = 1.196_{3,11}$, $p = 0.219$). There is no evidence for differences in the number of living C. *nemoralis* among treatments (GLM 2-way ANOVA, $F = 1.196_{3,11}$, $p = 0.3565$). There is no evidence for differences in the number of dead C. nemoralis among blocks (GLM 2-way ANOVA, $F = 5.801_{3,11}$, $p = 0.6482$), but there is evidence for the differences in the number of dead snails between treatments.

Significantly more C. nemoralis were found dead in the bait treatment than either the no bait ($p = 0.00378$, Tukey's test) and sham bait treatment ($p = 0.00479$, Tukey's test). Their was a significant increase in the number of dead snails found in the bait treatment between week one and week two (χ^2 = 9.305, d.f. = 1, p = 0.0022). No significant increase in the number of dead snails was found in the no bait treatment (χ^2 = 2.276, d.f. = 1, p = 0.1313) or the sham bait treatment (χ^2 = 1.80, d.f. = 1, p = 0.1797) between week one and week two. Over three-quarters (75.6%) of all C. nemoralis surveyed in the bait treatment was found to be dead (Table 5.1). The physical parameters (temperature and humidity) among the blocks were not different (Table 5.2).

DISCUSSION

Iron phosphate is an effective molluscicide for killing C. nemoralis. Significantly more *C. nemoralis* were found dead in the bait treatment than in the no bait or sham bait treatments. The number of dead snails between week one and week two in the baited areas increased significantly from 41.8% to 75.6%. Iron phosphate killed more adults than it did juveniles indicating the bait may target older snails. No evidence was found to indicate that the number of living snails was different or decreased among the treatments or between week one and week two. This finding indicates that C. *nemoralis* moved between treatments and has a high population density (See Chapter 4). Plots were adjacent to one another and snails could move in and out of treatment zones. Reservoirs (i.e. trees) for living snails may have also played a role in no net decrease in the number of living snails. The number of living snails in the sham bait treatments actually increased from week one to week two (Table 5.1) indicating the presence of a snail reservoir.

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The symptoms of intoxication for C. nemoralis in the lab are consistent with the Sluggo® literature. However, in the lab intoxicated snails do seem to lose some muscle tonus. Loss of muscle tonus was seen when intoxicated snails would show lethargy and hang the foot and part of the body outside the shell. In some cases the snail would not retreat back into the shell even if poked with forceps and probe. Many intoxicated snails would retreat into their shells and never again emerge with death following within six to seven days. Juvenile snails seemed to die faster than adult snails and the adults would feed longer on the bait sometimes for an entire hour.

^I concluded that iron phosphate is an effective chemical that can be used to control a large pest population of C. *nemoralis*. This study was carried out at the manufacturers recommended application of 0.45 Kg/92.9 m². The manufacturers suggested amount was meant to be used in small gardens and not in an area with dense vegetation. In dense vegetation, similar to the SC, adequate coverage is not obtained using the manufactures suggested amount. It was shown that iron phosphate can kill C. nemoralis, however, the density of this population was not significantly impacted by use of the bait. To significantly decrease the number of C. nemoralis in a large, wild population more iron phosphate would need to be used. It is the recommendation of this author that the quantity of bait being applied to infested areas be increased to at least 1.8 Kg bait/92.9 m². One set-back to using iron phosphate to control a large population is the cost. The amount of iron phosphate needed to treat ¹ acre is approximately 4.54 Kg at a cost of \$42 U.S./4.54 Kg (Baute and DiFonzo, unpublished). Baute and DiFonzo have suggested that Sluggo® is too expensive for use on field crops. However, iron phosphate even applied at 4 times the manufacturers recommended application amount would still

be a worthwhile investment to control isolated populations of C. *nemoralis*. Bait containing iron phosphate can last in the environment for up to one week (personal observation). After a weeks time the pellets begin to break down and become covered with a white fungus.

What makes iron phosphate an ideal molluscicide even with the high cost is that does not have an impact on mammals, birds, fish and aquatic invertebrates. In this study no other animals were found dead within the sampled areas. Iron phosphate seems to be target chemical product having an impact only on molluscs. One fall back to using iron phosphate is that it cannot discriminate between native and pest gastropods. However, this is an acceptable trade-off when one considers the toxicological effects of other molluscicides.

Table 5.1. The mean \pm SE of live and dead C. nemoralis found before treatment and during week one and week two post-application, the total number of adults and juveniles found in each treatment group and the percent dead C. nemoralis Table 5.1. The mean \pm SE of live and dead *C. nemoralis* found before treatment
and during week one and week two post-application, the total number of adults
and juveniles found in each treatment group and the percent Table 5.1. The mean \pm SE of live and dead *C. nemoralis* found before treatment
and during week one and week two post-application, the total number of adults
and juveniles found in each treatment group and the percent after treatment for SC in 2005.

* NC = Not counted, but dead snails were removed from study area.

 \dagger A = Total Adult C. nemoralis; \ddagger J = Total Juvenile C. nemoralis.

Table 5.2. The mean \pm SE temperature (°C) relative humidity (%) in each of the 5					
blocks per week of treatment in SC 2005.					
Physical Parameter	Block A	Block B	Block Block C	Block D	Block E
Week One					
Temperature	29.2 ± 0.36 \mathbf{v}	26.1 ± 0.69 W	24.8 ± 0.17 w, x	25.1 ± 0.17 w, x, y	26.4 ± 0.34 w, x, y
Relative Humidity	82.7 ± 0.69 \mathbf{v}	92.7 ± 3.1 w, x	95.8 ± 0.92 w, y	87.3 ± 1.6 v, w, x, y, z	84.2 ± 2.2 v, w, x, z
Week Two					
Temperature	32.2 ± 1.5 \mathbf{v}	29.8 ± 0.12 v, w	27.0 ± 1.4 W	26.9 ± 0.78 $\boldsymbol{\mathsf{w}}$	27.5 ± 0.27 v, w
Relative Humidity	62.5 ± 5.3 V	73.2 ± 3.6 V	76.0 ± 8.2 V	70.9 ± 3.9 $\mathbf v$	72.0 ± 1.9 \mathbf{v}

Table 5.2. The mean \pm SE temperature (°C) relative humidity (%) in each of the 5 Table 5.2. The mean \pm SE temperature (°C) relative humidity (%) in each of the 5
blocks per week of treatment in SC 2005.

A lack of significant difference (Tukey's Test, $p > 0.05$) between pairs in a single row is indicated by shared letters.

Figure 5.1. The mean $(\pm S)$ number of live snails found per block before application of rmlluscicide.

CHAPTER 6: GENERAL CONLUSIONS AND RECOMMENDATIONS

General Conclusions

In Europe, where this species is native, the natural dispersal is much less when compared to its dispersal in Michigan. This finding indicates that perhaps this species disperses greater distances when playing the exotic role. However, this hypothesis was not tested and remains open for exploration. The mark and recapture techniques used in Europe were inaccurate due to the low recapture rates. However, recapture rates using harmonic radar were much higher and the tracking was performed over shorter time intervals. It cannot be stated that this species can disperse greater distance when it is invasive, but it can be said that the European reports underestimated the dispersal capabilities of this species. Therefore, if management agencies rely on dispersal information that was acquired for this species in its native habitat it is plausible that the rate of spread could be miscalculated. For example, Goodhart (1962) estimated that adult C. nemoralis, in England, would not disperse more than 10.92 m in ⁴ years. The results of the present study are drastically different. In the preferred woodland habitat adult C. nemoralis were found to have a mean dispersal of 4.98 m/week (2004) and 2.1 m/day (2004). There was also variation in the dispersal of individual C . *nemoralis* indicated by the 'big movers' that could disperse distances of nearly 40 meters in less than two weeks. Even though these 'big movers' were rare (Appendix G) their role in establishing a new population could be important. This species is a hermaphrodite and capable of storing sperm for long periods; an individual snail moving great distances could establish a new population by itself.

Similar to the above mentioned observations, Baker (1988) reported that Theba

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pisana dispersed greater distances when it was invasive. This snail species is native to Western Europe and found from the Mediterranean to the United Kingdom. Cowie (1984) reported on the dispersal of T . *pisana* from South Wales found this species moved a maximum of 300 centimeters over a 100 day period. Cowie concluded that T. pisana was a "sedentary" snail and showed a "reluctance to migrate". In the 1920's this species was introduced to Australia and has become a very costly pest species (Baker, 2002). Baker (1988) reported T. pisana in Australia moved greater than 55 meters in a single month and greater than 75 meters in 3 months. The dispersal capabilities reported for T. pisana in its native range and from areas where it is invasive are drastically different. The data on T. pisana dispersal would indicate a snail species that is certainly not "sedentary". The mark and recapture techniques used by Baker (1988) were similar to the techniques used in Europe. These techniques involved marking a large sample of snails with paints, releasing them at a given starting point, and recapturing individuals after some time interval (usually a month or greater).

Recently, Ozgo (2205a and 2005b) has hypothesized that habitat (primarily temperature) is responsible for inter- and intrapopulation banding and color variation of C. nemoralis. A strong association had been reported in the literature that indicated banded and dark morphs prefer woodland habitats while the non-banded and light morphs preferred grassland habitats (Cain and Currey, 1968; Jones et al., (1977); Ozgo (2005a and 2005b). Ozgo, in Poland, demonstrated that habitat types are an important selection force. This author hypothesized that banded individuals are more susceptible to over heating in grassland habitats where the radiant energy is greater and the dark bands cause the shell to absorb more solar radiation. Further, non-banded individuals are less likely to

overheat in grassland habitats due to the absence of dark shell pigmentation and lighter overall shell color. In general open habitats are less humid and have higher temperatures while shaded habitats are more humid and have lower temperatures (Ozgo, 2005a and 2005b). The association of a particular C. *nemoralis* morph to the environment was also reported by Cain and Currey (1968). These authors found no five banded C. nemoralis in the Marlborough Downs, England study site, however, they do mention an association between dark shells and nettle patches (areas with dense vegetation) and light pink and yellow shells found in grassland habitats. These authors reported that C. nemoralis had much higher population densities $(6 - 10/m^2)$ in the nettle patches than in the grassland habitat (0.3 – 0.8/m²). The population density of C. *nemoralis* in Ingham County was also higher in the woodland habitat $(11.6 - 12.1/m²)$ than in the grassland habitat $(0.0 0.05/m^2$).

Here in the U.S. the most commonly reported C . *nemoralis* morph is banded and dark in color. This is true with the Ingham County population that was the focus of this study. This morphological characteristic of C. nemoralis is a very important factor that influences the natural short-distance dispersal of this snail. For C. *nemoralis* to disperse naturally, under its own power, it must creep through its environment on a trail of mucus. Mucus is costly for the snail to produce and is approximately 96 — 97% water (Denny, 1980). The more mucus a land gastropod produces the more water it will lose (Baur and Baur, 1990; and Denny (1980)). Environments that maintain and keep moisture are more suitable for snails because water is readily available and easily acquired. A woodland habitat which offers a dense canopy and herbaceous layer is ideal for maintaining higher moisture levels at the soil surface and promotes C. *nemoralis* dispersal. In Ingham

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County, the surrounding habitats of the study site are grassland, open with little shade, and tend to dry out during the summer months. Therefore, it may be difficult for this population of C. nemoralis to naturally spread beyond the source woodland habitat. The environmental conditions of the surrounding sink habitats are not suitable for this snail species and may be acting as barriers preventing further dispersal. However, during times of heavy rainfall (rain events lasting for several continuous days) the grassland habitat does seem to maintain high enough moisture levels to support C. *nemoralis* dispersal. One individual C. nemoralis moved nearly 40 meters in 11 days within the grassland habitat. During this time rain events were frequent. This is an important finding which demonstrated that natural barriers to dispersal may be breached if weather conditions are favorable.

Cepaea nemoralis was first deliberately introduced to the U.S. 149 years ago. It is not known how far this species has spread within the U.S. This is a result of a lack of interest and research. Populations of C. nemoralis most likely go unnoticed and only receive attention when they become a pest. The USDA-PPQ considers C. nemoralis to be established and no eradication attempts will be conducted (Sullivan et al., 2004). An established population is breeding and successfully creating offspring that can also reproduce. There are several reasons that ^I feel this is not necessarily a good decision for the USDA-PPQ to take. First, not enough information is known about how far this species has spread and whether it is truly established. Established populations are those that have individuals that are successfully reproducing. It may be that isolated populations are established but it is not clear if the USDA-PPQ truly considers this species established throughout the U.S. It is the opinion of this author that this species is

not broadly established and small isolated populations should be eradicated, if possible, whenever they are found.

Second, no research has ever been conducted to investigate the impact C. nemoralis has had on the native gastropod communities or native ecosystems in areas where this species has been introduced. The data reported herein indicate that C. nemoralis can live at high population densities as an exotic and has the potential to dominate native gastropod communities. This species could have long lasting effects and seriously impact native gastropods and perhaps drive local native populations to extinction. This is a serious issue and should be researched further.

Third, C. nemoralis is known as a pest species in Europe. In the U.S. C. nemoralis has only been labeled ^a pest from vineyards in New York (Martinson, 1999). Cepaea nemoralis may appear to be benign throughout its non-native range, however this current scenario could easily be changed. Grosholz (2005) documented a case where a non-native bivalve in California, introduced 50 years ago, was thought of as benign and having relatively no impact on the native ecosystem. However this non-native bivalve quickly became a serious problem with the introduction of another non-native species of marine crab. This phenomenon is called "invasional meltdown" and it suggests that an ecosystem is more easily invaded with increasing numbers of exotic animals and that the interaction between these exotics may allow them to become more invasive (Ricciardi, 2001). In the case presented by Grasholz the introduced crab began to eat native bivalves, thus creating new niche opportunities for the relatively 'quiet' non-native bivalve which has now allowed for the rapid spread of the non-native bivalve. It is likely that another non-native species could be introduced allowing for C. nemoralis to utilize

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newly created niche opportunities and become a serious pest species here in the U.S. The economic impact on agriculture could be serious if C. *nemoralis* became as pestiferous here in the U.S. as it is in Europe.

Fourth, the dispersal capabilities of C. nemoralis in the U.S. are poorly understood. This study is the first to quantify the short-distance dispersal of C . *nemoralis* in a non-native environment. The abiotic (temperature and humidity) and biotic (vegetation) conditions of the environment are very important for snail dispersal. Knowing how snail dispersal is closely tied to these conditions will allow for better recognition of source and sink habitats for invading snail species. Identifying sink habitats will allow those agencies responsible for the management of invasive species to evaluate the disruptive properties of natural barriers to snail dispersal. Corridors can also be identified and potentially modified, if needed, to prevent further spread. Much more research is warranted to determine the dispersal ecology of invasive land snails in a nonnative environment.

Every year more and more exotic snail species are identified coming into the U.S. and little attention is paid to these invaders. Between 1999 and 2001 seven new species of land snails were identified coming into the U.S. (Robinson and Slapcinsky, 2005). Sullivan et al. (2004) reported that 12% of containers found at container yards in Detroit, Michigan were infested with one or more species of exotic snail (Xerolenta obvia, Candidula intersecta, Monacha cartusiana, and Hygromia cinctella). Cepaea nemoralis was also found at several of these sites in Detroit but no attempt to eradicate them was made because this species is considered established. The USDA-PPQ eradicated some of the snails $(X, obvia and M,$ cartusiana) found at these container yards. The USDA-PPQ

admits that exotic snails have been overlooked as a pest problem (Sullivan, 2004). They also suggest that many exotic snails have become naturalized over the last 100 years with minimal impact to agriculture. They further admit that "the biology of many snails is poorly described and they may not be recognized as damaging pests (Sullivan, 2004)". This author feels that we should remain cautious and not become complacent with regards to these "naturalized" exotic snails. Very little biological and ecological information exists about many of these exotic snails in non-native ranges and we should not assume them to be benign. We should also not look to find answers to the biological and ecological questions we have about these exotic land snails in the literature regarding them in there native ranges. As this current research has demonstrated that natural history traits and dispersal ecology information may be different from native to nonnative ranges.

Exotic species have major economic and ecological impacts. Controlling and managing them has become a serious problem in the U.S. Simberloff et a1. (2005) suggested that it is inadequate research and funding, insufficient policy, and gaps in scientific knowledge that has lead to this problem in management and control. This rings true for the exotic land snail dilemma as well. Cowie (2005) called for better quarantine strategies, pre-entry regulations and screening, and establishing a rapid response to eradicate new populations of invading land snails as a means to prevent establishment and spread of an invader. Sullivan et al. (2004) however has stated that the USDA-PPQ does attempt to prevent exotic snails from entering the U.S., but they do very little when it comes to eradicating them. It seems that if a local population is deemed "established" no eradication attempts will be made. ^I am concerned, however, with the policy that sets

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the criteria for whether a population is established or not. There is a "hurry up and wait" atmosphere when it comes to dealing with exotic land snails and doing nothing is becoming the norm. The stand of the USDA-PPQ is that the invading land snail has to be causing damage before eradication attempts are made (Sullivan et al., 2004).

It is the opinion of this author that the complacency and attitude of the USDA-PPO towards C. nemoralis may be regretted in the future. This research has shed light upon the short-distance dispersal capabilities and population dynamics of C . *nemoralis* as an exotic and invader. Cepaea nemoralis has the potential to become another example of "what can go wrong" if the threat of an invading organism is overlooked. Lack of knowledge and information on dispersal and natural history make research into C. nemoralis and other invasive land snail species very important.

Recommendations

Land snail dispersal can be determined accurately using harmonic radar tracking techniques. This new technique offers a high degree of accuracy without the labor intensive mark-and-recapture methods traditionally used to estimate dispersal. Further work needs to be done to determine the dispersal of non-banded exotic C. *nemoralis* in grassland habitats. There have been reports of non-banded C. nemoralis populations in New York. A comparative dispersal study using HR should be performed placing nonbanded C. nemoralis in woodland habitats and in grassland habitats. Further research needs to be conducted in Europe to determine the dispersal capabilities of this species and others using harmonic radar. This would allow for direct comparisons of dispersal between this species in its native range to snails in North America. Understanding the natural history and short-distance dispersal of any invasive land snail in more detail will

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help with future control and eradication.

The example of *Achatina fulica* (See Chapter 1 for a review of A. fulica) has also demonstrated that many of these exotic snails may be harboring organisms that can cause disease in humans or wildlife. It is not known what parasitic organisms these introduced land snails could be bringing into the U.S. No research is being conducted to monitor and survey this potential threat to both humans and wildlife. There are examples in the literature of introduced species harboring parasites that could infect native species. Irizarry-Rovira et al. (2002) reported that a panther chameleon, *Furcifer pardalis* Cuvier, 1829, found in Indiana was infected with the microfilarial nematode, *Foleyella* sp. Panther chameleons, and this species of nematode, are native to Madagascar and this individual chameleon was imported to the U.S. through the pet trade. This particular species of nematode can cause disease (thrombosis, edema, and necrosis) in reptiles and the vector for this parasite is the mosquito (*Culex sp.* and *Aedes sp.*). Here in the U.S. we have native species of mosquito that could serve as a vector for this parasite. It is easy to see that an epizootic could have occurred in our native reptiles if this parasite had spread via the mosquito vector. A serious threat exists from many of these exotic species because they may carry infectious agents that could potentially lead to outbreaks of disease in both human and wildlife populations. Snails (aquatic and land) and molluscs in general serve a vital role in all digenetic trematode life cycles. Surveys should be conducted to identify any parasites that these non-native snail species are harboring.

The population of C. nemoralis in Ingham County was most likely introduced when green ash trees were planted by a commercial nursery. The Snail Central site was a field before the trees were planted in the late 1980's and early 1990's. This particular

morph of C. *nemoralis* does not survive well and is unlikely to establish a population in an open field. Therefore, it is probable that this population was introduced during the time of tree planting. This demonstrates the importance of human activity in the movement of this snail species throughout the country. This population has been at this location for over 15 years and has not managed to spread beyond the study site. This is a strong indicator that the surrounding areas are indeed sink habitats and act as barriers to the short-distance dispersal of C. nemoralis. However, it is only a matter of time before individuals are transported to far off places. Currently, SC has been put up for sale by the landowners. It is likely that the property will be developed and houses will be built. It is plausible that as this development takes place and the land is cleared that individual C. nemoralis could be removed and transported to distant places. This type of long-distance dispersal must be prevented and it is the recommendation of this author that this population of C. nemoralis be eradicated.

Appendix A

Table A.1. The types of plants identified from each of the 5 habitats found at the study Table A.1. The types of plants identified from each of the 5 habitats found at the studenties in Ingham County, Michigan.

Table A.1. The types of plants identified from each of the 5 habitats found at the stud					
site in Ingham County, Michigan.					
Plant Species	Snail Central	Blue Spruce	South Field	North Field	Homestead
Green Ash, Fraxinus pennsylvanica	X		X		
White Ash, Fraxinus americana	X				
Silver Maple, Acer	X	X			X
saccharinum Domestic Apple, Malus	X	X			
pumila Trembling Aspen,	X	X			
Populous tremuloides					
Pin Oak, Quercus palustris Honey Locust, Gleditsia	X	X X			
triacanthos White Mulberry, Morus					
alba	X	X			
Blue Spruce, Picea pungens		X			
Staghorn Sumac, Rhus typhina		X	X	X	
Poison Ivy, Rhus radicans	X	X	X	X	
Common Dandelion, Taraxacum officinale	X	X	X	X	X
Canada Golden Rod,	X	X	X	X	
Solidago canadensis Fleabane, Erigeron	X	X			
canadensis Curled Dock, Rumex	X		X		
crispus					
Common St. Johnswort, Hypericum perforatum			X		
Black Medick, Medicago lupulina	X				
White Cockle, Silene			X	X	
pratensis Ox-eye Daisy,	X		X		
Chyrsanthemum leucanthemum					
Lamb's-Quarters,			X	X	
Chenopodium album Sulphur Cinqefoil,	X	X	X	X	
Potentilla recta Milkweed, Asclepias			X	X	
syriaca					
Water Hemlock, Cicuta maculate	X				
Chicory, Cichorium intybus	X	X			

Appendix B

Figure B.1. Compass designations for determining directionality in C . nemoralis dispersal from the SC and SF in Ingham County, Michigan.

Appendix C

TAG	Transponder	Shell Diameter	Age	Habitat
Designation	Type	(mm)		
X ₁	Monopole	22	Adult	SC
X ₂	Monopole	21	Adult	SC
X ₃	Monopole	21	Adult	SC
X4	Monopole	22	Adult	SC
X ₅	Dipole	20	Adult	SC
X6	Monopole	20	Adult	SC
X ₇	Monopole	21	Adult	SC
X8	Monopole	21	Adult	SC
X9	Monopole	20	Adult	SC
X10	Monopole	21	Adult	SC
X11	Monopole	21	Adult	SC
X12	Monopole	20	Adult	SC
X13	Monopole	21	Adult	SC
X14	Monopole	22	Adult	SC
Y ₁	Monopole	19	Juvenile	SC
Y ₂	Monopole	17	Juvenile	SC
B9	Monopole	15	Juvenile	SC

Table C. l. TAG designation, transponder type, shell diameter (mm), age, and habitat Table C.1. TAG designation, transponder type, shell diameter (mm), age, and habitate
release site for individual C. *nemoralis* tracked in 2003. release site for individual C. nemoralis tracked in 2003. C.1. TAG designation, transponder type, shell diameter (mm), age, and habitat
site for individual C. nemoralis tracked in 2003.
AG Transponder Shell Diameter Age Habitat
nation Type (mm)

Appendix D

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Table D.1. TAG designation, transponder type, shell diameter (mm), age, and habitat Table D.1. TAG designation, transponder type, shell diameter (mm), age, and habita
release site for individual *C. nemoralis* tracked in 2004. release site for individual C. nemoralis tracked in 2004.

Appendix E

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		Table E.1. TAG designation, transponder type, shell diameter (mm), age, and habitat		
	release site for individual C. nemoralis tracked in 2005.			
TAG Designation	Transponder Type	Shell Diameter (\mathbf{mm})	Age	Habitat
B1 B2	Monopole	20 21	Adult Adult	SC SC
B3	Monopole Monopole	20	Adult	SC
B4 B5	Monopole Monopole	20 21	Adult Adult	SC SC
B6	Monopole	20	Adult	SC
B7	Monopole	21	Adult	SC
B8	Monopole	21	Adult	SC
B9 B10	Monopole Monopole	20 20	Adult Adult	SC SC
M1	Monopole	20	Adult	SF
M ₂	Monopole	20	Adult	SF
M3	Monopole	20	Adult	SF
M ₄ M ₅	Monopole Monopole	22 20	Adult Adult	SF SF
M ₆		21	Adult	SF
M ₇				
	Monopole Monopole	21	Adult	SF
M8 M9	Monopole Monopole	21 21	Adult Adult	SF SF

Table E.1. TAG designation, transponder type, shell diameter (mm), age, and habitat Table E.1. TAG designation, transponder type, shell diameter (mm), age, and habitat
release site for individual *C. nemoralis* tracked in 2005. release site for individual C. nemoralis tracked in 2005.

Appendix F

Table F.1. The 33 sites that were surveyed for the presence of C. nemoralis from Table F.1. The 33 sites that were surveyed for the presence of *C. nemoralis* from
Ingham County, Michigan in 2003 – 2005.

Ingham County, Michigan in 2003 - 2005.

Appendix G

Figure G.1. Frequncy histogram of C. nemoralis daily dispersal from SC in 2004.

Dispersal (meters)

Figure G2. Frequncy histogram of C. nemoralis daily dispersal from SF in 2004.

Figure G.3. Frequncy histogram of C. nemoralis weekly dispersal from SC in 2004.

Figure G.4. Frequncy histogram of C. nemoralis weekly dispersal from SF in 2004.

Figure G.5. Frequncy histogram of C. nemoralis daily dispersal from SC in 2005.

Figure G.6. Frequncy histogram of C. nemoralis daily dispersal from SF in 2005.

Appendix H

Figure H.1. Daily dispersal of snail 21 over a 14 day period from $\ddot{}$ $\mathbf{S}\tilde{\mathbf{C}}$ in 2004.

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Figure H.10. Daily dispersal of snail 210 over a 14 day period from SC in 2004.

Figure H.15. Daily dispersal of snail B5 over a 14 day period from SC in 2004.

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Appendix ^I

Figure 1.1. Design of the short-term experimental study. The five blocks are labeled A, B, C, D, and E and each contains three treatment plots that were 10 x 10 meter in size with a 3 x 3 meter sub-plot (treatment zone) located in the center. The three treatments were bait, no bait and sham bait.

LITERATURE CITED

Ackerman, J. D., B. Sim, S. J. Nichols, and R. Claudi. 1994. A review of the early life history of zebra mussel (*Dreissena polymorpha*): comparisons with marine bivalves. Canadian Journal of Zoology 72:1169-1179.

Arnold, R. 1969. The effects of selection by climate on the land-snail Cepaea nemoralis (L.). Evolution 23:370-378.

Backeljau, T., A. Baur, and B. Baur. 2001. Population and Conservation Genetics. Pages 383-412 in The Biology of Terrestrial Molluscs. Edited by G. M. Barker. CABI Publishing, New York.

Baker, G. H. 1988. Dispersal of Theba pisana (Mollusca: Helicidae). Journal of Applied Ecology 25:889-900.

mm. 2002. Helicidae and Hygromiidae as pests in cereal crops and pastures in southern Australia. Pages 193-215 in Mollusca as Crop Pests. Edited by G. M. Barker. CABI Publishing, New York.

Barker, G. M. 2001. The Biology of Terrestrial Molluscs. CABI Publishing, New York. 558 pages.

------ . 2002. Molluscs as Crop Pests. CABI Publishing, New York. 468 pages.

Baur, A., and B. Baur. 1990. Are roads barriers to dispersal in the land snail *Arianta* arbustorum? Canadian Journal of Zoology 68:613-617.

------, and mm. 1992. Effect of corridor width on animal dispersal: A simulation study. Global Ecology and Biogeography Letters 2:52-56.

------, and ------. 1993*a*. Climatic warming due to thermal radiation from an urban area as possible cause for the local extinction of a land snail. Journal of Applied Ecology 30:333-340

------, and ------. 1993b. Daily movement patterns and dispersal in the land snail Arianta arbustorum. Malacologia 35:89-98.

Baute, T, and C. DiFonzo. Bugs n Slugs. Presentation given to the Ontario Soybean Growers.

Brazee, R. D., H. Zhu, E. S. Miller, M. E. Reding, M. G. Klein, and B. E. Nudd. 2004. Development of harmonic radar transponders to track black vine weevil behavior in nurseries. Asae Annual International Meeting. Paper no. 041033.

Brooks, S. T., and B. W. Brooks. 1934. A new colony of *Helix nemoralis* with some observations on their color. Nautilus 47:96-100.

Bruno Baur. 2005. Personal Communication, Department of Integrative Biology, University of Basel, Basel, Switzerland.

Brussard, P. F. 1975. Geographic variation in North American colonies of Cepaea nemoralis. Evolution 29:402-410.

------, and G. F. McCracken. 1974. Allozymic variation in a North American colony of Cepaea nemoralis. Heredity 33:98-101.

Burch, J. B. 1955. Some ecological factors of the soil affecting the distribution and abundance of terrestrial gastropods in eastern Virginia. The Nautilus 69:62-69.

------. 1962. How to Know The Eastern Land Snails. Wm.C Brown Company, Dubuque, Iowa. 214 pages.

Canadian Food Inspection Agency (CFIA). 2003. List of pests regulated by Canada. www.inspection.gc.ca/english/plaveg/protect/listpespare.shtml. Downloaded March 10, 2003.

Cain, A. J., L. M. Cook, and J. D. Currey. 1990. Population size and morph frequency in a long-term study of Cepaea nemoralis. Proceedings of the Royal Society of London Series B 240:231-250.

------, and J. D. Currey. 1963a. Differences in interactions between selective forces acting in the wild on certain pleiotropic genes in *Cepaea. Nature* 197:411-412.

------, and ------. 1963b. Area effects in *Cepaea. Philosophical Transactions of the* Royal Society of London Series B-Biological Sciences 246:1-81.

------, and ------. 1968. Studies on *Cepaea III.* Ecogenetics of a population of *Cepaea* nemoralis (L.) subject to strong area effects. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 253:447-482.

Cain, A. J., and P. M. Sheppard. 1950. Selection in the polymorphic land snail Cepaea nemoralis. Heredity 4:275-294.

------, and ------. 1954. Natural selection in Cepaea. Genetics 39:89-116.

Cameron, R. A. D. 1970. The survival, weight-loss and behaviour of three species of land snail in conditions of low humidity. Journal of Zoology London 160:143-157.

Cameron, R. A. D. 1992. Change and stability in Cepaea populations over 25 years: a case of climatic selection. *Proceedings of the Royal Society of London Series B* 248:181-187.

------, and P. Williamson. 1977. Estimating migration and the effects of disturbance in mark-recapture studies on the snail Cepaea nemoralis (L.). Journal of Animal Ecology 46: ¹ 73-1 79.

Carreck, N. L., J. L. Osborne, A. E. Capaldi, J. R. Riley. 1999. Tracking bees with radar. Bee World 80:124-131.

Chang, H. 1991. Food preference of the land snail Cepaea nemoralis in a North American population. Malacological Review 24:107-114.

Clarke, B., and J. Murray. 1962. Changes of gene-frequency in Cepaea nemoralis (L.); the estimation of selective values. Heredity 17:467-476.

' dr-

Cohen, A. N. 2002. Success factors in the establishment of human-dispersed organisms. Pages 374-394 in Dispersal Ecology: The 42nd Symposium of the British Ecological Society. Edited by J. M. Bullock, R. E. Kenward, and R. S. Hails. Blackwell Publishing.

Cook, L. M. 1998. A two-stage model for Cepaea polymorphism. Philosophical Transactions ofthe Royal Society London Series B-Biological Sciences 353:1577-1593.

------, R. H. Cowie, and J. S. Jones. 1999. Change in morph frequency in the snail Cepaea nemoralis on the Marlborough Downs. Heredity 82:336-342.

Cowie, R. H. 1984. Density, dispersal and neighborhood size in the land snail Theba pisana. Heredity 52:391-401.

------. 2005. Alien non-marine molluscs in the islands of the tropical and subtropical Pacific: A review. American Malacological Bulletin 20:95-103.

Currey, J. D., R. W. Arnold, and M. A. Carter. 1964. Further examples of variation of populations of Cepaea nemoralis with habitat. Evolution 18:111-117.

Davison, A. 1999. Isolation and characterization of long compound microsatellite repeat loci in the land snail, Cepaea nemoralis $L - (Mollusca, Gastropoda, Pulmonata)$. Molecular Ecology 8:1760-1761.

------, and B. Clarke. 2000. History or current selection? A molecular analysis of 'area effects' in the land snail Cepaea nemoralis. Proceedings of the Royal Society of London Series B 267:1399-1405.

Denny, M. 1980. The role of gastropod pedal mucous in locomotion. Nature 285(5761)l60-16l.

Diver, C. 1939. Aspects of the study of variation in snails. Journal of Conchology 21 :91-141.

Dundee, D. S., P. H. Phillips, and J. D. Newsom. 1967. Snails on migratory birds. Nautilus 80(3):89-91.

Ehrlich, P. R. 1986. Which species will invade? Pages 79-95 in Ecology of Biological Invasions of North America and Hawaii. Edited by H. Mooney and J. Drake. Springer-Verlag, New York.

Garton, G. W., D. J. Berg, A. M. Stoeckmann, and W. R. Haag. 1993. Biology of recent invertebrate invading species in the Great Lakes: The spiny-water flea, Bythotrephes cederstroemi, and the zebra mussel, Dreissena polymorpha. Pages 63-84 in Biological Pollution: The Control and Impact of Invasive Exotic Species. Edited by B. H. McKnight. Indiana Academy of Science, Indianapolis.

Glassner-Shwayder, K. 1998. Biological invasions: How aquatic nuisance species are entering North American waters, the harm they cause and what can be done to solve the problem. Great Lakes Panel on Aquatic Nuisance Species. Great Lakes Commision, Ann Arbor, Michigan.

Godan, D. 1983. Pest Slugs and Snails: Biology and Control. Eugen Ulmer GmbH & Co., Stuttgart, Germany. 445 pages.

Goodhart, C. B. 1962. Variation in a colony of the snail Cepaea nemoralis (L.). Journal ofAnimal Ecology 31 :207-23 7.

Greenwood, J. J. D. 1974. Effective population numbers in the snail Cepaea nemoralis. Evolution 28:513-526.

Grosholz, E. D. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proceedings of the National Academy of Sciences of the United States of America 102(4):1088-1091.

Hadfield, M. G., S. E. Miller, and A. H. Carwile. 1993. The decimation of endemic Hawaiian tree snails by alien predators. American Zoologist 33(6):610-622.

Harris, L.D., and G. Silva-Lopez. 1992. Forest fragmentation and the conservation of biological diversity. Pages 197-237 in Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management. Edited by P. L. Fiedler and S. K. Jain. Chapman and Hall, New York.

Heath, D. J. 1975. Colour, sunlight and internal temperatures in the land-snail Cepaea nemoralis (L.). 0ecologia 19:29-38.

Heller, J. 2001. Life History Strategies. Pages 413-445 in The Biology of Terrestrial Molluscs. Edited by G. M. Barker. CABI Publishing, New York.

Henderson, I., and R. Triebskorn. 2002. Chemical control of gastropods. Pages $1 - 31$ in Mollusca as Crop Pests. Edited by G. M. Barker. CABI Publishing, New York.

Irizarry-Rovira, A. R., A. Wolf, M. Bolek, J. A. Christian, and D. B. DeNicola. 2002. Blood smear from a wild-caught Panther Chameleon (Furcifer pardalis). Veterinary Clinical Pathology 31(3):]29-132.

Jones, J. S., B. H. Leith, and P. Rawlings. 1977. Polymorphism in Cepaea: A problem with too many solutions. Annual Review of Ecology and Systematics 8:109-143.

Lamotte, M. 1951. Recherches sur la structure genetique des populations naturelles de Cepaea nemoralis (L.). Bulletin Biologique de la France et de la Beligique, Supplement $35:1-239.$

Lovei, G. L., I. A. N. Stringer, C. D. Devine, and M. Cartellieri. 1997. Harmonic radar — A method using inexpensive tags to study invertebrate movement on land. New Zealand Journal of Ecology $21(2):187-193$.

------, S. M. Bassett, M. J. McLean, J. McCartney, and G. R. Parrish. 2003. Biology and conservation of the rare New Zealand land snail Paryphanta busbyi watti (Mollusca, Pulmonata). Invertebrate Biology ¹ 12(3):241-251.

Lozek, V. 1962. Soil conditions and their influence on terrestrial gasteropoda in central Europe. Pages 334-342 in Progress in Soil Zoology. Edited by P. W. Murphy. Butterworth Inc., U.S.A.

MacFarlane, D. W., and S. P. Meyer. 2005. Characteristics and distribution of potential ash tree hosts for emerald ash borer. Forest Ecology and Management 213:15-24.

Mack, R. N., D. Simberloff, W. K. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10(3):689-710.

Martinson, T. E. 1999. Biology and control of the striped garden snail Cepaea nemoralis in vineyards. Finger Lakes Grape Program, Report to National Grape Cooperative. 8 pages.

Mascanzoni, D., and H. Wallin. 1986. The harmonic radar: A new method of tracing insects in the field. Ecological Entomology 11:387-390.

Michigan State University — Integrated Pest Management (MSU - IPM). 2001. Land snails in baled hay. Field Crop Advisory Team Alert vol. 15, no. 18. www.msue.msu.edu/ipm/CAT00_field/FC02-02-01.htm. Downloaded March 10, 2003. Murray, J. J. 1962. Factors affecting gene frequency in some populations of *Cepaea*. Doctor of Philosophy Thesis. University of Oxford.

Murray, J. 1964. Multiple mating and effective population size in *Cepaea nemoralis*. Evolution 18:283-291.

National Agricultural Pest Information Systems (NAPIS). 2003. www.ceris.purdue.edu/napis. Downloaded March 8, 2003.

Odenkirk, J., and S. Owens. 2005. Northern snakeheads in the tidal Potomac River system. Transactions of the American Fisheries Society 134:1605-1609.

O'Neal, M. E., D. A. Landis, E. Rothwell, L. Kempel, and D. Reinhard. 2004. Tracking insects with harmonic radar: A case study. American Entomologist 50(4):212-218.

Ozgo, M. 2005a. Cepaea nemoralis (L.) in southeastern Poland: Association of morph frequencies with habitat. Journal of Molluscan Studies 75:93-103.

------. 2005b. The effect of shell colour on activity of the land snail Cepaea nemoralis in outdoor cage experiments. Bulletin of the Malacological Society of London 44:9.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 1999. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53-65.

Raut, S. K., and G. M. Barker. 2002. Achatina fulica Bowdich and other Achatinidae as pests in tropical agriculture. Pages $55 - 114$ in Mollusca as Crop Pests. Edited by G. M. Barker. CABI Publishing, New York.

Reed, C. F. 1964. Cepaea nemoralis (LINN.) in eastern North America. Sterkiana 16:11-18.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 58:2513-2525

Richardson, A. M. M. 1975. Food, feeding rates and assimilation in the land snail Cepaea nemoralis L. 0ecologia 19:59-70.

Riley, J. R., P. Valeur, A. D. Smith, D. R. Reynolds, G. M. Poppy, and C. Löfstedt. 1998. Harmonic radar as a means of tracking the pheromone-finding and pheromonefollowing flight in male moths. Journal of Insect Behavior 11:287-296.

------, D. R. Reynolds, and A. D. Smith. 1999. Compensation for the wind by foraging bumble bees. Nature 400: 126.
Roland, J., G. McKinnin, C. Backhouse, and P. D. Taylor. 1996. Even smaller radar tags on insects. Nature 381 :120.

Sakovich, N. J. 2002. Integrated management of *Cantareus aspersus* (Muller) (Helicidae) as a pest of citrus in California. Pages 353 — 360 in Mollusca as Crop Pests. Edited by G. M. Barker. CABI Publishing, New York.

Schnetter, M. 1951. Veranderungen der genetischen Konstitution in naturlichen Populationen der polymorphen Banderschnecken. Zoologischer Anzeiger, Supplement ¹ 5: ¹ 92-206.

Shigesada, N., and K. Kawasaki. 2002. Invasion and the range expansion of species: Effects of long-distance dispersal. Pages $350 - 373$ in Dispersal Ecology: The $42nd$ Symposium of the British Ecological Society. Edited by J. M. Bullock, R. E. Kenward, and R. S. Hails. Blackwell Publishing.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. TRENDS in Ecology and Evolution 17(4):170-176.

Simberloff, D., I. M. Parker, P. N. Windle. 2005. Introduced species policy, management, and future research needs. Frontiers in Ecology and the Environment 3(1): 12-20.

Smith, J. W. 2005. Recently recognized risk of importing the giant African snail, Achatina fulica Bowdich, 1822, and its relatives into the United States and the efforts of the U.S. Department of Agriculture to mitigate the risk. American Malacological Bulletin 20:133-141.

Speiser, B. 2001. Food and Feeding Behavior. Pages 259-288 in The Biology of Terrestrial Molluscs. Edited by G. M. Barker. CABI Publishing, New York.

Stringer, I. A. N., S. M. Bassett, M. J. McLean, J. McCartney, and G. R. Parrish. 2003. Biology and conservation of the rare New Zealand land snail, Paryphanta busbyi watti (Mollusca, Pulmonata). Invertebrate Zoology 122(3):241-251.

Stiling, P. D. 1996. Ecology Theories and Applications, 2nd Edition. Prentice-Hall Inc., Simon and Schuster, New Jersey. 539 pages.

Sullivan, B., D. Dehn, J. Manor, and D. McKay. 2004. Report and commentary: Exotic snails discovered to be established in container yards in Detroit, Michigan. Report prepared by the United States Department of Agriculture, Animal and Plant Health Inspection Service.

United States Department of Agriculture (USDA). 1959. Land slugs and snails and their control. Farmer's Bulletin No. 1895. 8 pages.

United States Department of Agriculture — Animal and Plant Health Inspection Service (USDA-APHIS). 2005. New Pest Response Guidelines. Giant African Snails: Snail Pests in the Family Achatinidae. USDA/APHIS/PPQ/PDMP, Riverdale, Maryland. www.aphis.usda.gov/ppq/manuals/

United States Department of Agriculture — National Agricultural Library for the National Invasive Species Council (USDA-NAL). 2003. Invasive Species. www.invasivespecies.gov. Downloaded March 8, 2003.

United States Environmental Protection Agency (USEPA). 2005. Iron (Ferric) Phosphate (034903) Technical Document. www.cpa.gov/pesticides/biopesticides/ingediants/tech_docs/tech_034903.htm. Downloaded November 24, 2005.

University of California Integrated Pest Management (UCIPM). 2006. How to Manage Pests: Pests in Landscapes and Gardens. www.ipm.ucdavis.edu/PMG/PESTNOTES/pn7427.html. Downloaded January 8, 2006.

Walters, L. J., K. R. Brown, W. T. Stame, and J. L. Olsen. 2005. E-commerce and Caulerpa: Unregulated dispersal of invasive species. Frontiers in Ecology and the Environment 4(2):75-79.

Washington State Department of Ecology (WSDE). Non-native Freshwater Plants: Purple Loosestrife. www.ecy.wa.gov/programs/wq/plants/weeds/aqua009.html. Downloaded 2004.

Waugh, C. A., S. Shafir, M. Wise, R. D. Robinson, M. L. Eberhard, and J. F. Lindo. 2005. Human Angiostrongylus cantonensis, Jamaica. Emerging Infectious Diseases 11(12):]977-1978.

Williamson, P., and R. A. D. Cameron. 1976. Natural diet of the landsnail Cepaea nemoralis. Oikos 27:493-500.

Wolda, H. 1967. The effect of temperature on reproduction in some morphs of the landsnail Cepaea nemoralis (L.). Evolution 21:117-129.

------, and D. A. Kreulen. 1973. Ecology of some experimental populations of the landsnail Cepaea nemoralis (L.). II. Production and survival of eggs and juveniles. Netherlands Journal of Zoology 23:168-188.

------, A. Zweep, and K. A. Schuitema. 1971. The role of food in the dynamics of populations of the landsnail Cepaea nemoralis. Oecologia 7:361-381.

