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HERBIVORY AND DETRITIVORY BY THE LAND SNAIL CEPAEA NEMORALIS IN A TEMPERATE OLD FIELD

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HERBIVORY AND DETRITIVORY BY THE LAND SNAIL *CEPAEA NEMORALIS* IN A TEMPERATE OLD FIELD

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Abstract and Keywords

The European banded wood snail (*Cepaea nemoralis*) has become widespread throughout the northeast United States and Canada, thriving in woodlands, roadsides, disturbed habitats, grasslands, and old fields. I used exclosure experiments to investigate the effect of snail herbivory on the biomass of Canada thistle (*Cirsium arvense*), a highly palatable forb species. I measured grass litter within exclosures to determine the effects of detritivory on litter mass and used fecal analysis to determine the ratio of dead to live plant material in the diet. Snail exclosures had no effect on the total biomass of *C. arvense* or mass of grass litter. Live plants comprised approximately 10% of the overall snail diet with the remainder consisting of plant litter and soil. There was no clear seasonal trend in consumption of green material. However, snail herbivory increased with time from the last precipitation event, suggesting that snails consume live material to obtain water.

Keywords: herbivory, detritivory, terrestrial molluscs, *Cepaea nemoralis*, *Cirsium arvense*, gastropod diet

Co-Authorship Statement

Dr. Hugh Henry will be given co-authorship on any manuscripts published from the data chapters of this thesis. Dr. Henry provided invaluable guidance and direction during the design and implementation of these experiments, as well as during data analysis and interpretation.

Dedication

I would like to dedicate this thesis to my mother, father, and brother. They have always supported me and I am grateful that I have such a wonderful family.

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1.0 Introduction

1.1 Terrestrial herbivory

Terrestrial herbivores are influential components of ecosystem food webs (Cebrian 2004) making up roughly a third of all species and consuming 10% to 15% of the annual global net primary productivity (Crawley 1983, Cyr and Pace 1993). Although they occupy many ecological niches and habitats, their effects vary among systems; tropical and temperate grasslands as well as old fields are heavily grazed (4-25% of primary productivity removed), temperate and tropical forests are moderately grazed (2-15% of primary productivity removed), and tundra and deserts have on average lower amounts of grazing, but are prone to severe herbivore outbreaks (Cyr and Pace 1993, McNaughton et al. 1996). The prevalence of herbivory varies among taxa (Huntly 1991) but is particularly common in arthropods, molluscs, ungulates, and birds (Crawley 1983). A wide diversity of feeding modes (Table 1.1) allows herbivores to exploit a variety of tissues including fruits (frugivores), phloem (mucivores), seeds (granivores), and leaves (folivores) (Crawley 1983).

1.1.2 Direct effects of herbivory

Herbivory can have major effects on individual plants, community dynamics, and entire ecosystem processes (McNaughton 1983, Schmitz 2008) . It directly reduces plant growth and biomass (Wardle and Barker 1997) and alters plant shape and structure (Inouye 1982) by the removal of tissue or by the release of apical dominance (Huntly 1991). Photosynthetic activity is lost from the tissues that are directly consumed (Aldea et al. 2006); however, photosynthetic activity is also indirectly reduced in the surrounding ungrazed tissue (Zangerl et al. 2002). Plant re-growth after grazing depletes critical carbohydrate stores (Priestley 1970, Landhausser et al. 2003), thereby limiting the amount of resources the plant has for seed production or clonal spread (Cunningham 1997). Grazing on seedlings limits the recruitment and spread of plants by increasing seedling mortality (Hulme 1994).

Table 1.1. Herbivore feeding modes. Table modified from Crawley (1983).

Food items	Mode of feeding	Species example
Leaves	Clipping	Ungulates, slugs, sawflies, butterflies, etc.
	Skelotonizing	Beetles, sawflies, capsid bugs
	Holing	Moths, weevils, pigeons, slugs, etc.
	Rolling	Microlepidoptera, aphids
	Spinning	Lepidoptera, sawflies
	Mining	Microlepitdoptera, Diptera
	Rasping	Slugs, snails
	Sucking	Aphids, psyllids, hoppers, whitefly, mites, etc.
Herbaceous/ woody stems	Removal	Ungulates, sawflies, etc.
	Boring	Weevils, flies, moths
	Sucking	Aphids, scales, cochineals
Seeds	Predation	Deer, squirrels, mice, finches, pigeons
	Boring	Weevils, moths, bruchids
	Sucking	Lygaeid bugs
Flowers	Nectar drinking	Bats, hummingbirds, butterflies, etc.
	Pollen eating	Bees, butterflies, mice
	Receptacle eating	Diptera, microleptidoptera, thrips
	Spinning	Microlepidoptera
Fruits	Beneficial	Monkey, thrushes, ungulates, elephants
	Destructive	Wasps, moths, rodents, finches, flies, etc.

1.1.3 Indirect effects of herbivory

In plant communities, herbivory can shift the competitive balance among species by impairing the target plant's ability to compete with surrounding plants (Wardle and Barker 1997). Competitive relationships among plants are strong in terrestrial habitats and are potentially the most important factor driving community dynamics and composition (Goldberg and Barton 1992). Grazing is more likely to weaken a plant than to kill it, at which point competition from surrounding plants can be the main cause of the reduction in plant biomass (Tilman 1977, Dirzo and Harper 1980). For example, the competitive ability of dominant grasses can be impaired by grazing (Wardle and Barker 1997), allowing forb abundance to increase; however, under lower herbivore pressure, this effect can be reversed (Crawley 1983). In addition to altering plant competition, herbivores make plants more vulnerable to plant disease either through direct transmission from herbivore to plant (Hohn 2007, Fraedrich et al. 2008) or by increasing bacterial and fungal infection through grazer induced wounds (Friedli and Bacher 2001, Silliman and Newell 2003, Daleo et al. 2009). The interactive effects of grazing and fungal infection on productivity can also be greater than their additive effects alone (Daleo et al. 2009).

Although plant responses to herbivory are typically negative they can also be neutral or even positive (Maschinski and Whitman 1988). For example, low levels of leaf tissue removal by herbivores can expose shaded leaves lower in the canopy increasing photosynthetic activity (Mabry and Wayne 1997), increase growth rates (Houle and Simard 1996), and increase branching or tillering after release of apical dominance (Lennartsson et al. 1997). If losses from herbivory are compensated by these responses, then herbivory has a neutral or positive effect on plant performance (McNaughton 1983). However, compensatory growth appears to be rare in most natural habitats (Belsky 1986).

1.1.4 Plant defences against herbivory

Plant defences against herbivory vary across taxa and species (Huntly 1991, Strauss and Agrawal 1999). Plants use two strategies; they deter herbivory using plant defences or tolerate herbivory by reducing its impact on plant fitness (Crawley

1983, Stowe et al. 2000). There does not appear to be a trade-off between resistance and tolerance and species may maintain multiple defence strategies (Leimu and Koricheva 2006). For instance, graminoids impregnate their tissues with silica bodies to increase resistance (McNaughton 1983) and tolerate grazing better than dicotyledonous plants (dicots) because of their buried basal meristems (Johnson and Parsons 1985). As a result, dicots may not only be preferred by herbivores over grasses, but they also suffer more damage from herbivores when they are grazed (Grubb et al. 2008). Plants can also have inducible defences, which are triggered after they have been grazed upon, to increase resistance to herbivory (Dicke et al. 2003). Induced defences are common in perennial and longer lived species and typically include increases in physical defences (trichomes, spines, etc.) or secondary plant chemical compounds (Karban and Baldwin 1997). The specific strategies that plants use and the effectiveness of those strategies against herbivores are highly influential in determining the importance of herbivory within a given habitat (Strauss and Agrawal 1999).

1.1.5 Community scale herbivory effects

Herbivores can increase plant diversity and richness by consuming competitively dominant plants and therefore allowing weaker competitors to grow (McNaughton 1983, Huntly 1991). Herbivore size often influences the strength of this effect, with smaller herbivores having weak or negative effects on species diversity and larger herbivores making plant communities more diverse (Olff and Ritchie 1998). By consuming palatable species herbivores can shift the relative species abundance towards less palatable plants (Davidson 1993, Buschmann et al. 2005) thereby reducing herbivore carrying capacity (Augustine and McNaughton 1998). Herbivory can also alter the successional trajectories of plant communities, causing long term changes in the structure and biological composition of terrestrial habitats (Davidson 1993). Plants characteristic of early to mid-successional habitats are often highly palatable to herbivores and herbivory results in a slowing of succession. However, succession in late successional communities is accelerated by herbivory because herbivores preferentially feed on plants from earlier successional

seres (Davidson 1993). By shaping the community structure of terrestrial habitats herbivores can affect the functioning of entire ecosystems (Crawley 1983, Huntly 1991).

1.2 Detritivory

Most of the detritus in terrestrial systems is composed of dead plant material (Parsons and Tinsley 1975) with about 64% to 70% of that being leaf litter (Meentemeyer et al. 1982). Litter production is variable across systems and is affected by the net primary production (NPP) (Bray and Gorham 1964), climatic factors (Meentemeyer et al. 1982), and the amount of primary productivity consumed by herbivores (Facelli and Pickett 1991). Overall, global trends in litter production are strongly correlated with latitude (Meentemeyer et al. 1982). Old fields have high NPP which is almost all transferred to litter annually at the end of the growing season (Odum 1960, Golley 1965). Temperate forests and evergreen forests eventually transfer much of their production into litter (Facelli and Pickett 1991); however, time lags in litter production can be great with less than 50% of woodland productivity becoming litter each year (Olson 1963). Despite high primary productivity, heavy grazing often decreases litter accumulation in grasslands (Hunt 1978, Seastedt 1984).

Globally, 90% of the NPP of terrestrial ecosystems is eventually broken down by decomposers and detritivores (Crawley 1983, Nannipieri et al. 2003). Species specific plant traits including leaf toughness, litter quality (C:N), secondary chemicals, and lignin content modify decay rates by influencing microbial activity (Hattenschwiler et al. 2005). About 90% of all decomposition is performed by microbial and fungal decomposers (Seastedt 1984), that break down organic compounds within plant litter (Nannipieri et al. 2003) as well as mineralize nutrients (Coleman and Crossley 1996). However, invertebrate detritivores can be very influential in litter decomposition as well (Curry and Byrne 1997, Irmler 2000, Mayer et al. 2005). Invertebrate detritivores have been frequently acknowledged as important in aquatic habitats (Fazi and Rossi 2000), but there are relatively few studies that focus on terrestrial ecosystems (Aerts 1997, Mayer et al. 2005).

1.2.2 Detritivore feeding

Dominant invertebrate detritivores are microarthropods (mainly mites and collembolans) and macroarthropods (mainly millipedes and fly larvae) (Seastedt 1984), lumbricids (Edwards and Bohlen 1996), and molluscs (Spieser 2001). Functional feeding types of invertebrate detritivores include shredders (insects), collectors (filter feeders), scrapers (gastropods), and piercers (microcaddisflies) (Cummins and Klug 1979). Despite the direct effects of detritivore metabolism on litter decomposition being relatively neglibible (Mikola et al. 2002), their indirect influences on microbial activity are very important (Mason 1970, Seastedt 1984, Irmler 2000). Invertebrate detritivores accelerate litter fragmentation (Hattenschwiler et al. 2005), decreasing fragment size six-fold (Mcbrayer 1973) and thereby increasing the surface area available for microbial colonization (Elkins and Whitford 1982). The increased moisture retention and nutrient availability of detritivore fecal castes also provides a favorable substrate for microbial growth and increases microbial biomass (Tajovsky et al. 1992, Dangerfield and Milner 1996). However, fecal formation may be accompanied by a decrease in fungal decomposers because of the preferential digestion of fungus by detritivores (Maraun and Scheu 1996).

Plant litter often contains approximately half the nitrogen of live tissues (Killingbeck and Whitford 1996) because plants reabsorb and retain nutrients during senescence (Killingbeck 1996, Nooden et al. 1997). Litter also has a much lower level of secondary chemical compounds (Spieser 2001), although fresh detritus may retain high enough levels of chemical toxins to deter detritivores (Middleton 1984). Additionally, plant detritus may also be colonized with bacteria or fungi that are highly nutritious and invertebrates may feed on litter to obtain those microbes and fungi (Cummins and Klug 1979). Detritivores may selectively feed on plant litter with high nutrient quality (Graca et al. 2001) and their selective feeding can alter the composition of the litter and influence microbial growth (Hattenschwiler et al. 2005). Invertebrate detritivores are regulated by predators, plant species composition, and refugia (Mayer et al. 2005). Detritivores seek out preferable food patches and microhabitats (Kelaher et al. 2003) and therefore, detritivore mediated increases in decomposition can be concentrated around preferable habitats and are highly spatially

variable (Kelaher et al. 2003). In addition to their effects on microbial decomposition, when detritivores remove litter they can deposit up to 80% of it at their sheltered resting sites (Hassall et al. 1987). Consequently, they can be dominant habitat transformers by altering the physical characteristics of the litter layer and through the removal or relocation of litter (Lavelle et al. 1997, Scheu and Setälä 2002).

1.2.3 Effects of plant litter on plant growth

The litter layer directly affects plant growth (Bosy and Reader 1995), and is especially important in grassland and old field habitats where litter production is high (Tilman 1987, Carson and Peterson 1990). The physical and chemical effects of the litter layer strongly affect species richness due to the suppression of seedling germination (Xiong and Nilsson 1999). Physically, the litter layer may intercept up to 60% of light and alter the microclimate of the soil surface (Facelli and Pickett 1991), removing seed cues and reducing growth of established seedlings (Bosy and Reader 1995). Litter may also act as a mechanical barrier to shoot extension of new seedlings (Almufti et al. 1977) reducing their vertical growth and consequently limiting seedling emergence (Bosy and Reader 1995). Although not as influential as the physical effects (Hovstad and Ohlson 2008), leaching of allelopathic chemicals from plant litter can reduce plant growth and seed germination (Rice 1972, Werner 1975). For example, leachate of grass species can delay seedling germination between approximately 35-95% in other grassland species (Ruprecht et al. 2008). On the other hand, forb litter decomposes quickly (Facelli and Pickett 1991, Cornelissen 1996) and typically makes up a smaller percentage of the litter mass in these systems. Therefore, despite the chemical effects of forb litter (Xiong and Nilsson 1999), its overall importance may often be negligible (Olson and Wallander 2002).

1.3 Gastropod feeding

Important groups within the invertebrate herbivores and detritivores are the terrestrial gastropods (land snails and slugs), that play a major role in structuring the plant communities of terrestrial habitats (Crawley 1997). Gastropods are the most speciose class of the molluscan phylum and are the only class that has land dwelling

species (Ruppert et al. 2003). Terrestrial molluscs are highly successful and have invaded all types of habitats with a few particular species of gastropods becoming dominant invertebrates in terrestrial ecosystems (Barker 2001). Evaporative water loss is of particular importance to terrestrial gastropods (Prior et al. 1983, Prior 1985). Therefore they are typically nocturnal feeders, roosting during daytime high temperatures and migrating to food patches at dusk (Speiser 2001). Their locomotion is slow and restricted by the costly mucous layer they must lay down during movement (Denny 1980). Due to this type of locomotion, gastropods have developed a generalist feeding strategy (Speiser 2001) that allows them to consume a variety of food items across different habitats including both live material and detritus. As polyphagous generalist invertebrate grazers who are herbivores and detritivores (Grime and Blythe 1969, Richardson 1975, Williamson and Cameron 1976, Chevalier et al. 2001), terrestrial gastropods trade-off between maximizing nutritional quality and minimizing secondary chemical content in their food (Bernays et al. 1994). More importantly, by consuming both live and dead material, gastropods may affect ecosystems through both herbivory and detritivory (Seifert and Shutov 1981, Hulme 1994, Hanley et al. 1996, Buschmann et al. 2005).

It has been frequently demonstrated that gastropod herbivory can lead to significant changes in the relative abundance of plant species through the selective grazing of palatable plants and especially seedlings (Hanley et al. 1996, Hulme 1996 Buschmann et al. 2005, Peters 2007). Gastropod grazing may shift the relative species abundance of plants either directly or indirectly by negatively affecting adult plant vigour and fitness (Ehrlen 1995), plant growth and size (Hulme 1996, Ehrlen 2003), internal allocation of resources (Hulme 1996), and competitive relationships (Crawley 1988). Terrestrial molluscs are also important as detritivores, mainly consuming plant litter and especially dead grasses (Grime and Blythe 1969, Speiser 2001). By physically and chemically altering the litter, gastropods promote microbial and fungal growth that increases the rate of decomposition (Mason 1970) and, by removing litter, gastropod feeding may release seedlings from the suppressive effects of the litter layer (Thompson et al. 1993, Mayer 2008).

1.4 Study species – *Cepaea nemoralis*

The gastropod species, *Cepaea nemoralis* (banded wood snail), may alter plant communities through the consumption of both live and senescent plant materials (Grime and Blythe 1969). *Cepaea nemoralis* is a medium sized land snail native to Europe, and it has become locally abundant where introduced in North America (Pilsbury 1939). Over the last 150 years, *C. nemoralis* has spread rapidly and become a dominant invertebrate throughout southern Ontario and the northeastern United States (Whitson 2005). However, these new populations have received little attention (Brussard 1975). This snail is a generalist that prefers senescent material over live tissues (Richardson 1975, Chang 1991), but also shows very selective preferences for a few live plant species (Chang 1991, Grime et al. 1968). Forbs are more palatable than grasses (Grime et al. 1968, Wolda et al. 1971, Carter et al. 1979, Chang 1991) with live grasses being particularly unpalatable (Chang 1991, Grime et al. 1968). The composition and the relative amounts of herbivory and detritivory in the diet of *C. nemoralis* are highly variable across sites and appear to be site-specific (Wolda et al. 1971). Furthermore, the relative consumption of different plant materials can vary with season (Chang 1991, Wolda et al. 1971), plant species and abundance (Chang 1991, Grime et al. 1968), plant age (Grime and Blythe 1969) and plant structure (Chang 1991).

Currently, we have only a basic understanding of what determines food consumption in *C. nemoralis*, and we still do not know how snail grazing affects plant communities. Live plants that are palatable to *C. nemoralis* are rare in most habitats (Chang 1991, Grime et al. 1968). Consequently, only a few plant species make up most of the live material consumed by the snail (Richardson 1975 Williamson and Cameron 1976, Carter et al. 1979). As a result, *C. nemoralis* populations may apply intense feeding pressure on these highly palatable plants (Buschmann et al. 2005) and seedlings (Hulme 1994, Hulme 1996, Hanley et al. 2007), shifting the relative abundance of plant species. For example, the highly palatable nitrophilous plant *Urtica dioica* (stinging nettle) is often the dominant source of live material in the diet of *C. nemoralis* due to its high nutrient content as well as the protection it provides from mammalian predators (spiny trichome defences) (Grime and Blythe 1969, Carter

et al. 1979, Iglesias and Castellijo 1999). Carter et al. (1979) determined that *U. dioica* made up 75.8% of live material consumed by the snails in a chalk grassland. This concentrated grazing can remove significant amounts of leaf tissue from the plant (Grime and Blythe 1969).

In habitats where *U. dioica* is not available, specific dietary components required by the generalist snail (Williamson and Cameron 1976, Wacker and Baur 2004) may be obtained from other palatable plants. Like *U. dioica*, heavy snail grazing on these plants could significantly reduce plant biomass. One particular plant, *Cirsium arvense* (Canada thistle), is a highly palatable forb species that is common in the same habitats as *Cepaea nemoralis* (Grime et al. 1968, Wolda et al. 1971). *Cirsium arvense* also has spiny trichomes to deter mammalian herbivores (Tuberville et al. 1996) potentially providing predator refuge and like *U. dioica*, its trichome defences do not appear to impede *C. nemoralis* feeding (personal observation). *Cirsium arvense* is also nitrophilous (Obermaier and Zwolfer 1999) and may provide a rich source of nutrients for the snail in the absence of *U. dioica*. Carter et al. (1979) showed that *Cepaea nemoralis* fed disproportionately more on both *U. dioica* and *Cirsium arvense* than plant abundance would predict. In habitats without *U. dioica*, snail grazing may increase substantially on *C. arvense* in order to meet snail requirements for live material in their diet. *Cirsium arvense* is a vigorous perennial forb that grows vegetatively (clonal) and has large underground network of horizontal roots that may potentially share resources between individual plants within a clone (Hellstrom et al. 2006). Seeds are produced and recruitment to new habitats is mainly due to wind dispersal; however, clonal growth is the main method of spread once they are established (Amor and Harris 1975). Currently, we do not know how important *Cirsium arvense* is to *Cepaea nemoralis* under field conditions (Wolda et al. 1971) or how *Cepaea nemoralis* grazing affects plant biomass and the relative abundance of plant species.

Natural densities of *C. nemoralis* in the field are heavily influenced by the abundance of preferred plants (Chang 1991) and weather conditions (Chang and Emlen 1993). Weather conditions can cause localized increases around preferable microhabitats which may result in more intense grazing. For example, snails climb to

avoid ground heat (Jaremovic and Rollo 1979) and choose plants that provide both shelter and food in the hot summer months (Chang and Emlen 1993). *Cirsium arvense* is a broadleaf forb, and may provide both food and shelter during warmer months (Chang and Emlen 1993), making it vulnerable to exploitation by snails. Snail diet and grazing may vary with season and site due to these changes in microhabitat preferences. Additionally, through the consumption of litter material, *C. nemoralis* may remove the suppressive effects of plant litter and allow for greater forb germination (Bosy and Reader 1995, Wilby and Brown 2001) thus altering relative species abundance. Previous findings that *C. nemoralis* consumes mainly detritus (Grime et al. 1968, Wolda et al. 1971, Richardson 1975, Chang 1991) suggest that this snail may play an important role in litter removal.

My study investigated how grazing by *Cepaea nemoralis* affects the biomass of *Cirsium arvense* and overall litter abundance in an old field plant community in London, ON. The snail is very conspicuous at this site, and anecdotal observations (J. Bowles, personal communication) have suggested that the local populations in London, ON have been increasingly abundant over the last decade. I excluded snails using exclosures during the growing season to simultaneously measure the effects of snail feeding on *C. arvense* biomass and litter abundance. Additionally, using fecal analysis, I explored how snail feeding may be affected by weather, plant palatability, plant coverage, and season at my field site. Overall, I hypothesized that *Cepaea nemoralis* feeds heavily on *Cirsium arvense* and dead grasses, significantly reducing both the abundance of *Cirsium arvense* and the quantity of plant litter.

1.5 Objectives

Objective 1: *To determine how adult snail herbivory affects the aboveground biomass of C. arvense*. I predicted that the aboveground biomass of *C. arvense* would be increased in snail-exclosed plots relative to unexclosed control plots.

Objective 2: *To quantify the effect of detritivory by C. nemoralis on plant litter abundance.* I predicted that the density of plant litter would increase in snail-exclosed plots relative to unexclosed control plots.

Objective 3: *To determine the natural diet of C. nemoralis in the field including seasonal variation.* I predicted that *Cepaea nemoralis* would consume large amounts of senescent material, mainly grasses (Grime and Blythe 1969, Richardson 1975), but also consume green plant material, mainly *Cirsium arvense*. I predicted the amount of herbivory would vary seasonally and would be further affected by local weather patterns.

Objective 4: *To examine the relationship between vegetation and snail density.* I predicted that *C. nemoralis* density would increase around *C. arvense* because it is a palatable food plant and a good shelter plant.

2.0 Methods and Materials

2.1 Study site

The population of *C. nemoralis* I studied is located in a 0.4 ha old field at the Agriculture Canada Southern Crop Protection and Food Research Centre, in London Ontario (43° 01' 45" N, 81° 12' 50" W, 264 m a.s.l.). The site was sown with *Bromus inermis* Leyss and *Poa pratensis* L. and has been left unmanipulated since the early 1980's. The site is currently dominated by grasses with a patchy distribution of forbs and trees (Table 2.1). Weather data for the site during the experimental period are summarized in Table 2.2.

2.2 Snail exclosures (Objective 1 and 2)

I measured the effects of *Cepaea nemoralis* on *Cirsium arvense* transplants using circular exclosures (60 cm diameter, 0.33 m^2, 15 cm high). The two experimental treatments were: (1) exclosed (snail exclosures), (2) unexclosed (natural field densities), and (3) cage control (exclosure with the bottom 3 cm removed). I made all exclosures from mesh with 0.7 cm x 0.7 cm openings. This screening excluded *C. nemoralis* (> 0.7 mm), but allowed the passage of soft bodied slugs, worms, and other invertebrates. Commercially available Nixalite Copper Blocker™ copper mesh screening was attached to the top 3 cm of the interior and exterior of the exclosures to deter terrestrial gastropods from entering the plots. Copper mesh screening has been used successfully to deter terrestrial gastropods (Hata et al. 1997, Grewal et al. 2001, Peters 2007).

I used *C. arvense* as the focal forb species to investigate herbivory due to its high palatability (Grime et al. 1968) and local abundance at the site. I haphazardly selected thirty plots (ten replicates of each treatment) which had a homogenous litter layer and were at least 5 m away from any existing *C. arvense* plants. On 10 April 2008 I transplanted thirty *C. arvense* juvenile plants from their genets into the centers of the plots (one per plot). Transplanting was intended to reduce variation in plant vigour among ramets caused by resource sharing between mother and daughter plants. I gave the transplants a one time application of approximately 200 ml of water

Table 2.1. Visual plant cover estimates at the Agriculture Canada study site assessed using 128 (25 m^2) quadrats during July 2008 around the time of peak biomass.

Species	Percent Cover (%)
Graminoids	
Poa pratensis L. and *Bromus inermis* Leyss	81.6
Forbs	
Solidago altissima L.	7.5
Lotus corniculatus L.	5.4
Cirsium arvense L.	3.5
Daucus carota L.	0.5
Asclepias Syriana L.	0.2
Other Species	
Cornus and *Crataegus*	1.3
Melilotus alba Medikus	< 0.1
Aster ericoides L.	< 0.1
Fissidens taxifolius Hedw.	< 0.1
Brachythecium salebrosum (Hoffm.) Bruch & Schimper	< 0.1

Table 2.2. Weather data from May to October 2008 the London International Airport weather station (6 km from the field site) including mean temperature, maximum average temperature, minimum temperature average, total precipitation, and number of precipitation days. Data from Enivronment Canada (http://weatheroffice.gc.ca/canada_e.html).

	Mean Temp (°C)	**Max Temp Avg (°C)**	**Min Temp Avg (°C)**	**Total Precipitation (mm)**	**Precipitation Days**
May	11.3	17.1	5.5	89.4	15
June	19.4	24.2	14.6	70.9	14
July	21.0	26.8	15.2	74.8	11
August	19.3	25	13.6	60.0	8
September	16.8	22.7	10.9	61.7	7
October	8.7	14	3.4	74.5	14
	16.1	21.6	10.5	431.3	69

to reduce transplant stress. I grouped the plots into 10 blocks of three based on their spatial proximity. I then randomly assigned one of the three treatments to the plots within each block. I checked the plots weekly for any snails that had breached the exclosures and any excess snails were removed.

On 8 October 2008, the aboveground biomass of *C. arvense* plants was destructively harvested. Stems and leaves were separated and stem length along with leaf number were determined. I dried all of the aboveground biomass for 72 hours in a 60° C drying oven and then weighed it. I determined average leaf weight, total leaf weight, stem weight, leaf number, and total shoot mass. Within the same experimental plots, I assessed litter removal by *C. nemoralis* by collecting three 70 cm^2 litter sub-samples and averaging their mass. Only litter of the two dominant grasses at the site, *Poa pratensis* (Kentucky bluegrass) and *Bromus inermis* (smooth brome) were investigated.

2.3 Snail enclosures (Objective 2)

Twenty-four 0.10 m^2 circular plots were grouped into 8 blocks of three and were established across the field site in early September 2008, a highly active period for terrestrial molluscs. Plots were haphazardly selected that had a homogenous litter layer and only included the graminoid species (*Poa pratensis* and *Bromus inermis*). Each plot was surrounded by an aluminum barrier that was buried 5 cm into the ground and extended 10 cm above the surface. The top of each barrier was covered by aluminum screening (1 mm mesh) and clipped off at the top. The plots were then randomly assigned to one of three possible treatments, control (0 snails), medium density (1 snail representing 10 snails/m^2), and high density (2 snails representing 20 snails/m^2). I used high overall densities to follow the suggested protocol for mollusc feeding experiments proposed by Hanley et al. (2003). After six weeks, all litter was removed from the plots, dried, and weighed to determine the amount of litter removal.

2.4 Fecal analysis (Objective 3)

I divided the field site into thirty-two 10 m x 10 m sampling areas with a 1 m buffer zone for walking surrounding them. I collected snails on 12 dates throughout the growing season (22 June, 26 June, 3 July, 15 July, 22 July, 3 August, 13 August,

20 August, 27 August, 9 September, 23 September, 29 September). When possible, I collected one small juvenile (9-14 mm diameter), one medium juvenile (15-19 mm diameter), and one adult (mature, 18-24 mm) from each of the thirty-two sampling areas of the field. Snails were taken to the lab, kept in individual Petri dishes, and fed moist filter paper. When filter paper was seen in the feces it was assumed that all the contents from the gut had been egested (Williamson and Cameron 1976). The snails were then weighed (wet weight) and had their shell diameters taken before being returned to their respective sections in the field. Feces were collected from the Petri dishes and put into a freezer (-20°C) until analysis (Carter et al. 1979).

I classified the condition of the fecal string item as green (live) or brown (dead), which is an accurate indication of the food condition at consumption (Williamson and Cameron 1976). *Cirsium arvense* was the only plant identified down to the species level based on cell structure and presence of trichomes. Additionally, I recorded the proportion of the fecal string by volume that was from live plants, plant litter, or soil (Williamson and Cameron 1976). This type of analysis has been used to determine the natural diet of *C. nemoralis* in the past (Williamson and Cameron 1976, Carter et al. 1979, Wolda et al. 1971).

2.5 Snail density estimates (Objective 4)

Density sampling was conducted with ground searches (McDade and Maguire 2005). I divided each of the 32 sampling sections across the site into quarters (see section 2.3). On 30 July and 14 August I randomly placed 1 m^2 quadrats within these quarters and exhaustively searched each quadrat recording the number of adult and juveniles snails (112 searches total). The results were then pooled across both dates because overall densities did not differ significantly. I estimated the plant coverage (5% increments) for each quarter that was sampled.

2.6 Statistical analysis

All statistical analysis was done using JMP 4.0 (SAS Institute).

2.6.1 Snail exclosures

I used a multivariate analysis of covariance (MANCOVA) with a covariate of intital *C. arvense* height to test treatment effects on *C. arvense* total shoot biomass, *C. arvense* stem length, leaf number, and *C. arvense* stem weight. Graminoid biomass and litter was analyzed with a one way analysis of variance (ANOVA). *C. arvense* total plant mass and graminoid biomass were log transformed and total leaf number was square root transformed to improve normality and homogeneity of variance. Transformations were unsuccessful at obtaining a normal distribution for *C. arvense* total leaf mass and subsequently a Wilcoxon ranked sums non-parametric test was used to test for treatment effects.

2.6.2 Snail enclosures

I analyzed the amount of litter mass removed from snail enclosures with a one way ANOVA. One block was removed from the analysis due to control plot laying more than two standard deviations outside of the block mean because of a dense patch of litter within the plot. *Bromus inermis* leaf litter and total litter mass was log transformed after the Shapiro-Wilk test for normality was significant indicating a non-normal distribution.

2.6.3 Fecal analysis

A Pearson chi-square was used to test for differences across sampling dates in both the proportion of individuals that consumed live material and the percentage of live material in the diet. A linear regression was performed to compare the relationship between mean percentage of live material in the diet and the proportion of green in the diet per sampling date with the number of days after precipitation event. The differences between adult and juvenile diet for overall greenness, total green *C. arvense,* and soil, were analyzed using a one-way ANOVA.

2.6.4 Snail density estimates

I used Pearson correlations to examine the relationships between vegetation cover and snail density at the site. I log transformed adult and total snail density to obtain normal distributions.

3.0 Results

3.1 Snail exclosures

Cirsium arvense total shoot biomass (Fig. 3.1), stem length, stem weight, and number of leaves did not differ significantly between unexclosed and exclosed treatments after correcting for initial plant height ($p = 0.473$). Additionally, no treatment effects were found for *C. arvense* total leaf mass ($p = 0.691$; Table 3.1). Excluding snails from grazing also had no significant effect on graminoid litter ($p = 0.213$) or graminoid biomass ($p = 0.419$).

3.2 Snail enclosures

Bromus inermis leaf litter was reduced by approximately 8 g m^{-2} in high snail density plots relative to control plots, indicating a trend of decreasing *B. inermis* leaf mass with increasing snail density ($p = 0.052$, Table 3.2). However, artificially increasing densities to 10 snails/m^2 and 20 snails/m^2 had no significant effect on the dry mass of *P. pratensis* litter ($p = 0.114$), *P. pratensis* and *B. inermis* total litter mass ($p = 0.657$), *P. pratensis* live shoots ($p = 0.404$), *B. inermis* live shoots ($p = 0.164$), or total live material ($p = 0.478$).

3.3 Fecal analysis

Green material was found in 29.2% of snails sampled over the summer and made up 4.2% to 17.6% of the total diet (adults and juveniles pooled, n= 948) with a seasonal mean of 9.3%. Live material made up approximately 30.4% of the fecal string in snails who had live material present in their diet. Adult and juvenile snails did not differ in either the proportion of snails consuming live material ($p = 0.397$), the proportional consumption of live material ($p = 0.082$) , or the average proportion of live material in the fecal string ($p =0.503$). However, the adult diet contained 4.1% live *C. arvense*, 2.0% more than the juvenile diet over entire summer ($p = 0.014$). *C. arvense* made up a combined total of 2.9% of the diet and made up a third of the live material eaten by *C. nemoralis*. Juveniles diets contained

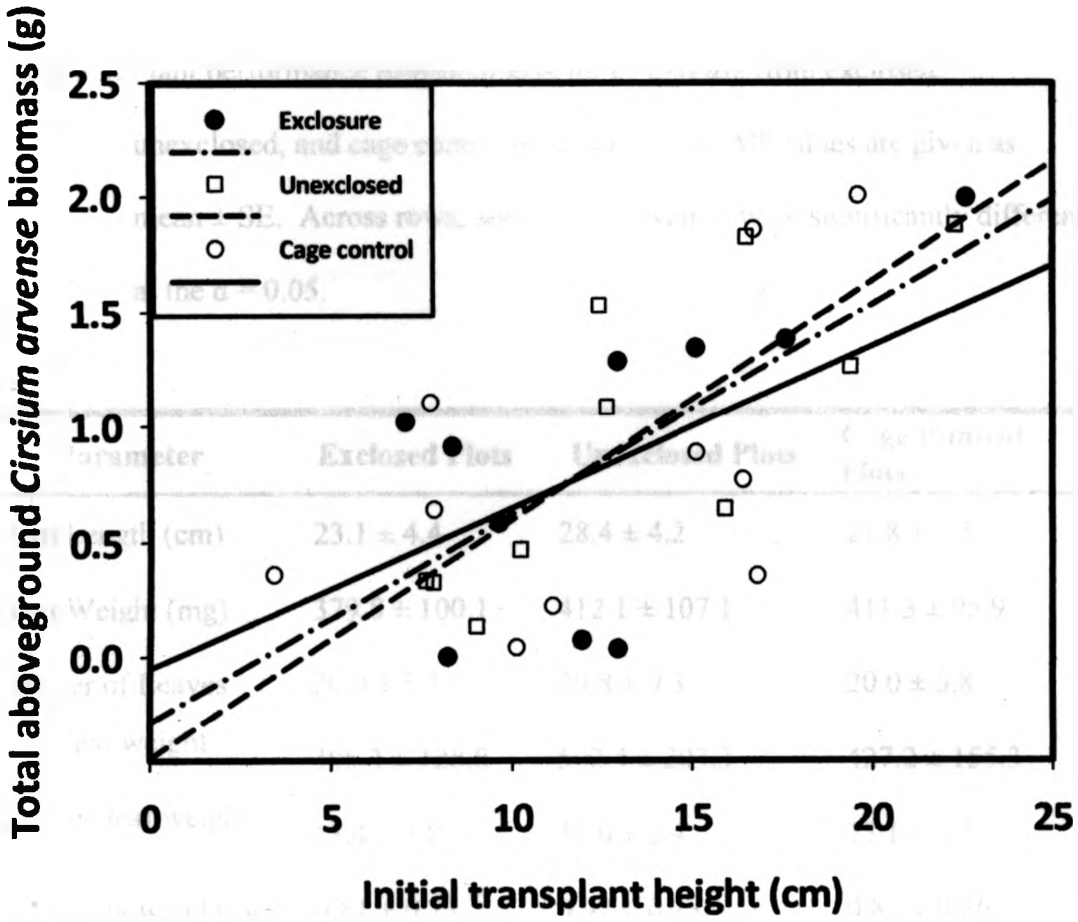

Figure 3.1. Total aboveground biomass of *C. arvense* from exclosed, unexclosed, and cage control plots with corrections for initial transplant height.

Table 3.1. Plant performance measurements for *C. arvense* from exclosed, unexclosed, and cage control treatment plots. All values are given as mean ± SE. Across rows, none of these values were significantly different at the $\alpha = 0.05$.

Parameter	Exclosed Plots	Unexclosed Plots	Cage Control Plots
Stem Length (cm)	23.1 ± 4.4	28.4 ± 4.2	21.8 ± 3.5
Stem Weight (mg)	379.8 ± 100.1	412.1 ± 107.1	411.3 ± 95.9
Number of Leaves	20.9 ± 5.3	29.8 ± 9.3	20.0 ± 5.8
Total leaf weight (mg)	405.3 ± 128.8	502.4 ± 203.3	427.2 ± 155.3
Average leaf weight (mg)	13.4 ± 3.8	13.0 ± 2.4	15.1 ± 3.7
Total plant weight (g)	0.81 ± 0.23	0.92 ± 0.23	0.82 ± 0.26

Table 3.2. Litter mass (g dry weight) and graminoid biomass in snail enclosures of 0 snail m^{-2}, 10 snails m^{-2}, and 20 snails m^{-2}.

	0 snails m^{-2}	**10 snails m^{-2}**	**20 snails m^{-2}**
Poa litter (g)	42.2 ± 4.6	50.6 ± 4.5	52.0 ± 5.8
Bromus leaf litter (g)	15.9 ± 3.5	9.7 ± 0.7	8.0 ± 1.3**
Bromus stems (g)	45.6 ± 6.6	42.7 ± 6.1	37.4 ± 5.0
Total litter including stems (g)	103.7 ± 10.9	103.1 ± 9.7	97.5 ± 5.6
Poa live (g)	14.1 ± 1.7	17.6 ± 2.1	13.7 ± 2.0
Bromus live (g)	6.5 ± 1.3	7.3 ± 1.0	8.9 ± 1.8

** Signifcant at the $\alpha = 0.05$ level

approximately 15% soil, which was significantly higher than the 9% found in adult diets ($p = 0.036$; Table 3.3).

Significant changes were observed in both the proportion of individuals consuming live material ($p < 0.001$) and the overall percentage of live material in the diet ($p < 0.001$, Fig. 3.2) across sampling dates. There was no clear seasonal trend in this variation. However, the proportion of live material in the diet increased significantly with the number of days after a precipitation event ($R^2 = 0.764$, $p < 0.001$, Fig. 3.3). This correlation was driven by an increase in the percentage of the green consumed by snails that consumed live material ($R^2 = 0.627$, $p = 0.002$, Fig 3.4) and not by an increase in the number of individuals that had green in their diet ($R^2 = 0.097$, $p = 0.324$).

3.4 Snail density estimates

Solidago altissima cover was significantly correlated with adult snail density (Pearson's $r = 0.76$, $p < 0.01$, Fig. 3.5) and total snail density (Pearson's $r = 0.44$, $p = 0.02$). but not juvenile density (Pearson's $r = 0.16$, $p = 0.42$). *Cirsium arvense* cover did not correlate with juvenile (Pearson's $r = 0.11$, $p = 0.582$), adult (Pearson's $r = -0.34$, $p = 0.133$), or log total snail density (Pearson's $r = -0.08$, $p = 0.695$, Fig. 3.6). *Lotus corniculatus* cover did not correlate significantly with juvenile (Pearson's $r = 0.011$, $p = 0.953$), adult (Pearson's $r = -0.332$, $p = 0.142$), or total snail density (Pearson's $r = -0.01$, $p = 0.957$, Fig. 3.7). *Cirsium arvense* did not correlate significantly with *S. altissima* cover (Pearson's $r = -0.255$, $p = 0.1582$).

Table 3.3. Differences in the diet of adult and juvenile *C. nemoralis* in overall greeness, total green *C. arvense*, and soil content. All values are given as mean ± SE.

	Adults (n=438)	**Juveniles (n=680)**	**Significance**
Overall Green (%)	10.7 ± 1.0	8.3 ± 0.8	p = 0.503
Live C. arvense (%)	4.1 ± 0.6	2.1 ± 0.5	p =0.014**
Soil (%)	9.3 ± 1.6	15.1 ± 1.3	p = 0.036**

** Significant at the $\alpha = 0.05$ level

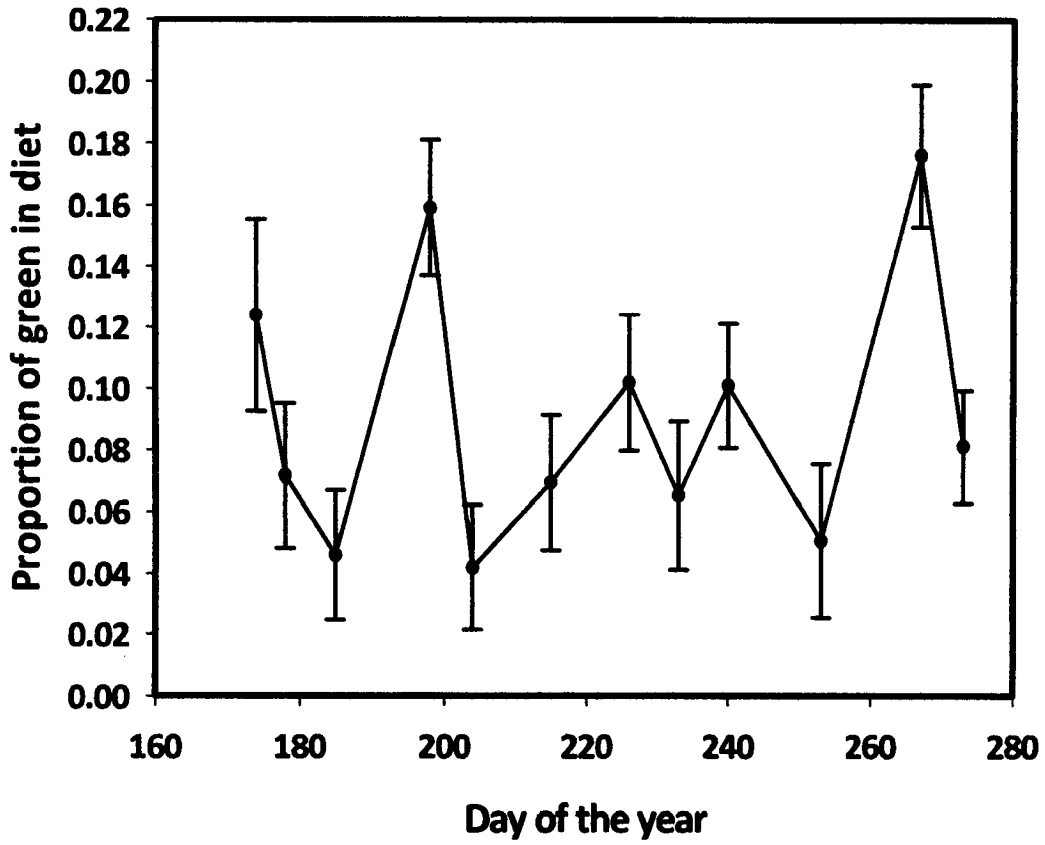

Figure 3.2. Seasonal variation in the percent of green plant material (herbivory) in the snail diet (all individuals) over feces sampling dates during the growing season. Sampling dates were 22 June, 26 June, 3 July, 15 July, 22 July, 3 August, 13 August, 20 August, 27 August, 9 September, 23 September, and 29 September.

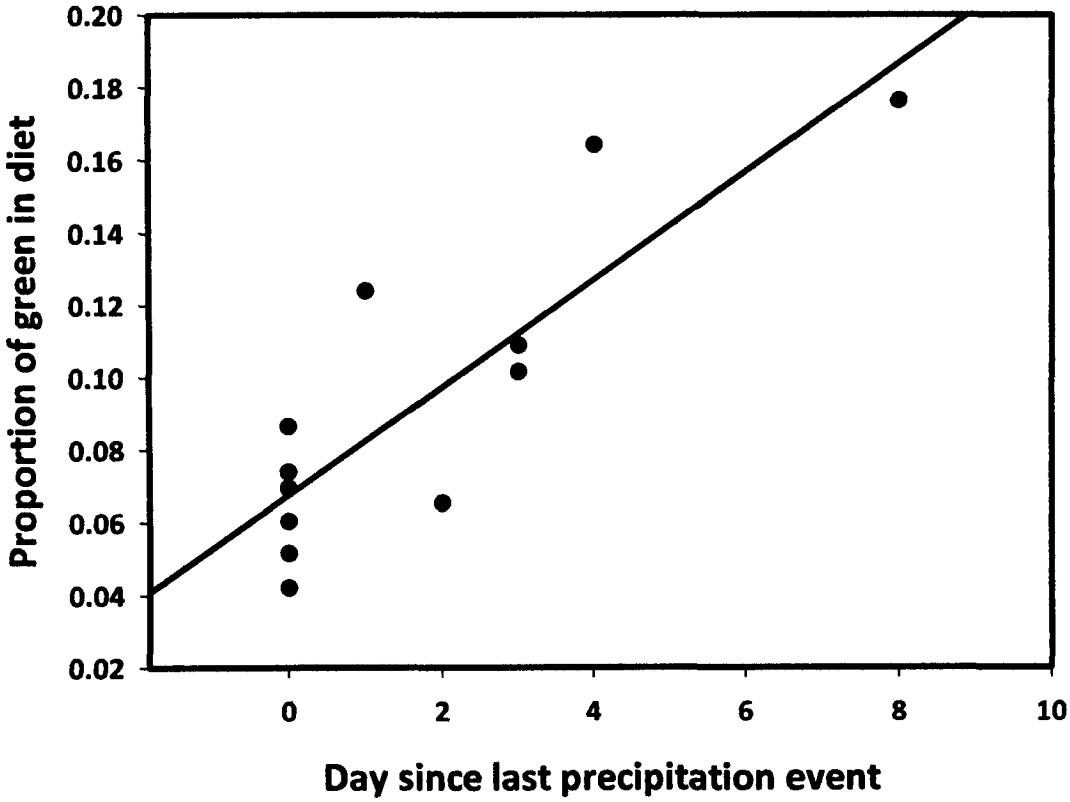

Figure 3.3. The proportion of green plant material in the snail diet of all snails versus the number of days since the last precipitation event. Precipitation days were calculated as how many days it had been since a precipitation event. In order to account for the nocturnal feeding habits of *C. nemoralis*, 7:00 am to 7:00 am was a full day.

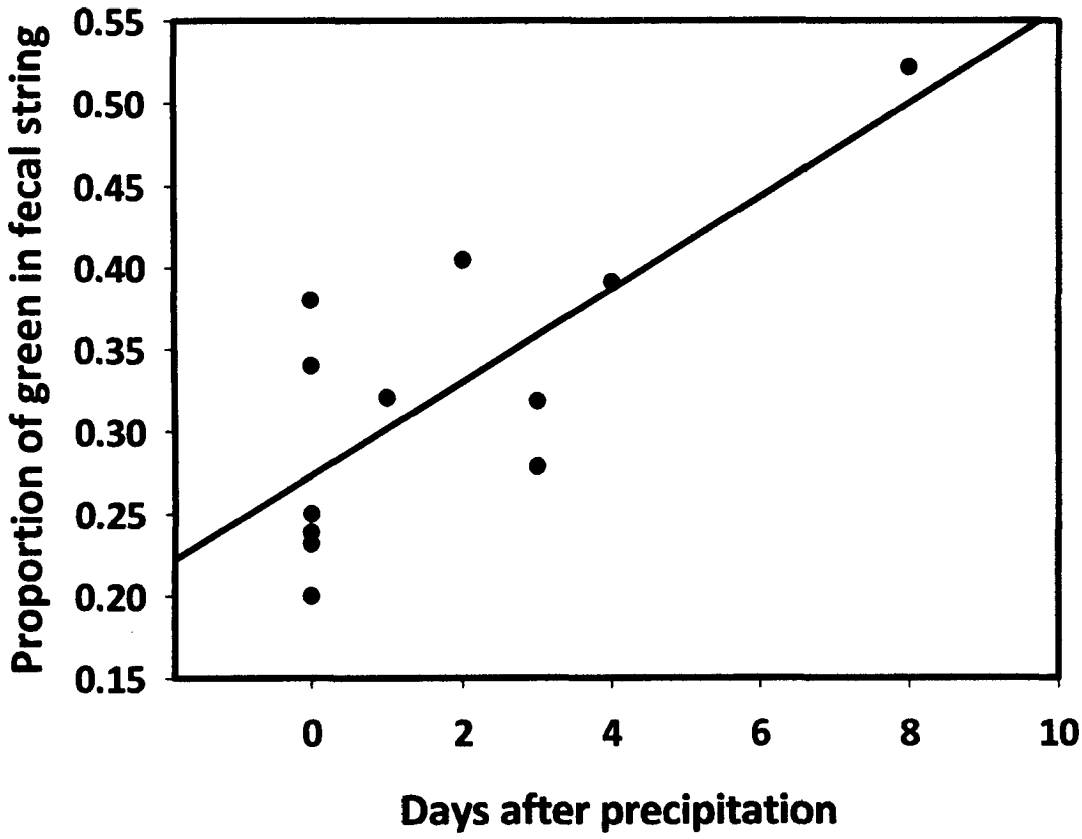

Figure 3.4. The proportion of green in the fecal string of individual snails who consumed green plant material versus the number of days since the last precipitation event. Precipitation days were calculated as how many days it had been since a precipitation event. In order to account for the nocturnal feeding habits of *C. nemoralis*, 7:00 am to 7:00 am was a full day.

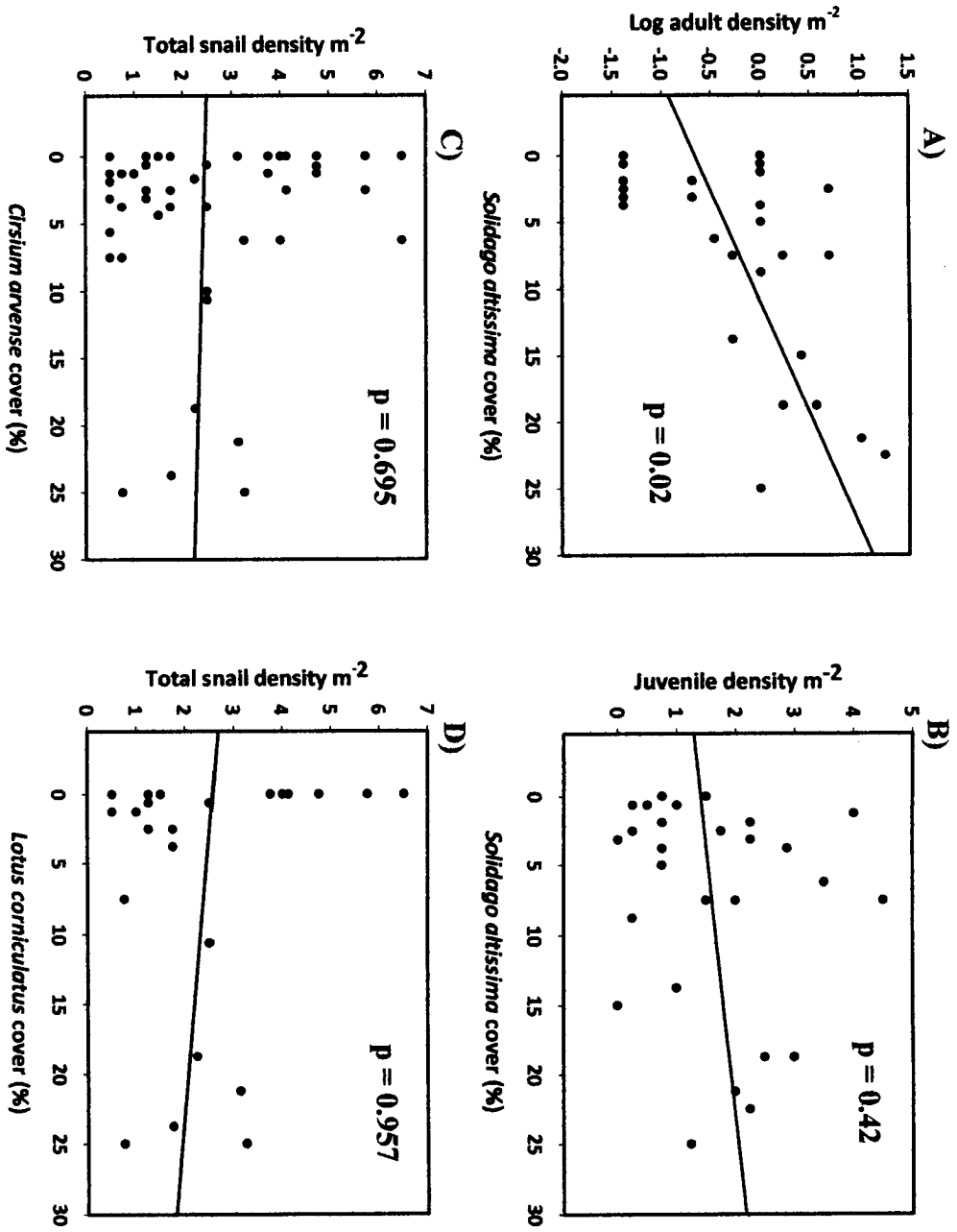
A)
Log adult density m-2
Solidago altissima cover (%)
p = 0.02
B)
Juvenile density m-2
Solidago altissima cover (%)
p = 0.42
C)
Total snail density m-2
Cirsium arvense cover (%)
p = 0.695
D)
Total snail density m-2
Lotus corniculatus cover (%)
p = 0.957

Figure 3.5. Correlations of A) adult snail density m^{-2} and *S. altissima* coverage, B) juvenile snail density and *S. altissima* coverage, C) total snail density and *C. arvense* coverage, and D) total snail density and *L. corniculatus* coverage.

4.0 Discussion

4.1 Snail herbivory

Despite *Cirsium arvense* being highly palatable to *Cepaea nemoralis* (Grime et al. 1968, Wolda et al. 1971), my study demonstrated that snail feeding did not significantly alter the biomass of this species. Edwards et al. (2000) found similar results, concluding that excluding molluscs had no effect on the recruitment of seeds, aboveground biomass, or shoot biomass of *C. arvense* in an acid grassland. My fecal analysis revealed that live *C. arvense* made up only 3% of the overall snail diet, indicating that snail grazing intensity on *C. arvense* is low at our field site. Carter et al. (1979) found that snails fed disproportionately more on *C. arvense* in the field than would be expected by the relative abundance of plant species. In contrast, overall thistle consumption by *Cepaea nemoralis* matched well with *Cirsium arvense* coverage at my site where *Cirsium* is at 3.5% cover.

Snails prefer only a small selection of the live vegetation that is available to them (Chang 1991, Spieser 2001) with only a few species consumed live (Wolda et al. 1971). For example, Carter et al. (1979) found that live plants made up 40% of the snail diet where *U. dioica* were present. However, similar to Williamson and Cameron (1976) I found that only 9% of the overall diet was live. Plant palatability is often negatively correlated with percent coverage (Chang 1991), and low encounter rates of snails with palatable live plants may explain why observed herbivory levels were low. However, when snails do encounter a palatable plant they typically increase their feeding (Grime and Blythe 1969). In my study, neither the number of snails consuming thistle nor the percentage of live thistle in the fecal string correlated positively with increasing *C. arvense* cover. This suggests that even when snails do encounter *C. arvense*, they do not feed heavily on the plant. Snails only feed until their crop is full and the fecal string generally contains 3 food items from separate feeding bouts (Williamson and Cameron 1976, Spieser 2001). Accordingly, in my study green plants made up about a third of the fecal string collected from snails that had consumed at least some live plants. Therefore, live material did not exceed the

average amount of intake for a single food item in the diet. This suggests that upon encountering palatable live material snails do not localize feeding or feed continuously, despite the higher palatability of live plants.

Snail grazing on palatable plants can be intensified due to higher snail densities around preferable plant species (Cain and Currey 1968, Chang and Emlen 1993). For example, snail densities within *U. dioica* patches can be much higher than average, typically reaching 10 snails m^{-2} (Cain and Currey 1968) to 20 snails m^{-2} (Grime and Blythe 1969), and the increased grazing can cause significant defoliation (Grime and Blythe 1969). At my study site, I predicted that snails would congregate around *C. arvense* because it was a highly palatable food plant and potentially a good roosting site. However, *Cepaea nemoralis* densities did not correlate significantly with increased *Cirsium arvense* density. Therefore, unlike with *U. dioica*, snails do not congregate around *C. arvense*, and consequently, thistles were not exposed to high levels of grazing. Additionally, the cover of *L. corniculatus*, another palatable plant at our site, did not correlate significantly with snail densities. Densities were positively correlated with *S. altissima* density, which is a preferable resting plant but a poor food plant (Chang and Emlen 1993). Increased grazing on plants near preferable resting sites has been observed (Frank 2003); however, thistle cover was not correlated with *S. altissima*, indicating that *C. arvense* was not in close proximity to preferred roosting sites. My study suggests that, unlike *U. dioica*, *C. arvense* is unable to support higher densities of snails and therefore there is no corresponding increase of live material in the diet. Furthermore, snails do not appear to select *C. arvense* as a preferred food plant in the field. *Urtica dioica* may be unique in its importance to gastropods because of its high phosphorous (Rorison 1968), protein and calcium content (Iglesias and Castelljo 1999) or its easily ascendable stems (Grime and Blythe 1969).

While high feeding rates on *C. arvense* in the laboratory (Grime and Blythe 1969) did not translate into high consumption in the field in my study, laboratory tests on palatability have been assessed using leaf discs cut from live tissue (Grime et al. 1968, Chang 1991) which may create unrealistic experimental artefacts (Grime et al. 1968, Wolda et al. 1971). Such artefacts include the absence of induced chemical

defences or allowing access to usually inaccessible feeding surfaces (Wolda et al. 1971). Alternatively, if laboratory palatability is representative of field palatability, limited or reduced access to plants may be decreasing consumption. Plants differ in their accessibility to snails in the field (Wolda et al. 1971) and in particular, plant-specific stem structure (stem hairs, roughness, etc.) limits snail feeding by blocking access to plant canopies (Grime et al. 1968). For example, adult snails consumed about double the amount of live *C. arvense* as compared with juveniles in my study, indicating age differences in palatability and/or ability to access plants. Large trichomes on the surface of *C. arvense* do not affect snail access to the plant (Tuberville et al. 1996). However, trichomes might limit juvenile feeding on *C. arvense* because of their smaller digestive tracts. Juveniles typically have higher nutrient demands for growth and therefore may consume more live material than adults (Iglesias and Castellijo 1999). However, in my study, mature and juvenile snails did not differ in the amount of overall live material they consumed, which is consistent with other studies on *C. nemoralis* (Richardson 1975, Williamson 1976). Soil consumption was significantly higher in juveniles, a phenomenon that has previously been reported (Richardson 1975, Williamson 1976). Soil made up approximately 12% of the overall snail diet, and although the role of soil in nutrition is not fully understood, snails may extract humic acids (Elmslie 1998), calcium (Fretter and Graham 1962), or be digesting soil organisms (Williamson and Cameron 1976).

4.2 Detritivory

In accordance with other studies (Grime et al. 1968, Richardson 1975, Williamson and Cameron 1976), my research confirmed snails are mainly detritivores, with plant litter making up approximately 78% of their overall diet. However, snail detritivory did not significantly alter litter mass during the experiment. The overall effect of gastropod detritivores depends on the amount of litter production and snail biomass in the system, which can be highly variable. In old field habitats, like the one in my study, litter production is relatively high (Carson and Peterson 1990). At my field site, ground searching showed the total density of snails

to be about 2.5 snails m^{-2}. Although this is higher than typical grassland densities of 0.3 snails m^{-2} (Cain and Currey 1968), snails at my site did not have the capacity to significantly consume the high litter input from *P. pratensis* (approximately 150 g m^{-2}). Mason (1970) found that snails did not have any effect in a beech litter forest, consuming 0.35- 0.43% of the litter. Seifert and Shutov (1981) calculated that the medium sized land snail *Bradybaena fruticum* (1 snail m^{-2}) could remove only 1.6-2.7% of the total litter in lime forests; however, a larger species, *Eobania vermiculata*, (4-5 snail m^{-2}) significantly contributed to litter removal. When I artificially increased densities in snail enclosures at my site, *B. inermis* leaf litter was significantly reduced by approximately 8 grams m^{-2} overall, but only in the high density plots (20 snails m^{-2}). In contrast, there was no reduction in the mass of *P. pratensis* litter. Snails may have preferred *B. inermis* leaf litter because of its greater surface area making tissues more accessible to grazing. However, *P. pratensis* litter is typically more important in seedling suppression (Bosy and Reader 1995), emphasizing the fact that *C. nemoralis* is unlikely to affect species composition indirectly through litter removal at this site. In systems with lower litter production, snails may have a greater influence on litter turnover.

4.3 Variability in feeding

The consumption of live material may vary seasonally because of increased plant availability, variation in nutritional quality, and potential decreases in plant secondary compounds later in the growing season (Hägele and Rahier 2001). However, my results show no obvious seasonal trends in the amount of live material consumed over time. Previous studies also found that although the species composition of the diet varied over the season, the proportion of live material did not change seasonally (Richardson 1975, Williamson and Cameron 1976). Although I did not formally quantify the relative abundance of species in all fecal samples, *L. corniculatus* appeared to make up most of the green material that was not *C. arvense*. Large seasonal variation in the consumption of *L. corniculatus* has been previously observed in *C. nemoralis* (Richardson 1975, Williamson and Cameron 1976);

however, regardless of seasonal differences in dietary species composition, total consumption of live material typically remains constant over the season.

Despite the lack of clear seasonal trends in the consumption of green material, there were distinct and significant peaks in the green material detected in the diet between sampling dates. Interestingly, overall diet greenness was significantly correlated with the number of days after a precipitation event (length of drought). The number of snails feeding on green material did not increase during drought; however, snails did increase the amount of green material they consumed. Therefore, snails did not seek out plants during dry periods, likely because locomotion is a major source of water loss (Machin 1975) but, when snails did encounter a palatable plant, they actively consumed more live material as the length of drought increased. Terrestrial gastropods have high rates of evaporative water loss through their integument, lungs, and mucous deposition during movement (Prior 1985), and water loss can be as great as 30-40% of initial body weight within the course of two hours (Dainton 1954). By forming an epiphragm across the shell aperature during aestivation, *C. nemoralis* reduces evaporative water loss by two thirds (Machin 1975); however, when active, adult snails can lose approximately 4 mg – 8 mg of water h^{-2} (Cameron 1970). By feeding on wet foods, snails can stop further water loss (Prior 1983) by taking up water from food items (Machin 1975). Plant litter and top soil become quite dry in drought periods (Ogee and Brunet 2002); however, live plant tissues contain between 80-85% water (Hägele and Rahier 2001). Based on laboratory consumption rates of 12 mg dry weight daily (Grime et al. 1968) and typical assimilation efficiencies (Richardson 1975), snails take up approximately 8 mg of water from live plants (based on 30% of the fecal string). Typical values for most terrestrial gastropods range between 3-7 mg of water uptake per hour through food consumption (Machin 1975). Even by increasing feeding on live materials by only 10-20% in the fecal string, as we see in lengthier drought periods, would result in greater recovery of water losses for active snails.

5.0 Conclusions

Overall, despite the high paltability of *C. arvense* and contrary to my hypothesis, snail grazing did not reduce the biomass of *C. arvense* and consumption of the plant was fairly low. Furthermore, snail detritivory did not remove significant quantities of grass litter from unexclosed plots. There were no overall seasonal trends in the amount of live material consumed; however, significant peaks in greeness across sampling dates were observed. These peaks were driven primarily by the length of time since a previous precipitation event, suggesting that snails feed more heavily on live plants in times of drought in order to obtain water.

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