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**Seed predation and dispersal in a deciduous forest understorey herb,
wild ginger (*Asarum canadense*)**

by

Angela M. Muir, B.Sc. (Honours) 1994

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Master of Science

Department of Biology
Carleton University
Ottawa, Ontario

April 17, 1997

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The undersigned recommend to the Faculty of Graduate
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Thesis Supervisor

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ABSTRACT

Wild ginger (*Asarum canadense*) was used as a model system to study seed predation and dispersal in understorey plants. Flower predation was severe and killed nearly 98% of ginger flowers. Predator exclusion cages identified small predators (*Arion fasciatus* slugs) to cause a significant decrease in flower survival in 1995 and 1996, and large predators (*Peromyscus leucopus* mice) to cause a significant decrease in flower survival in 1995, 1996, and seedling emergence in 1996. Further, a matrix-based simulation predicts this predation has a significant negative impact on long term population growth. Seed dispersal by ants was observed and average distances were 32 to 39 cm (excluding two remarkable distances, 23.5 and 36 m!). Unfortunately, seed dispersal operates after predation, and predation is so high that there are few seeds remaining to be dispersed. Implications for conservation of this plant and temperate understorey herbs in general is discussed.

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I. INTRODUCTION

Endangered plant species

It has been proposed that nearly 25% of the estimated 250 000 species of vascular plants in the world may become extinct within the next 50 years (Schemske et al. 1994).

Important causes of this mass extinction include: overexploitation, introduction of predators and disease, loss of mutualists, and habitat destruction (Purves et al. 1995).

Over the last 300 years, European settlement in Canada and the United States has had a devastating impact on North American vegetation (Argus & Pryer 1990).

Urbanization, industrialization, agriculture, and forestry have all contributed to the dramatic loss in both plant species and population numbers (Argus & Pryer 1990). In the United States, nearly 50 % of the 728 federally listed threatened or endangered species are plants (Schemske et al. 1994). As well, almost 35% of Canada's species "at risk" are native plants (Environment Canada 1996).

The deciduous forests of eastern North American have incurred widespread habitat alteration (Argus & Pryer 1990, Vankat 1979, Soulé 1986). Following European settlement, extensive areas of forest were cut down for timber and slash fires were set to clear land for agricultural use. This early deforestation followed by years of fragmentation due to agriculture, urbanization, and the later introduction of several European diseases (Purves et al. 1995) were among the factors that reduced and fragmented the forests of eastern North America (Soulé 1986). Plants that were once common in the deciduous forests of northern United States are now rare (Argus & White 1977). Some of these

plants are still represented in eastern Canadian deciduous forests and may represent the only viable populations of these plants left (Argus & White 1977). However, these plants are quickly disappearing. Currently, almost one quarter of the Priority 1 (dangerously in peril) plant species in Canada are understorey plants. And of the 331 plants species recognized as rare in Ontario, 103 of them are forest understorey plants (Argus & Pryer 1990).

Conservation biology

Conservation of rare species has received much attention over the last 20 years. Most scientists approach conservation from either an ecological or a genetic perspective (Schemske et al. 1994). Ecologists assert that the key to conservation is defining the biotic interactions and habitat requirements of an endangered species. Ecologists focus on measuring extrinsic limitations, such as plant associations and competitive interactions, habitat requirements (Loehle & Li 1996), pollination limitations and predation levels (Pavlik et al. 1993). Whereas geneticists insist that as genetic variation drives evolutionary adaptation, demographic genetic measurements should be the focus of study for long term survival of the species. Geneticists concentrate on collecting demographic profiles on biochemical (isozymes) and molecular (DNA) polymorphisms that are often difficult to directly relate to plant fitness (Ellstrand & Elam 1993). The problem that arises repetitively with all of the aforementioned measures used, is that they are often chosen arbitrarily and are hence ineffective predictors of population fitness and long term plant survival.

Schemske et al. (1994) proposed a “top-down,” three-tiered approach to any conservation plan for choosing measurement parameters. First, the biological status of the species should be determined (i.e., is it endangered?). Second, the life history stages that affect the population growth and species persistence must be identified. Third, the causes of variation (such as the measures described above) involved in those life history stages that have an impact on species survival must be determined. These three steps should take place before any ecological or genetic measurement is made.

Deciduous understorey herbs

Deciduous understorey herbs live in an environment of low light throughout the summer where nutrients, particularly nitrogen, are very limited in the soil (Brundrett & Kendrick 1990, Vankat 1979). Most deciduous understorey herbs can reproduce by both clonal and sexual reproduction (Bierzychudek 1982, Cook 1985, Silander 1985). In clonal reproduction, the plant propagates vegetatively by sending out “runners” or “rhizomes” to produce offspring that are clones of itself. As sexual reproduction is energetically costly (Agren 1988, Delph et al. 1993, Harper 1977, Mendez & Obeso 1993, Michaels & Bazzaz 1986, Muir 1995, Pitelka & Ashmun 1985, Snow and Whigham 1989, Sohn & Policansky 1977, Westley 1993), resource-limited understorey herbs persist by propagating clonally, while storing energy for less frequent sexual reproduction (Silvertown et al. 1993). Though understorey herbs generate a substantial number of flowers (Offer 1992), the seeds produced rarely establish themselves (Helliwell 1975, Peterken & Game 1984, Primack & Miao 1992, Whitney & Foster 1988) and do not

significantly add to the intrinsic growth rate of the plant population (Damman & Cain, in press, Silvertown et al. 1993).

Understorey herbs rely heavily on clonal propagation to maintain populations. However, the habitat for deciduous understorey herbs has become fragmented and is disappearing. Persistence in local clumps will not protect this group of plants from extinction. Metapopulation dynamic processes demand that for a species to persist, it must colonize new habitats as frequently as it becomes extinct in others (Chambers & MacMahon 1994, Doak & Mills 1994, Loehle & Li 1996, Schemske et al. 1994, Soulé 1986). The future survival of this group is dependent upon its ability to sexually reproduce, disperse its seed, and colonize new habitats effectively (Ehrlén 1996, Peterken & Game 1984, Primack & Miao 1992).

The variables that influence a plant's ability to disperse its seeds and colonize new habitats include: abiotic resource levels in the surrounding environment, pollination mechanisms, seed predation, and seed dispersal (Janzen 1969, Janzen 1971b, Pavlik et al. 1993). It has been established that the frequency of an understorey herb's sexual reproduction depends upon restrictions imposed by its nutrient- and light-limited environment (Campbell & Halama 1993, Harper 1977b, Watson 1984). These environmental restrictions are dictated by the natural understorey microhabitat. Pollination requirements and techniques differ greatly from one understorey herb to another (Bierzychudek 1982). The key obstacle that understorey herbs share and must hurdle to successfully colonize new habitats is seed predation (Bierzychudek 1982, Ruhren & Dudash 1996).

Understorey herbs suffer high rates of seed predation (Heithaus 1981, Ruhren & Dudash 1996, Turnbull & Culver 1983). For instance, seed predation accounts for losses of as much as 83.7% of seeds in the understorey herb *Lathyrus vernus* (Ehrlen 1996), 30% in *Viola* spp. (Culver & Beattie 1978), 40% in *Asarum canadense*, 47% in *Jeffersonia diphylla*, 43% in *Sanguinaria canadensis* (Heithaus 1981), 86% in *Carex pilulifera* (Kjellsson 1985). Seed predators vary from ground beetles to birds, but the most predominant predators are rodents (Bierzychudek 1982, Heithaus 1981, Ruhren & Dudash 1996). Seed predation will be the primary variable studied in this paper.

Plants have evolved different mechanisms to protect their seeds from predators. These include physical deterrents such as protective ovaries and seed coats, and chemical deterrents such as toxic alkaloids or uncommon amino acids in the seeds or protective tissues (Janzen 1969). Some plants use “predator satiation” and flood the environment with seeds to ensure that at least some will survive (Eriksson 1995, Janzen 1969, Kjellsson 1985). Other plants use temporal fluctuations in seeding (e.g., masting) to discourage dependency on their seeds as a food source (Harper 1977a, Janzen 1971a, Kelly 1994, Pucek et al. 1993). Lastly, some plants have developed specific dispersal mutualisms that move the seed away from the parent plant where seeds are less likely to be eaten (Harper 1977a, Janzen 1969). It is this last mechanism that is used most by understorey herbs. Among forest understorey herbs in eastern North American, ants represent perhaps the most common seed dispersal agent (Handel et al. 1981).

Myrmecochory (seed dispersal by ants) is the most widespread mechanism used by understorey plants to resist seed predation (Beattie 1985, Beattie & Lyons 1975,

Bierzzychudek 1982, Culver & Beattie 1978, Handel 1978, Heithaus 1981, Ruhren & Dudash 1996). Myrmecochory is relied upon by approximately 40 % of the herbaceous biomass in mesic deciduous forests (Handel et al. 1981), including *Asarum canadense* (Heithaus 1986, Offer 1992), *Carex pilulifera* (Kjellsson 1985, Kjellsson 1991), *Dicentra cucullaria* (Lobstein & Rockwood 1993), *Erythronium americanum* and *Trillium sessile* (Ruhren & Dudash 1996), *Jeffersonia diphylla* (Heithaus 1981), *Sanguinaria canadensis* (Heithaus 1986), and *Viola* spp. (Culver and Beattie 1978, Culver and Beattie 1980). As the seed's distance from the parent plant increases, the likelihood of being preyed upon decreases (Horvitz & Schemske 1994, Janzen 1971b, O'Dowd & Hay 1980). Also, Heithaus (1981) found that removal of the elaiosome decreased the ability of foraging rodents to detect seeds. Thus, once ants have removed the seed's elaiosome, the seed is less likely to be found and eaten. Ant dispersal will be the secondary variable observed in this study.

Seeds of myrmecochorous plants possess a fleshy appendage rich in fatty acids and diglycerides called an elaiosome (Beattie 1985). Foraging ants are attracted to seeds with elaiosomes. Foraging ants carry these seeds back to the ant nest where they remove and consume the elaiosomes (Culver & Beattie 1978, Kjellsson 1985). The remainder of the seeds, intact minus their elaiosomes, are deposited on refuse heaps, either inside or directly outside of the nest depending upon the ant species (Culver & Beattie 1978, Heithaus 1986). Some of these seeds will be picked up from the refuse heaps and dumped on the pathway back to the seed collection site (Kjellsson 1985, Sudd 1967).

Though predation is perhaps the strongest selective force for myrmecochory in

deciduous understorey herbs (Beattie & Lyons 1975, Heithaus et al. 1980, Ruhren & Dudash 1996), myrmecochory may have other benefits to the plant. For example, relocation away from the parent plant has been shown to decrease competition with parent and sibling plants (Beattie 1985, Handel 1978, Kjellsson 1991). Further, dispersal may result in the seed reaching a better environment for germination (Beattie 1985, Culver & Beattie 1978, Handel 1978).

Much debate has focussed on the benefits/drawbacks of seed germination in refuse piles inside of ant nests or beside nest entrances (Handel 1978). Though top soil horizons of the mesic deciduous understorey are often nutrient and water poor, soil contained in the lower horizons is rich in minerals, particularly nitrogen and phosphorus, and moisture (Culver and Beattie 1978). This soil is excavated during nest creation and development and deposited in refuse piles where abandoned intact seeds are also located (Sudd 1967). It is postulated that the nutrient content of this soil (Wang et al. 1995), the smaller particle size (Wang et al. 1995), and moisture content (Culver & Beattie 1978) are all advantageous to understorey herb seed germination and seedling success. In studies by Culver and Beattie (1980), the nest environments of myrmecochorous ants significantly improved seed germination and seedling growth of *Viola* sp. Scarification of the seed coat, caused by ant mandibles and maxillae (Brian 1978) also increased seedling emergence (Culver & Beattie 1980). In addition, studies in Costa Rican lowland rainforests have indicated that several shrub species' seeds have higher rates of germination on *Pheidole* sp. refuse piles than on topsoil (Levey & Byrne 1993). In contrast, work by Kjellsson (1985) has shown that less than 20% of (1400) foraged seeds

were dispersed following elaiosome removal, over a 3 week period. The remaining seeds were left in refuse piles that laboratory studies showed were vulnerable to pathogens, decreasing their viability (Kjellsson 1985).

Study

Following Schemske's top-down approach, it has been determined here that understorey herbs are a group of plants that are at risk due to habitat disappearance and fragmentation. A life-history stage or mechanism that is imperative to the ultimate survival of understorey herbs is the colonization by seed of new habitats. A variable threatening the success of colonization of new habitats in understorey herbs is seed predation. As a secondary variable, seed dispersal will be observed. To study seed predation and dispersal in understorey herbs one study plant was chosen that was typical of mesic forest understorey plants. Seed predation in this plant will be studied in order to collect natural history information that is vital for the long term conservation of this species and other understorey herbs (Kareiva 1994). The study plant is *Asarum canadense*.

Asarum canadense, wild ginger (Aristolochiaceae), is a herbaceous perennial that commonly inhabits the forest understorey of deciduous hardwood forests in eastern North America (Brundrett and Kendrick 1990, Gleason 1963). *A. canadense* shares this habitat with wild sarsaparilla (*Aralia nudicaulis*), wild lily-of-the-valley (*Maianthemum canadense*), white trillium (*Trillium grandiflorum*), and *Viola* species, the dominant canopy vegetation is comprised of sugar maple (*Acer saccharum*), eastern

hemlock (*Tsuga canadensis*), and eastern white cedar trees (*Thuja occidentalis*).

A. canadense, like many understorey herbs (Bierzychudek 1982, Ruhren & Dudash 1996), is a spring ephemeral that grows rapidly following snowmelt before the canopy closes. Wild ginger sometimes produces a burgundy flower by mid-summer. Shoots grow slowly and steadily until senescence in late autumn (Brundrett and Kendrick 1990). Wild ginger propagates asexually by vegetative rhizome. Lateral shoots are produced that are clones of the parent plant. These plants remain connected to the parent plant by rhizomes for 3 to 5 years. The rhizomes are the storage organs that overwinter from which shoots emerge in the Spring. Wild ginger often reproduces sexually by seed. The flowers are hermaphroditic, common in understorey herbs (Bierzychudek 1982), and self-fertilizing (Wildman 1950), though they are capable of cross-fertilization. *A. canadense* has no known animal pollinators (methods for pollination in understorey herbs differ greatly (Bierzychudek 1982)). Seeds possess elaiosomes and are dispersed by foraging ants. Myrmecochory is a widespread dispersal mechanism of understorey herbs (Bierzychudek 1982, Handel 1978, Ruhren & Dudash 1996). Seeds exhibit epicotyl dormancy thus form roots the same year that they are dispersed but initiate shoot growth in early spring the following year. *A. canadense*, like most understorey herbs has no substantial seed bank (Baskin & Baskin 1986, Bierzychudek 1982, Damman, personal communication) .

Rodents are thought to be the primary predator of ginger seeds (Heithaus 1981). However, Offer (1992) suggests that *Arion fasciatus* Férussac slugs may be a threat to ginger seeds due to their abundance at his ginger sites. This slug as a potential predator is

interesting, because it is a non-native species introduced to North America by Europeans (Getz 1959, Runham & Hunter 1970). Its presence and occurrence in large congregations is unlike native species of slugs (Chichester 1973). Thus, this species of slug and its effect on wild ginger populations is an example of human intervention into the ecology of an established plant community.

Wild ginger possesses a favourable combination of traits that make it suitable for the project. Wild ginger sexually reproduces often enough to pursue a study involving sexual reproduction over a short period of time. Wild ginger does not have a seed bank, thus seedling emergence can be measured with some degree of precision. Wild ginger is self-fertilizing, so covering plants with predator exclusion cages will not interfere with plant pollination. Finally, only one species of *Asarum* grows in Southern Ontario (Offer 1992).

This study is a preliminary natural history examination of seed predation and dispersal in a typical deciduous understorey herb. I will measure the amount of seed predation occurring in natural populations of *Asarum canadense*, the effects of differential predation on ginger flowers and seeds, and seed predators will be identified. Seed dispersal by ants will also be observed.

II. METHODS

Description of study sites

Six sites containing large numbers of wild ginger were identified. The sites were located just north of Cantley, Quebec. The area had been logged in the late 1800s to early 1900s for timber and now is late-succession deciduous forest composed predominantly of sugar maple (*Acer saccharum*), hemlock (*Tsuga canadensis*), and eastern white cedar trees (*Thuja occidentalis*). The forest understorey is heavily populated by white trillium (*Trillium grandiflorum*), and to a lesser extent by red and painted trillium (*T. erectum* and *T. undulatum*), bloodroot (*Sanguinaria canadensis*), common blue violet (*Viola papilionacea*), wild lily-of-the-valley (*Maianthemum canadense*) and wild ginger (*Asarum canadense*). In areas where ginger occurred close to the forest edge, where the woods intersect with agricultural land, sensitive fern (*Onoclea sensibilis*), staghorn sumac (*Rhus typhina*), and middle-succession plants occurred. All six sites were within 4 km² of one another.

The six sites contained 17 predation plots and 18 predator exclusion plots. The predation plots were used to measure seed predation over the course of the field season, and to identify predators. The predator exclusion plots measured the effect of differential predation upon ginger flowers and seed using cages to exclude groups of predators based on size.

Predation plots

In May 1995, seventeen 1 m² plots containing wild ginger were established at five of the six ginger sites. The plots were used to measure the amount of ginger flower predation, to identify predators, and to compare predator populations. The plots varied greatly in their number of flowering ginger (range: 6-119 flowers) and contained a mean of 42.2 ± 10.3 ($\bar{x} \pm \text{SE}$) flowering ginger.

The degree of predation in each plot was assessed by observing the number of damaged flowers both at the onset of the experiment late spring (late May) and mid-summer (late June), prior to flower dehiscence. Unexpectedly, a great deal of predation had already occurred by the time the experiment was set up. Degree of predation was measured by counting flowers that had been gutted or had holes exposing an ovule or seeds.

At the end of June, flower remnants were studied to identify the predators of the ginger flowers. Flowers that had been preyed upon by rodents were bitten off, leaving a straight-edged cut on the stalk (Heithaus 1981). Flowers typically lay beside the stalk ripped and torn with sharp, square, slash marks, empty of seeds. Flowers that had been preyed upon by slugs were often still attached to the stalk and bore rounded, groove marks. Seeds were sometimes seen scattered beneath these flower remnants.

To minimize population differences between plots, the percentage of flowers preyed upon was calculated:

$$\frac{\text{Flowers}_{\text{May}} - \text{Flowers}_{\text{July}}}{\text{Flowers}_{\text{May}}} \times 100$$

Parametric assumptions were not met so Kruskal-Wallis one-way analysis of variance for non-parametric data was used to test for differences between plots. To test for correlations between two continuous variables, Spearman's rank-order correlation test was performed (Siegel and Castellan 1988).

Predator exclusion experiment

In May 1995, eighteen 1 m² plots of wild ginger were identified, 3 at each of the six sites. All seedlings were removed, and the number of flowering ginger were counted. The mean number of ginger flowers varied greatly from plot to plot (range: 14-114 flowers), the mean was 49.61 ± 6.73 (SE) ginger flowers.

This experiment was used to measure the effect of flower and seed predation on wild ginger. Predators were excluded from clumps of ginger using cages of different mesh size. Three treatments were used: protected, semi-protected, and unprotected. Protected plots were protected from all predators. Semi-protected plants were protected from large predators (rodents), but exposed to small predators (slugs). And unprotected plants were subject to all predator sizes. This experiment spanned 2 field seasons. The effect of predation during the first field season (1995) was estimated by measuring the number of flowers preyed upon, and the number of seedlings that emerged the following spring. To ensure that the seedlings counted in (1996) were from 1995 seeds, all existing seedlings were removed in 1995 in all plots. Predation during the second field season was estimated by measuring the number of flowers eaten (1996).

Protected plots were covered by hardware-cloth cages (with 1 X 2 mm holes). It was assumed that these hardware-cloth cages excluded all large and small predators (rodents and slugs), thus protected plots should yield the greatest number of flowers by the end of the growing season, seedlings the following spring, and flowers the following summer. The hardware-cloth cages were also expected to exclude dispersal agents (ants). Before erecting the cages, the soil surface was scoured for slugs and all those found were removed. To kill those slugs that remained hidden and those residing in the soil, metaldehyde slug pellets were deposited evenly (5 per 10 cm²) on the soil surface (pelleting) and were sprinkled with water to activate (Hunter & Symonds 1970, Runham & Hunter 1970). To ensure that all slugs within the plot were killed, protected plots were re-pelleted 10 days later (as the pellets were only guaranteed to be effective for 10 days). After pelleting protected plots, trenches were dug around each plot perimeter and cages were painstakingly driven into these trenches and soil packed down. Cages were removed for re-pelleting and carefully replaced.

Semi-protected plots were covered by WB plastic fencing cages (with 2 X 5 mm holes). It was assumed that the WB plastic fencing would exclude large predators (rodents) but allow in small predators (slugs). Thus, semi-protected plots would yield fewer flowers by the end of the growing season, seedlings the following spring, and flowers the following summer, than protected plots.

Unprotected plots had no cage. All predators (rodents and slugs) had access to the plants in these plots. It was predicted that unprotected plots would suffer the greatest loss of flowers by the end of the growing season, seedlings the following spring, and

flowers the following summer.

In order to accurately count emergent seedlings, the boundaries for the semi-protected and unprotected plots were moved outward to accommodate the movement of seeds due to ant dispersal. Eighty-seven percent of ants will move a ginger seed within 60 cm of its former position (see experiment described under “Ant dispersal”). Based upon this, cages for semi-protected and unprotected plots covered the plot and this area (60 cm from the perimeter). Seedlings that emerged within the plot or 60 cm from the plot perimeter were counted in the following spring. To ensure that local seedlings from plants outside of the experimental area were not counted, ginger flowers and seedlings were removed within a 1.6 m radius of the plots a year earlier.

Once cages were erected, they were checked for damage regularly during the spring, summer, and fall, and any holes or open seams were mended. In late May and again in early July, the number of flowers in each plot was counted. The following spring, emergent seedlings were enumerated, plots were re-pelleted, and damaged flowers were counted mid-summer.

Damage done by large predators (rodents) can be estimated by subtracting predation values in semi-protected plots from unprotected plots. Damage done by small predators (slugs) can be estimated by subtracting predation values in protected plots from semi-protected plots. (Figure 1)

Analyses

For the predator exclusion experiment, the primary dependent variables analysed

were the percentage of flowers preyed upon in 1995, number of emergent seedlings in 1996, and percentage of flowers preyed upon in 1996. The percentage of flowers preyed upon was calculated to minimize population differences between plots:

$$\frac{\text{Flowers}_{\text{May}} - \text{Flowers}_{\text{July}}}{\text{Flowers}_{\text{May}}} \times 100$$

Each of the dependent variables (percentage of flowers preyed upon in 1995, 1996, and number of emergent seedlings in 1996) was used to detect proposed differences between treatments. The design was balanced and assumptions for parametric analysis were met, so analysis of variance was used. When a significant difference was detected between treatments ($P < 0.05$), Fisher's Protected LSD post-hoc test was used for further analysis (Schultz 1989). Site to site variation was used as a blocking factor, though the difference between sites was not significant ($P = 0.4118$).

Lighting

To determine the effect of the predator exclusion cages on lighting, a radiometer was used to measure the amount of white light penetrating both of the cage materials used in the above experiment.

To test the effect of predator exclusion cages on seed set a light exclusion experiment was used. Independent plants were covered with cages to mimic the effects of cages on plants in the predator exclusion experiment. Seventy-five flowering ginger plants were located late May 1995, at 25 separate sites. At each location, there was a protected

Figure 1. A sample graph showing the damage done by large predators (rodents) as estimated by the difference between semi-protected and unprotected plots. Damage done by small predators (slugs) is illustrated by the difference between protected and semi-protected plots.

plant (covered by a hardware-cloth cage), a semi-protected plant (covered with a WB plastic cage), and an unprotected plant. Plants were left to grow until late June, their flowers were picked, and seeds per flower were counted. The seeds were kept and used in the tracking experiments (see experiment described in Predators: Rodents).

Simulation

A matrix-based simulation was used to estimate the long term effects of predation on ginger populations. Seedling emergence measured in this paper was used in conjunction with clonal demographics (Cain & Damman, in press) collected from another location (Garretton, Ontario). The model included both demographic and environmental stochasticity, and assumed no density dependent effects on growth (Cain & Damman, in press). The simulation was run for 25 time periods, each representing one year of growth.

Predators

Slugs

At the 17 predation plots, slugs were identified (Chichester 1973), counted, and tested for predation of ginger flowers. To estimate the number of slugs at each site, slugs were counted in all predation plots by searching the soil surface and litter in late spring (late May) 1995. To account for those slugs residing beneath the soil surface during the day, and to better estimate the density of slugs per plot, soil cores (Runham & Hunter 1970, Southwood 1978) were extracted from each plot in mid-summer (late June). Three soil cores, each with the dimensions 15 X 15 X 10 cm, were dug from each plot and sifted

with a 2.5 mm mesh soil sifter (Southwood 1978).

Offer (1992) postulated that *Arion fasciatus* slugs were preying upon the ginger seeds at his sites in Guelph, Ontario as they were frequently “caught in the act” of seed consumption. To see if *A. fasciatus* would eat ginger seeds, slugs were collected from ginger sites and placed into arenas with transplanted flowering ginger with mature seeds. Each arena was a plastic container that was kept very moist and filled with soil and leaves from the ginger site. Slugs were provided with ginger flowers and pieces of fruit for food. Slugs remained in containers for one week and what was eaten was recorded. Five replicates were done.

Rodents

At the 17 predation plots, rodents were identified, their numbers were estimated, and their predation of ginger flowers was monitored.

Tracking paper was used to identify rodents and estimate the level of traffic that occurred at each site. On June 28, 1995, two small tubes containing tracking paper baited with both mature ginger seeds possessing elaiosomes and flower tissue were placed within 1 m of each of the 17 predation plots. Though Heithaus (1981) found that rodents could use their sense of smell to locate seeds with elaiosomes, flower tissue was also placed with the seeds to mimic natural conditions under which rodents would search and locate ginger seeds. After 5 days, tracking papers were collected and rodent foot prints were identified. Tracking papers also provided information on the presence of slugs. Slugs were sometimes found directly on the tracking paper, but their presence was primarily indicated

by slug tracks.

On June 23, four live traps were placed in the vicinity of each of 17 predation ginger plots. Traps were baited with sunflower seeds (as ginger seeds are a precious commodity). Live traps (Harland et al. 1979, M'Closkey 1975, Adler et al. 1984) were set out in the evening then checked early the next morning, as most rodents are nocturnal. Traps were also set in the morning and checked at noon (to account for diurnal rodents). This procedure was repeated on June 26th.

Rodents caught in live traps were released into a temporary home where they could be identified and tested for ginger predation. Each home was a '10-gallon aquarium,' partially filled with soil and bark covered by a piece of wood with holes drilled for air. Rodents were provided with water, sunflower seeds, and four transplanted flowering ginger with mature seeds. After twenty-four hours, damage to ginger flowers and the number of sunflower seeds eaten was assessed and each animal was returned to its site of capture.

Ant dispersal

To eliminate loss of seeds due to ant dispersal, boundaries of semi-protected and unprotected plots in the predator-exclusion experiment were moved outward. To determine the distance that the boundaries needed to be moved outward, the distance of seed dispersal due to ants was estimated. Two experiments were used: one using a fluorescent powder to track seed movement, the other using direct observation. Both were employed during the natural seed dispersal period for wild ginger.

Fluorescent powder was used to mark seeds prior to dispersal for later measurement of dispersal distances. Twenty drop-sites for seeds were located and marked with flags in areas with naturally occurring wild ginger. Sites were more than 15 m from one another. Peanut butter, approximately one tablespoon on a flat plastic disk, was placed at each site for 24 hours. The peanut butter was used as bait to attract local scavenging ants to establish trails between the site and their nests. Twenty-four hours later, the peanut butter was replaced with a pile of 10 ginger seeds per site. Each seed had been dipped in fluorescent powder. The seeds were left for one full night, to account for nocturnal ant activity, and one full day, to account for diurnal ant scavenging. On the evening of the second day, I searched for dispersed ginger seeds by scanning the litter layer around each site with an ultra-violet light. An area up to 100 m², measuring 10 m in any direction away from each drop-site, was searched for seeds.

In addition, seed carries were observed directly during the day. Six sites were located and marked with a flag within vision of one another, in an area with naturally occurring wild ginger. As was done in the above method, peanut butter was placed at each site for one full day and one full night. After 24 hours, the peanut butter was replaced with piles of 5 seeds on bright green ginger leaves. Though ginger flowers typically contained approximately 25 seeds, piles of 5 seeds were used because ginger seeds were scarce. The sites were watched closely for a 3 h period to observe ant dispersal of seeds. This method was carried out by 3 researchers at once, in different locations in the forest, and repeated 2 additional times.

III. RESULTS

Degree of predation experiment and flower remnants

Predation of ginger flowers had already begun late spring (Figure 2A). Flower remnants that were observed at this time were all left by slugs. *Arion fasciatus* littered the ground around clumps of ginger and was often found on ginger plants. Ginger leaves and stems were not preyed upon by the slugs, only the flower tissue contained slug groove marks. By mid-summer, ginger flower predation was severe (Figure 2B). The average percentage of ginger flowers preyed upon was $97.9 \pm 0.9\%$ ($\bar{x} \pm \text{SE}$); the range was 95.6 % to 100 %. Though there was large variation in the initial number of ginger flowers per plot, no difference was found in the percentage of flowers preyed upon between plots. In mid-summer, a census was done of the flower remnants left by predators. There were significantly more ($P = 0.0183$, $F = 7.6628$, $df_{\text{effect, sample}} = 1,8$) rodent flower remnants than slug remnants, using averages for each site (Figure 2C). This implied that of the predation that had been observed (Figure 2B), more was due to rodents than slugs. However, the greater number of rodent remnants observed is likely a consequence of slugs consuming the “evidence” of their predation, the whole flower. In fact, results from the predator exclusion experiment (below) support this suggestion.

Predator Exclusion Experiment

Treatments that excluded predators had fewer flowers eaten and produced more seedlings than plots that were exposed to predators. Plots protected from all predators

(large and small) had fewer flowers eaten in '95 and '96 than plots protected from large predators only (semi-protected); this predation was due to small predators (slugs). Plots protected from small predators (semi-protected) had fewer flowers eaten in '95 and '96 and produced more seedlings in '96 than plots that were exposed to all predators (unprotected); this predation was due to large predators (rodents). It follows that plots protected from all predators had many fewer flowers eaten in '95 and '96 and produced many more seedlings in '96 than plots exposed to all predators (unprotected). (Figure 3, Table 1)

The result that varied from the above trend was the lack of a significant difference in emergent seedlings in '96 in protected versus semi-protected plots. The comparison between protected versus semi-protected plots was supposed to indicate the effect of protecting ginger seeds from small predators (slugs) (refer to sample graph, Figure 1). In a pairwise comparison, there was no difference in seedling emergence when plots were protected from slugs ($P = 0.4530$, Table 1).

The amount of damage done by small predators (slugs) was compared to the amount of damage done by large predators (rodents). I estimated the amount of predation caused by small predators by subtracting the parameters for semi-protected from protected treatments; and the amount of predation caused by large predators was estimated by subtracting the parameters for semi-protected from unprotected treatments (Figure 1). The amount of flower predation caused by large predators (rodents) was not significantly different from that of small predators (slugs) ($P = 0.7049$, $F = 0.1529$, $df_{\text{effect, sample}} = 1,9$).

Figure 2. Ginger flower predation was measured in seventeen plots at 5 sites late spring (A), mid-summer (B), and flower remnants left by predators (rodents and slugs) were identified (C).

A. Predation of ginger flowers in late spring had already begun.

B. The percentage of ginger flowers eaten by mid-summer was very high.

C. There were significantly more flower remnants left by rodents than by slugs.

Lighting

Radiometer measurements indicated that 85% of white light passed through the aluminum hardware-cloth cages (protected treatments). The WB plastic cages (semi-protected treatments) retarded a negligible amount of light. These results indicate that the cages used did not significantly reduce the light reaching the plants.

Unprotected and semi-protected plants suffered high rates of predation. As a result, of the 25 plants selected for each treatment, only 15 protected, 13 semi-protected, and 7 unprotected plants remained for seed counts. A Kruskal-Wallis test for non-parametrics confirmed that there was no significant difference in seed set between the 3 treatments. For example, the seed set for protected plants was 25.6 ± 2.2 , semi-protected was 23.3 ± 2.7 , and unprotected was 30.9 ± 4.8 ($\bar{x} \pm SE$). The chi-square statistic required to indicate a significant difference between groups is $H \geq 5.991$, and the statistic for this experiment was $H=2.435$ (where $0.5 \geq P \geq 0.1$). Thus, the predator exclusion cages did not effect wild ginger's seed set.

Simulation

The population growth simulation that used the seedling emergence results from the predator exclusion experiment predicts that seed predation has severe effects on ginger populations. After 25 time periods, a population exposed to all predators would be expected to triple in size. However, a population that was semi-protected, exposed to only small predators like slugs but protected from larger predators like rodents, would increase by 78 times its original size. Further, a population completely

Figure 3. Ginger plots were subject to different treatments using cages that excluded predators based upon mesh size. The effect of exclusion treatments on flower and seed predation was measured by the percentage of flowers eaten in 1995 (A), the number of emergent seedlings in 1996 (B), and the percentage of flowers eaten in 1996 (C).

A. Ginger plots protected from all predators (rodents and slugs) had the least flowers eaten, (semi-protected) plots protected from large predators (rodents) but exposed to small predators (slugs) had a greater percentage of flowers eaten, and plots exposed to all predators suffered the most flower predation in 1995.

B. Ginger plots protected from all predators (rodents and slugs) produced the most seedlings, (semi-protected) plots protected from large predators (rodents) but exposed to small predators (slugs) produced fewer seedlings (though not significantly), and plots exposed to all predators produced the least number of seedlings in 1996.

C. Ginger plots protected from all predators (rodents and slugs) had the least flowers eaten, (semi-protected) plots protected from large predators (rodents) but exposed to small predators (slugs) had a greater percentage of flowers eaten, and plots exposed to all predators suffered the most flower predation in 1996.

Treatment

Table 1. A statistical summary of the effects of exclusion treatments on flower and seed predation.

Variable	Statistic ^a	Pairwise Comparison ^b	P Value
Percentage of flowers eaten in '95	P = 0.0001 F = 28.2762	Prot * Semi	0.0060
		Prot * Unprot	0.0001
		Semi * Unprot	0.0019
Number of emergent seedlings in '96	P = 0.0070 F = 8.4992	Prot * Semi	0.4530
		Prot * Unprot	0.0030
		Semi * Unprot	0.0109
Percentage of flowers eaten in '96	P = 0.0001 F = 42.6259	Prot * Semi	0.0010
		Prot * Unprot	0.001
		Semi * Unprot	0.0009

^a Parametric analysis of variance was used, $df_{\text{effect, sample}} = 2, 15$.

^b Fisher's LSD test for multiple comparisons was used. Prot = protected plots; Semi = semi-protected plots; Unprot = unprotected plots; * = versus.

protected from predators would be expected to increase by 242 times its original size.

(Note: these numeric values illustrate estimated differences in population growth due to variation in predation, but are not realistic values for population growth. For example, the matrix does not account for resource depletion in the environment.) (Figure 4)

Predators

Slugs

Arion fasciatus was by far the most predominant slug at the ginger plots. (The only other slug identified at these plots was *A. circumscriptus*.) *Arion fasciatus* occurred at very high densities in ginger plots beginning in early spring, and their numbers waned by early summer. *A. fasciatus* was observed in situ to lay on top of ginger flowers curling its head and end over the sides of the flower. Its head probed and absorbed flower tissue in a circular motion leaving round holes exposing the immature, white-coloured, small, ginger seeds. Ginger flowers were immature while slug densities were at their highest (flowers begin to sprout late April and develop until mature at the end of June/early July). The holes made by slugs were often small (<4 mm in diameter, one third of the whole flower diameter), though sometimes large (exposing one whole side of the flower). On a few occasions, I observed more than 3/4 of the flower tissue to have been eaten. Exposed seeds would turn brown then black. Sometimes if the hole in the flower was small, only the seeds in the exposed ovule would turn black in colour. The flower would continue to grow, seeds in other ovules would develop into mature seeds, and the flower would dehisce normally mid-summer. (Table 2)

Figure 4. Matrix-based simulation predicting the effect of seed predation on long term growth of ginger populations.

Large numbers of *Arion fasciatus* were counted on the litter layer and soil surface at ginger sites in late spring. As many as 24 slugs were counted in a 1 m² area. The number of slugs differed significantly from one site to the next. A Kruskal-Wallis test for non-parametric data produced an H value = 10.759 ($0.05 \geq P \geq 0.025$, $df_{\text{effect, sample}} = 4, 16$), where $H \geq 9.488$ is significant. To see whether slug numbers correlated with the amount of predation caused by small predators (slugs), slug counts were compared to values for small predator predation from the predator exclusion experiment. I estimated the amount of predation caused by small predators (slugs) in the predator exclusion experiment by subtracting the parameters for semi-protected from protected treatments (Figure 1). These values were compared to average slug counts for each site using linear regression. No correlation was found between slug counts and the percentage of predation in '95 flowers, '96 flowers, or the number of '96 seedlings ($P = 0.2024$, $F = 2.6444$; $P = 0.8193$, $F = 0.0621$; $P = 0.2129$, $F = 2.4871$, respectively with $df_{\text{effect, sample}} = 1, 3$).

As a large number of slugs reside and move through the top 10 cm of the soil layer (Getz 1959), soil cores were dug early summer to estimate the true number of slugs present. Unfortunately, due to an unusually dry summer (no rain for fifteen days prior to the removal of soil samples) very few slugs were found, thus a comparison between plots was impossible using this data. Research has indicated that slugs will reside deeper in the soil during drought (Runham & Hunter 1970).

Five *Arion fasciatus* were placed in 5 separate arenas with flowering ginger plants containing mature seeds. All were found to eat the alternative fruit (grapes and plums) available to them. Though they were often found languidly covering ginger flowers, only

Table 2. Summary of ginger damage by slugs and rodents.

Damage	Slug	Rodent
When	Begins early spring and continues to early summer (late May/early June)	Exclusively mid-summer (mid-June/early July)
Description of damage: Flowers	Round holes left in flower tissue	Flower tissue is torn beyond repair
Seeds	Immature seeds in ovule are exposed and do not develop into mature seeds	Mature seeds are eaten
Extent of damage	May be partial damage to flower affecting only a portion of the seeds; sometimes whole flower is damaged and flower development ceases thus no seeds mature	Whole flower is ravaged for seeds, though some seeds may fall to the ground and evade initial predation

the flower tissue and elaiosome of the ginger seeds were consumed. Flowers were often fully consumed so that no remains were left. The seeds themselves always remained uneaten. (Table 2)

Rodents

No flower remnants left by rodents were found in the spring or early summer. However, large numbers of flower remnants left by rodents began to appear mid-summer when ginger flowers contained mature seeds (Table 2). There was no significant variation in the number of rodent remnants between sites (Figure 2C).

In late June, nearly all of the 510 ginger seeds used for bait in the tracking experiment were carried off. The tracking paper was often chewed and torn. Almost all tubes contained *Peromyscus leucopus* (white-footed mouse) tracks (Table 3). There were also *Tamias striatus* and *Mus musculus* tracks. As no *M. musculus* was caught in the live traps (see experiment described below), the species' affinity for ginger seeds could not be tested. There appeared to be no obvious pattern to where the tracks occurred. Tracking paper also indicated the prevalence of slugs at ginger plots. Almost all tubes of tracking paper contained tracks left by slugs, and slugs were often found on the tracking paper.

Three eastern chipmunks (*Tamias striatus*) and one deer mouse (*Peromyscus leucopus*) were captured using live traps and identified (Adler et al. 1984, Barry & Francq 1980, Burt & Grossenheider 1961, Forsyth 1985, M'Closkey 1975). One eastern chipmunk was captured near site 2, the other two were caught at site 3. The *Peromyscus* sp. was also caught at site 3. Interestingly, neither site 2 nor 3 had disproportionately

more rodent tracks. One problem with the live trapping experiment was that some of the traps were discovered with their trap doors sprung shut, yet no animal inside. It is possible that some of the live traps were too sensitive, hence were sprung prematurely and did not capture all rodents around the clumps of wild ginger (as may be suggested by the finding of *Mus musculus* paw tracks in the tracking paper experiment).

One rodent of each species (*P. leucopus* & *T. striatus*) was tested for predation of ginger flowers with mature seeds. Following the 24 hour exposure to ginger flowers, rodents were removed from their temporary homes. The chipmunk ate solely sunflower seeds and did not prey upon any of the flowering ginger parts. However, the *Peromyscus* sp. ate all of the sunflower seeds provided and preyed upon all four of the flowers on the transplanted ginger. Each ginger flower had been removed from the plant leaving a precisely cut flower stalk. Seeds had been removed from the flower, and the ravaged flower tissue remained. I observed the mouse boldly eating one of the flowers. He held the flower with both paws rotating it as he pilfered the ovules for seeds. A few seeds dropped to the ground and were left. (Table 2)

Ant dispersal

Almost all of the ginger seeds marked with fluorescent powder were carried off. Of the nearly 200 seeds moved, I managed to locate 40. Though a 100 m² area was searched for dispersed seeds, all seeds were found within a 1 m radius of the nearest drop-site. The average distance seeds moved from the nearest drop-site was 39 ± 5 cm ($\bar{x} \pm$ SE). There was often an ant hole visible within 50 cm of the drop-site. Those seeds that

Table 3. Predator activity at the seventeen predation plots.

Site	Plot	Slug Counts on Litter and Soil	Tracking Paper ^a		Rodent Live Traps
			Slug Tracks	Rodent Tracks	
1	1	24	✓✓		
2	2	0	✓	<i>P. leucopus</i> x 2	
2	3	3	✓	<i>P. leucopus</i>	<i>T. striatus</i>
2	4	3	✓✓	<i>P. leucopus</i> x <i>T.</i> <i>striatus</i>	
2	5	4	✓		
1	6	11	✓	<i>P. leucopus</i>	
4	7	5	✓	<i>P. leucopus</i>	
4	8	10	✓✓	<i>P. leucopus</i> x 2	
4	9	5		<i>P. leucopus</i>	
3	10	3	✓	<i>P. leucopus</i> x 2	
3	11	5	✓	<i>M. musculus</i>	<i>T. striatus</i>
3	12	0	✓	<i>P. leucopus</i>	<i>T. striatus</i> & <i>P.</i> <i>leucopus</i>
6	13	2	✓✓	<i>P. leucopus</i>	
6	14	0	✓		
6	15	2	✓	<i>P. leucopus</i> x 2	
6	16	3	✓✓	<i>P. leucopus</i>	
6	17	2	✓✓	<i>P. leucopus</i> x 2	

^a Two tubes of tracking paper were placed at each plot. ✓ indicates that slug tracks were found on one of the tracking papers, ✓✓ indicates that slug tracks were found on both tracking papers. Rodent x 2 indicates that rodent tracks were found on both tracking papers.

were located rarely had their elaiosomes.

During direct observations, of the 270 seeds laid out, only 13 of the seeds were moved. Nine of those seeds were dispersed within 1 m of the drop-site. The average distance moved was 32 ± 5 cm ($\bar{x}$, $\pm$ SE) remarkably similar to the average distance (39 cm) obtained for seeds dispersed in the fluorescent powder experiment. Remarkably, two seeds were displaced by great distances; 23.5 m and 36 m! Also, two seeds disappeared unnoticed while researchers were closely following other seeds being dispersed.

Of the 53 distances measured (including both the fluorescent powder and direct observations), 87% of them occurred within 60 cm of the drop-site (place of origin). This was the distance used in (semi-protected and unprotected treatments) the predator exclusion experiment to accommodate seed dispersal. Thus, the 60 cm displacement accounted for the outward movement of 87% of ginger seeds.

When ants encountered seeds, they sensed them with their antennae, and half the time left the seed. The other half of the time, the ant would perhaps examine the seed with its mouthparts (usually focusing on the elaiosome) then grasp the seed with its mandibles and try to carry it away. Because the species of ants that approached the ginger seeds were often quite small relative to the seeds, the ant would often drag the seed while crawling backward for a distance. Sometimes the ant would drag the seed, then attempt to pick it up and walk forward, only to continue dragging it, presumably back to the nest. Sometimes the ant would “give up” and leave the seed after a distance, and continue to forage.

In both instances when an ant carried a ginger seed for an extremely long distance,

the ants appeared to be travelling in a constant direction, and slowly forged onward carrying the seed. In one instance, the ant finally dropped the seed after carrying it for 23.5 m. In the other instance, we lost sight of the ant in the debris of the litter layer. This ant may have reached its final destination (the nest).

IV. DISCUSSION

Predation

Wild ginger suffered extreme levels of flower and seed predation. By mid-summer in 1995, 97.9 % of over 700 ginger flowers examined in the 17 predation plots were destroyed. The effect of this predation on the population biology of wild ginger was illustrated in the predator exclusion experiment. The percentage of flowers that were eaten in '95 and '96, increased greatly with exposure to small predators (slugs), and increased further with exposure to large predators (rodents) (Figure 3). Seedling emergence the year following predation declined significantly in plots that had been exposed to predators (Figure 3). A simulation was used to predict the long term effects of this predation on wild ginger (Figure 4). Following 25 time periods, populations protected from large predators would increase by 27 times that of unprotected populations, and populations protected from small predators would increase by 56 times that of unprotected populations.

The levels of predation that were recorded in this study were higher than expected for *A. canadense*. Heithaus (1986) found that 40 % of wild ginger seeds were consumed by predators and Offer (1992) found that 42 % of ginger seeds were destroyed by predators. However, flower and seed predation in understory herbs are known to fluctuate from year to year (Ehrlén 1996). As well, flower and seed numbers may have been higher than normal due to restrictions imposed by the experiment itself. Clumps of ginger are rare and widely fragmented in the forest understory. I may have increased the

predation pressure on unprotected clumps of ginger when protective cages were placed over some of the available. In addition, there is evidence to suggest that understory herbs have temporally staggered seed maturation, to accommodate generalist myrmecochores (Ruhren & Dudash 1996). Hence predators would be specifically targeting mature ginger seeds for a short window of time when other herb seeds have passed maturation or have not ripened. During this short period of time, ginger would be under heavy predation pressure.

Predators

Arion fasciatus is a dominant presence in the habitat in which *Asarum* grows. Offer (1992) also found them to be abundant at his field sites in Guelph, Ontario. These slugs are conspicuous on the soil and litter layer surrounding clumps of ginger in early spring and remain common as long as the soil remains moist, until the end of May at my sites (Cantley, Quebec). This is the period that ginger flowers are heavily attacked by *A. fasciatus*. Slugs consume the ginger flower tissue, prematurely exposing juvenile seeds. Slugs may also be able to absorb nutrients from the immature soft-coated seeds, hence killing them. Exposed seeds or seeds in an ovule damaged by slug predation do not continue to develop (as described in the Results section under *Predators: Slugs*). Thus, these seeds are not viable and likely do not produce offspring. I expected to find that ginger exposed to slugs would have decreased seedling emergence the year following predation. However, this was not the case. In the predator exclusion experiment, exposure to seeds did not significantly decrease seedling germination. Perhaps, an

experiment with a larger sample size might be more sensitive to the effects of slug predation. A matrix-based simulation (Figure 4), using the seedling germination results, found that population growth was significantly altered with exposure to small animals (slugs). It is predicted that ginger populations exposed to small animals will increase at 1/56th the rate of populations protected from small animals.

By mid-summer slugs are not a threat to ginger flowers. Ginger flowers by this time contain mature seeds with thick protective seed coats that slugs cannot penetrate. Consumption of the flower and ovule tissue at this point would not be lethal to the seed, as it can survive on its own. By mid-summer, slug movements are restricted anyway. The ground is less moist and slug travel is more difficult, so their presence at clumps of ginger is limited.

By mid-summer ginger is being threatened by an other predator. Rodents begin to prey upon ginger seeds about the time that ginger seeds mature, as indicated by the sudden appearance of flower remnants left by rodents late June. Rodent predation may occur mid-summer because rodents are able to detect the ripened elaiosomes on mature seeds within the flowers (Heithaus 1981).

The predominant rodent at ginger sites, as indicated by tracks left in the tracking paper experiment was *Peromyscus leucopus* (white-footed mouse). *P. leucopus* occurs widely in northeastern United States and southeastern Canada in deciduous woodland habitats (Adler et al. 1984, Barry & Francq 1980, Burt & Grossenheider 1961, Harland et al. 1979, M'Closkey 1975). *P. leucopus* was directly observed to eat ginger seeds in arena experiments. This was an expected finding, as rodents, particularly *Peromyscus*

spp., are known as predominant seed predators of understory herbs (Ruhren & Dudash 1996, Kjellsson 1985, Pucek et al. 1993) including *A. canadense*, *Jeffersonia diphylla*, and *Sanguinaria canadensis* (Heithaus 1981).

There may be ginger flower and seed predators other than *A. fasciatus* and *P. leucopus*. However, there has been no evidence to suggest other animals as potential predators of ginger. Though the predator exclusion experiment was specifically created with mesh sizes for excluding slugs (protected cages) and rodents (semi-protected cages) from ginger, other predators may have contributed to the predation that was observed.

The ants that carried off ginger seeds are unlikely predators of the seed. Many granivorous (seed eating) ants are found in Mediterranean climates such as Australia, South Africa, California, and Italy (Aronne & Wilcock 1994, Espadaler & Gomez 1996). However, in temperate climates myrmecochorous seeds possess fleshy appendages high in fatty acids and diglycerides that attract scavenging ants. The elaiosomes are the food item of interest and seeds are abandoned after elaiosome removal (Beattie 1985, Handel 1978). Offer (1992) confirms this belief by describing myrmecochory in wild ginger and that ants eat the elaiosome then abandon the seed.

Dispersal

Myrmecochory (ant dispersal) was the dispersal mechanism observed repeatedly in this study. The purpose of the ant dispersal observations was to determine an average seed dispersal distance. In the predator exclusion experiment, the boundaries for counting emergent seedlings in plots (semi-protected and unprotected) exposed to ants were

adjusted for this ant-dispersal distance. The average dispersal distance observed was between 32 cm (fluorescent powder observations) and 39 cm (direct observations). These observations are consistent with dispersal distances typical of temperate understorey herbs. In a study of 9 *Viola* species, Culver & Beattie (1978) found ants to move seeds an average distance of 75 cm. In studies by Kjellsson (1985) conducted in Denmark, the myrmecochorous herb *Carex pilulifera* was dispersed as far as 1.4 m. In addition, Heithaus (1986) observed ginger seeds being dispersed by ants an average of 80 cm (range: 71-94 cm).

Two very long dispersal distances were recorded during the 13 observed seed carries (23.5 m & 36 m!). The observed distances created a precedent in the literature on myrmecochory of woodland herbs. In a comprehensive review, Cain et al. (in press) present an average ant dispersal distance for forest herbs of 1.38 m. All of the maximum distances shown are less than a few metres, with the exception of one study by Pudlo et al. (1980) that describes a maximum dispersal distance for *Maianthemum canadense* of 17 m. Even this extraordinary dispersal distance is well under the two that were observed in this study. Interestingly, this study only takes into account primary dispersal. Secondary dispersal, would move seeds even further.

Arion slugs are unlikely to be effective dispersal agents of ginger seeds or other understorey seeds. Ginger seeds are relatively large and heavy and could not be dispersed by slugs. Even very small seeds might cling to the slimy slug exudate for a short period, but the distance dragged would not be very far. There are no studies to suggest that slugs would be effective seed vectors.

Rodents are often cited as dispersers of seeds (Vander Wall 1993, Vander Wall 1994). However, most of this effective dispersal occurs late summer and fall while rodents are caching food in preparation for the onset of winter. Understorey herbs typically emerge early spring and seed soon thereafter (Bierzychudek 1982, Ruhren & Dudash 1996). Food available at this time of the year is not cached by rodents, rather, it is eaten 'on the spot.' Though some seeds are likely transported as happenstance, rodents are thought to be unlikely effective dispersal agents of understorey plants (Barry 1976, Heithaus 1981).

Conservation of Understorey Herbs

Deciduous forest understorey herbs are at risk due to habitat disappearance and fragmentation. A mechanism that is imperative for the ultimate survival of this group is the effective colonization of new habitats. A significant obstacle threatening the success of colonization is seed predation.

Wild ginger suffers severe flower and seed predation. Ginger seed predation was shown to decrease the number of emergent seedlings the year following predation. In addition, a matrix-based simulation illustrated that seed predation over a long period has pronounced negative effects on population growth. Other studies have shown temperate understorey herbs to suffer high levels of seed predation (Heithaus 1981, Ruhren & Dudash 1996, Turnbull & Culver 1983). For example, 86% of seeds are eaten in the understorey herb *Carex pilulifera* (Kjellsson 1985), 83.7% of seeds in *Lathyrus vernus* (Ehrlén 1996), 47% in *Jeffersonia diphylla*, 43% in *Sanguinaria canadensis* (Heithaus

1981), and 30% in *Viola* spp. (Culver & Beattie 1978). The effects of this seed predation on populations of understorey herbs should receive further study.

A. fasciatus was shown to heavily prey upon ginger flower tissue in the spring. This (small animal) predation significantly decreased flower numbers in 1995, 1996, and the simulation that I used projects long term negative effects on population size (Figure 4). *Arion* spp. slugs were recently introduced by European migration. Ginger has probably not evolved the protective mechanisms necessary to effectively defend itself from this relatively new predator. Further study should be done to indicate whether *Arion* spp. are preying upon other understorey herbs. The introduction of predators to unprepared habitats is a commonly cited reason for plant endangerment and extinction (Janzen 1969, Janzen 1971a, Janzen 1971b, Purves et al. 1995).

Rodents preyed upon ginger seeds heavily in mid-summer. Rodent (large animal) predation significantly decreased flower numbers in 1995, 1996, and seedling emergence in 1996. The simulation conducted projects that exposure to large predators restricts ginger population growth by 1/27th. Rodents are common predators of deciduous understorey herbs (Ruhren & Dudash 1996, Kjellsson 1985, Pucek et al. 1993). Rodents can destroy large numbers of seeds (Vander Wall 1994) and rodent predation can detrimentally effect the establishment of plant populations and restoration ecology efforts (Hoffmann et al. 1995). Their effects on other understorey herbs should be documented.

The seed dispersal mechanism used by ginger is common to other understorey herbs (Beattie 1985, Beattie & Lyons 1975, Bierzychudek 1982, Culver & Beattie 1978, Handel 1978, Handel et al. 1981, Heithaus 1981, Ruhren & Dudash 1996). Ants that

disperse understorey seeds are generalists (Ruhren & Dudash 1996). Thus, ants that disperse ginger seeds disperse other herbs. We may assume that the dispersal distances measured in this study are representative of other understorey plant systems. If so, we can conclude that the extraordinary dispersal distances measured in this study are occurring in the deciduous forest understorey. These dispersal distances would play a positive role in effective colonization of new habitats (Andersen 1988).

However, seed dispersal by ants occurs only after flower dehiscence (late June/early July). And seed predation takes place before flower dehiscence. Seed predation is so severe that there are few seeds remaining to be dispersed. It may be that this dispersal mechanism functioned well before the introduction of the slug. However, now, this primary mechanism for colonizing new environments to establish replacement populations is not working effectively. Other understorey plants may be suffering a similar fate.

This is a preliminary study exploring the mechanisms imperative for the survival of wild ginger and other understorey plant species. Further natural history observations of other understorey plants are necessary to confirm the primary obstacles interfering with successful colonization. Particularly, research evaluating the effects of *A. fasciatus*, or similarly European introduced slugs, on other understorey plant species. Future conservation plans may include predator satiation of rodents using economic seed such as millet, or more likely, the introduction of a biological control such as a natural parasitoid of the European introduced slug (Chambers & MacMahon 1994).

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