EFFECTS OF FOREST COVER AND FOOD LIMITATION ON THE GROWTH AND SURVIVAL OF JUVENILE AND ADULT NORTHWESTERN SALAMANDERS (*AMBYSTOMA GRACILE* BAIRD)

by

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ABSTRACT

Forest harvesting alters microclimate and structure, which may affect amphibians directly, as well as affect the abundance, diversity and/or availability of amphibian prey. As a result, the foraging efficiency of amphibians in harvested areas may be reduced, lowering body condition, and perhaps survival. I experimentally tested the hypotheses that: 1) body condition would be lower in clearcuts than forested sites; and 2) salamanders would be food limited in clearcuts but not in forest, and food addition to clearcut enclosures would improve body condition, while food addition to forest enclosures would have no effect. We used 24 large-scale field enclosures in a randomized split-plot block design (3 blocks) with forest type (1 clearcut and 1 forest site in each block) and food level (supplemental mealworms, ambient) as factors to examine the effects on growth and survival of adult and juvenile northwestern salamanders. In trial one, which started in October 2003, each of the 24 enclosures received 14 marked and measured juveniles. Juveniles were recaptured and re-measured in April/May 2004. In trial two, each of the enclosures received 7 marked and measured adult salamanders in May 2004, and adults were recaptured and re-measured in October/November 2004. Mealworms were added weekly to half the enclosures at each site. We used an analysis of variance to test for differences between clearcut and forest, supplemental food and ambient food, and any interactions on the weight change of animals and on the proportional survival for each enclosure. We found no significant effect of forest type or food level on growth of juveniles or adults, or on proportion of juveniles recaptured at the end of the experiment. However, for adults, there was a significant effect of forest type on the proportion recaptured ($p < 0.001$), with fewer animals recaptured in clearcut enclosures. These results indicate that clearcuts may provide unsuitable habitat for salamanders during summer in the Pacific Northwest, but not during winter.

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INTRODUCTION

The habitats available to species have different characteristics in terms of abiotic factors, food supply, predators, competitors, and the longevity of suitable conditions, among others. These characteristics affect the fitness of individuals (in terms of the number of young produced), and the demography and dynamics of their populations (Southwood 1988). Through selection, species evolve a life history strategy that maximizes individual fitness in a particular habitat; this habitat might then be called the preferred habitat of the species (e.g., mature forest, native grassland etc.) (Southwood 1988). An individual's fitness may be reduced in habitats that have different characteristics than the preferred habitat (e.g., differences in food supply, more predators).

Anthropogenic activities (e.g., forest harvesting, agriculture) cause changes to habitat characteristics that may have effects on the individual fitness of organisms. Forest harvesting can cause a number of physical changes to habitat: a greater range in microclimate (Chen et al. 1993); increased soil compaction (Dyrness 1965, Sidle and Drlica 1981); and increased surface and soil temperatures, decreased soil and air moisture, and changes to the amount and decay class of downed wood, leaf litter depth and type, soil/humus acidity and hardwood shrub abundance (Geiger 1971). These physical changes may cause harvested areas to become less suitable habitat for many species adapted to forest conditions (Richardson et al. 2005). Vagile species may attempt to disperse into adjacent forest until conditions in harvested areas become more favourable (Ash and Bruce 1994). Many small species (e.g. some invertebrates, some amphibians) have low vagility and are frequently unable to leave harvested areas (Blaustein 1994, Petranka 1994). Individuals that remain in harvested areas may have reduced survival and body condition (and therefore fitness) as a result of habitat changes.

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Amphibians have become a focus of research on the effects of forest harvesting due to their physiology and associated specialized habitat requirements. Amphibians are poikilotherms (cold-blooded) that need to regulate their body temperature behaviourally, and they have moist, permeable eggs, gills and skin (deMaynadier and Hunter 1995, Stebbins and Cohen 1995). Amphibians have small home ranges, are highly philopatric, and have limited dispersal ability, making them sensitive to local environmental perturbations (Blaustein et al. 1994, Duellman and Trueb 1994, Stebbins and Cohen 1995, Beebee 1996). Most species are alternately exposed to either aquatic or terrestrial environments throughout their life cycle, and therefore are sensitive to disturbances in either (Stebbins and Cohen 1995, Semlitsch 2003). Since amphibians have such specialized requirements, they have been proposed as indicators of habitat quality and environmental changes (Bury and Corn 1988, Gibbons 1988, deMaynadier and Hunter 1995, Welsh Jr. and Droege 2001).

The responses of amphibian communities and populations to forest harvesting in North America have been well-studied, and results have varied (for a comprehensive review, see deMaynadier and Hunter 1995). In the eastern United States, many studies report reductions in amphibian population size and species richness in harvested areas (Pough et al. 1987, Petranka et al. 1993, Petranka et al. 1994, Ash 1997, Harpole and Haas 1999, Cromer et al. 2002, Knapp et al. 2003). In the Pacific Northwest, some studies have found large reductions of amphibians in harvested areas (Bury 1983, Dupuis et al. 1995, Cole et al. 1997, Davis 1998, Dupuis and Steventon 1999, Aubry 2000, Grialou et al. 2000, Naughton et al. 2000, Matsuda and Richardson 2005), while others have reported little change (Bull and Carter 1996, Richardson and Neill 1998, Maxcy 2000, Biek et al. 2002).

Three hypotheses have been proposed to explain observed patterns of amphibian decline in harvested areas. First, amphibians might be killed during the physical process of logging (deMaynadier and Hunter 1995, Chazal and Niewiarowski 1998). Second, amphibians might disperse out of harvested areas (emigration hypothesis), resulting in an observed decline in diversity and population size in

harvested areas (Ash and Bruce 1994). Emigrating amphibians may have difficulty establishing territories in adjacent forest habitat that contains resident animals (Petranka 1994). Third, amphibians might remain in harvested areas and vertically migrate into the substrate to escape adverse surface conditions (vertical migration hypothesis). Individuals that migrate into the substrate will be less likely to be encountered using traditional amphibian sampling techniques (pitfall traps, cover boards, litter searches), resulting in an apparent decline in abundance and diversity in harvested areas (deMaynadier and Hunter 1995). If surface conditions remain inhospitable for an extended period of time, these individuals may perish due to limited foraging opportunities in refuges, causing an actual decline in abundance and diversity in harvested areas (Petranka 1994, Petranka et al. 1994). There have been some attempts at distinguishing between these hypotheses. Johnston (1998) radio-tracked Coastal giant salamanders (*Dicamptodon tenebrosus*) in clearcut and forest habitats, and found reduced movement in clearcuts, results that are consistent with the vertical migration hypothesis. In contrast, northwestern salamanders (*Ambystoma gracile*) and ensatinas (*Ensatina eschscholtzii*) showed trends towards moving farther and with a higher rate of movement in harvested areas (Maxcy 2000), results more consistent with the emigration hypothesis. However, it is difficult to study movement patterns of amphibians due to their small size: many species are too small for radio-transmitters with sufficient battery life to permit tracking for an extended period of time. Using trapping grids to sample movement of animals is restricted by the typically low recapture rates, and the dependence on animal activity. If activity rates change in different habitats, trapping results can be confounded.

Although there remains uncertainty about how amphibians respond to harvesting in terms of movement patterns, it is still important to understand which conditions affect amphibians in harvested areas, as this understanding might permit management recommendations. Amphibians might be affected by the microclimate changes associated with harvesting: amphibians may experience high evaporative water loss due to the increased surface and soil temperatures and decreased soil and air moisture in harvested areas (Heatwole and Lim 1961, Jaeger 1971, Rothermel and Semlitsch

2002, Mazerolle and Desrochers 2005). Amphibians might also be affected by a change to the prey supply, i.e., invertebrates. Harvesting can reduce organic matter and increase temperature and moisture extremes beyond the tolerance range of most arthropods, resulting in a reduction in arthropod abundance and diversity (Vlug and Borden 1973, Bird and Chatarpaul 1986). Because of the change in conditions, forest-adapted invertebrate species may be unable to persist in harvested areas (Shure and Phillips 1991, Niemela et al. 1993, Heliola et al. 2001). These changes to invertebrate populations may affect the ability of amphibians to acquire sufficient high quality food resources, and may result in amphibians being food limited in harvested areas.

Both microclimate changes and prey population changes may interact to affect amphibians in harvested areas. Metabolic requirements of salamanders have been shown to increase with increasing temperature (Jaeger 1980a, Currens et al. 2002), while food assimilation efficiencies decrease (Merchant 1970, Jaeger 1980a). Salamanders can run a negative energy budget during warm, dry conditions (such as might be experienced in harvested areas), which has negative effects on the reproductive components of fitness (Jaeger 1980a). As a result, salamanders may compensate for food limitation by feeding at high rates when conditions are favourable (rainy weather), and store energy as fat reserves for later use (e.g., reproduction, maintenance during harsh climatic conditions) (Jaeger 1980a). If prey populations change in harvested areas such that high quality prey are limited, amphibians may be unable to acquire sufficient resources in this reduced foraging time.

To test the mechanisms underlying amphibian response to forest harvesting, an experimental approach is needed. The use of large field enclosures in amphibian studies has gained popularity in recent years: they have been used to study terrestrial ecology (Pearson 1955, Pechmann 1995), the effects of forest harvesting on body condition (Chazal and Niewiarowski 1998), and the influence of abundance of small-mammal burrows and conspecifics on density and distribution (Regosin et al. 2003). Although use of field enclosures has some limitations (e.g., some mortality factors may be reduced or increased within enclosures), field enclosures are ideal for experimental

manipulations: enclosures encompass the natural variation in habitat, animals are exposed to natural climatic conditions (unlike laboratory experiments), and individual animals can be followed through time using repeated sampling.

We designed an experiment using field enclosures to contrast growth and survival of Northwestern salamanders (Ambystomatidae: *Ambystoma gracile* Baird) from a common population when exposed to forest versus clearcut conditions, and to determine whether salamanders are food limited in clearcuts. Food limitation was tested by way of a food addition to half the enclosures. We examined the survival and the growth of salamanders in enclosures with two experiments: one during fall and winter using juvenile salamanders, and one during spring and summer using adults. For both experiments, we predicted: 1) that growth and survival would be lower in clearcuts than forested sites; and 2) that salamanders would be food limited in clearcuts, but less so, or not at all in forest, and food addition to clearcut enclosures would enhance survival and growth, while food addition to forest enclosures would have no effect. Environmental variables, including soil moisture, surface temperature, air temperature and precipitation, were monitored in each of the clearcut and forest sites throughout the experiments. Ambient invertebrate biomass, population size and diversity were periodically monitored outside each enclosure during both experiments.

METHODS

Study Animal

The northwestern salamander, a common species in the Pacific Northwest (Aubry 2000, Maxcy 2000), is an aquatic breeder (in ponds and slow-moving streams) that uses terrestrial habitat in the non-breeding season (Corkran and Thoms 1996). Mature adults migrate seasonally to breeding sites during late winter and spring, and return to the terrestrial habitat after breeding. There is evidence from recaptures that this species is capable of breeding migrations exceeding 1 km (Maxcy 2000). Metamorphosed juvenile salamanders emerge from their natal ponds during rainy

nights in the late summer, and mature in the surrounding terrestrial habitat. Like other ambystomatids, juveniles and adults are generally fossorial by nature: since they have limited ability to excavate their own burrows, they rely on existing small mammal burrows to gain access belowground (Semlitsch 1981, 1983, Madison 1997, Madison and Farrand III 1998, Faccio 2003). They may be found above ground at night during and after rain, and sometimes in soft logs or in bark and wood mounds at the bases of snags (Corkran and Thoms 1996). Because of the secretive nature of the species, little is known about the terrestrial phase: information is lacking on preferred prey, densities, home range sizes, and agonistic behaviours.

Study Area

This study took place in the University of British Columbia's Malcolm Knapp Research Forest (MKRF), located ~60 km east of Vancouver, British Columbia (122°34' W, 49°16' N). The MKRF is within the Coastal Western Hemlock biogeoclimatic zone, which is characterized by dry summers, and rainy, cool winters. The southern portion of the MKRF typically receives approximately 2200 mm of rain per year, and snowfall is rare. The forest is largely comprised of second-growth Western hemlock (*Tsuga heterophylla*) and Western redcedar (*Thuja plicata*) forest, which naturally regenerated after a stand-replacing fire in 1931. The MKRF is currently a patchwork of second-growth forest and small-scale logging operations (clearcuts, thinned stands). Northwestern salamanders are abundant in the MKRF (Maxcy 2000).

Three areas (blocks) were selected in the southern portion of the MKRF for this experiment: each block had one clearcut site (1.2 ha, 2.0 ha, or 8.7 ha; < 5 years old; ground harvested) and one second-growth forest site (>70 years old) (Figure 1, Table 1). All sites were between 225 and 310 m in elevation. Northwestern salamanders occurred naturally in all sites (personal observation). The clearcut sites, which were replanted after harvesting, all had a high percentage of downed wood cover (≥ 5 cm diameter; ≥ 1 m in length; 53% cover, SE = 7%) and had a high percentage of shrub and herb cover during the summer (shrub = 45%, SE = 6%; herb = 25%, SE = 5%). The forest sites had comparatively lower downed wood cover (18% cover, SE = 4%)

and shrub and herb cover (shrub = 7%, SE = 2%; herb = 8%, SE = 4%). Ground vegetation at forest sites was predominantly sword fern (*Polystichum munitum*), salal (*Gaultheria shallon*), deer fern (*Blechnum spicant*) and red huckleberry (*Vaccinium parvifolium*). Appendix 1 provides details on percent ground cover of vegetation species and downed wood at each site.

Enclosure Design

Four 6 m x 6 m enclosures were constructed in each site between May and September 2003 (n = 24). Enclosures were built in pairs (hereafter referred to as an "enclosure pair") such that each enclosure shared one short wall (the "dividing wall") with another enclosure (Figure 2). Enclosure pairs were constructed in random locations in each site, with the following restrictions: in forest sites, enclosure pairs were constructed >50 m from the edge of the forest, and the two enclosure pairs at each site were separated by >50 m; in clearcut sites, enclosure pairs were also separated by >50 m, were >20 m from road edges, and were >50 m from forest edges. Since amphibian species that are sensitive to harvesting have been found to be negatively affected up to 25 – 35 m from silvicultural edges (deMaynadier and Hunter 1998), our placement of forest enclosures >50 m from the forest edge should have been sufficient to ensure no negative edge effects.

Enclosure walls (other than the dividing wall) were built of 0.64 cm (¼") mesh hardware cloth (Figure 3). Hardware cloth was selected as the fence material as it permitted free passage of most invertebrates, but prevented salamanders from escaping. The hardware cloth was placed in 0.25 m - 0.5 m deep trenches dug by hand using a mattock and shovel (8 of 12 enclosure pairs), or using a small excavator with a narrow width bucket (4 of 12 enclosure pairs). The depth of the trenches depended on the soil at each site: in most cases, trenches were excavated until compacted soil/clay or bedrock was reached. In a few cases, compacted soil was not reached within 0.5 m of the surface due to a deep organic soil layer. In such cases, the trenches were excavated to a depth of 0.5 m. Trench excavation disturbed a ~1 m wide strip of ground. Hardware cloth was placed in trenches, with the bottom of the

fence folded over (~10 cm fold) towards the inside of the enclosure to provide a barrier to animals that may try to burrow down beside the enclosure walls. Above ground, enclosure walls extended 0.3 m to 0.5 m upwards, with the top of the fence folded over twice towards the inside of the enclosure to prevent salamanders from climbing out (Figure 3). In two clearcut enclosure pairs, exposed bedrock at or near the surface prevented excavation of portions of the trenches; in these cases, the bottom of the fence was folded over towards the inside of the enclosure and covered with a thick layer of quick setting concrete to fuse the fence to the rock.

The dividing wall separating the two enclosures in each pair was constructed with aluminum flashing to prevent invertebrates from passing from one enclosure to the other (Figure 4). The aluminum flashing was buried in trenches, which were excavated in the same way as for the perimeter walls. The top of the aluminum flashing was not folded over; aluminum flashing is slippery and salamanders should be unable to climb it (Pechmann 1995, Chazal and Niewiarowski 1998). An aluminum-flashing barrier was attached to support poles halfway up the height of the dividing wall to prevent salamanders from climbing the poles and moving between enclosures.

Cover boards and pitfall traps were added to each enclosure. Pitfall traps, which were installed in the corners of each enclosure, were constructed using 4 L ice cream pails (21.5 cm diameter; 13 cm deep) buried flush to the ground. A ~15 cm diameter hole was cut in the ice cream bucket lids and a ~15 cm diameter margarine container, with the bottom cut out, was placed in the hole to act as a funnel. Four cover boards were placed in each enclosure in random locations, with the restriction that they be reasonably accessible from the perimeter walls. Three cover boards were each placed over top of one of three ice cream bucket lids ("feeding tray"; depth 1 cm), with the cover board suspended ~2 cm, using small rocks, to allow access by the salamanders. The fourth cover board provided additional refuge for the salamanders.

Food Addition Treatment

One enclosure from each pair was randomly assigned to a food addition treatment; the other enclosure of each pair did not receive a food addition (ambient food level). The food addition treatment for the adult experiment was assigned to the enclosure that did not have the food addition in the juvenile experiment; this ensured that an enclosure was not assigned to the ambient food level for both experiments, which may have resulted in a depletion of naturally-occurring food resources.

In the first week of each experiment, mealworms (larvae of the beetle *Tenebrio molitor*) were added to each enclosure to allow all salamanders to acclimate to the enclosures. Every 5 to 10 days for the remainder of both experiments, mealworms were added to the food addition treatment enclosure of each pair only. For the juvenile experiment, 1.80 to 1.85 g of mealworms (approximately 28 to 32 small mealworms; weighed with an electronic balance) were added, while for the adult experiment, 2.50 to 2.56 g of mealworms (approximately 22 to 32 large mealworms) were added. The weights of mealworms selected for the food treatment for each experiment were based on the weekly weights of mealworms required by captive juvenile and adult northwestern salamanders for weight maintenance (personal observation). Mealworms were placed in ~0.5 cup of wheat bran (food for the mealworms), and were evenly distributed between the 3 feeding trays in the food addition treatment enclosures. At the same time, ~0.5 cup of wheat bran was evenly distributed between the three feeding trays of the ambient food enclosure so that the only difference between the enclosures was the addition of the mealworms. Any mealworms remaining on the feeding trays of the food addition enclosures from the previous weeks' feeding were counted and removed prior to adding new mealworms; wet bran on all feeding trays was discarded outside the enclosures. During both experiments, salamanders were observed sitting on or under the feeding tray in both the food addition and ambient food enclosures; we are reasonably sure that the salamanders were able to find the food resources in the food addition enclosures.

Determination of Salamander Density for Enclosures

Since estimates do not exist for the range of natural terrestrial densities of juvenile or adult northwestern salamanders, we used available literature on other pond-breeding ambystomatids from the United States to determine how many salamanders to place in each enclosure. A study in South Carolina reported that summer home ranges of mole salamanders (*Ambystoma talpoideum*) were 0.11 - 23.3 m^2 per individual, with median home range sizes of 0.25 m^2 for juveniles, 3.61 m^2 for males, and 5.29 m^2 for females (Semlitsch 1981). An enclosure study in South Carolina on mole salamanders (*A. talpoideum*) and marbled salamanders (*A. opacum*) found no effect on survival or growth with densities of 0.62 salamanders/m^2 (equivalent to a home range size of 1.61 m^2/salamander) (Pechmann 1995). We chose a density of 0.38 salamanders/m^2 (or 2.6 m^2/salamander) for the juvenile experiment, which equated to 14 salamanders per enclosure (n = 336). Since adults had two to three times the body mass of juveniles, we chose an adult density for the experiment that was half that of the juveniles. Thus, seven animals were assigned to each of the 24 enclosures (n = 168) for the adult experiment; this gave a density of 0.2 salamanders/m^2, and provided each animal with a potential home range of 5.1 m^2. This may have been a relatively high density for the adults: we made a trade-off between maximizing the amount of area available to each salamander, and maximizing the number of salamanders within each enclosure. For both experiments, we wanted to maximize the number of salamanders within each enclosure to increase the chances of recapturing some individuals at the end of the experiment. Total biomass and mean initial mass of animals added to each enclosure in the juvenile and adult experiments are shown in Tables 2 and 5, respectively.

Collection of Study Animals

Juvenile northwestern salamanders were captured as they emerged from a single natal pond (Mirror Lake; 1.4 ha; 1050 – 2555 m from study sites) in September and October 2003 using pitfall traps and drift fences partly encircling the pond. Pitfall traps were checked every 2 – 3 days, and trapping continued until ~350 salamanders had been captured. Juveniles were housed individually in ice cream buckets kept

outdoors until the required number of salamanders had been captured. Buckets contained ample moist moss, and salamanders were fed 2 – 3 mealworms once a week. Animals captured early in the trapping period were kept for up to 1.5 months. The average weight gain of juveniles in captivity was 0.15 g (n = 336; SE = 0.02) between capture and release. There was no significant difference in capture weight and release weight of juveniles ($t_{0.05(2),335} = 1.968$; $t < 0.01$; $p > 0.5$).

Adult northwestern salamanders were captured using the same pitfall traps and drift fences between March 15th and March 26th, 2004 as they began their post-breeding migration from Mirror Lake. Only salamanders moving away from the lake were kept. Salamanders were individually housed in ice cream buckets with moist moss, and 3 - 4 large mealworms were placed in each bucket weekly. Animals that were captured at the beginning of the trapping period were kept in captivity for up to 1.5 months. The average weight gain of adults in captivity was 0.32 g (n = 168; SE = 0.08) between capture and release. There was no significant difference in capture weight and release weight of adults ($t_{0.05(2),167} = 1.975$; $t < 0.01$; $p > 0.5$).

Enclosure Assignment, Marking and Measurements

For each experiment, animals were randomly assigned to enclosures. In each enclosure pair, the animals in one of the enclosures were all marked with one colour, while animals in the adjoining enclosure were marked with a different colour. In addition, each animal within an enclosure was given a unique elastomer dye (Northwest Marine Technology, Inc., Tumwater, Washington, USA) code via subcutaneous injections on the undersides of the forelegs and hind legs. All marking was done within one week of the commencement of each experiment; at the time of marking, weights of each salamander, to the nearest 0.01 g, were obtained using an electronic balance, snout-vent length (SVL) was measured to the nearest 0.1 cm using a ruler, and head width (taken at the widest point of the head) was measured to the nearest 0.1 mm using dial calipers.

Juvenile Experiment

Juveniles were released into the enclosures on October 20th, 2003, a rainy day. We did not trap salamanders out of the enclosures prior to commencing the juvenile experiment; since the enclosure walls were constructed before the onset of migration from natal ponds, there should not have been any unmarked recent metamorphs in the enclosures at the start of the experiment. The feeding treatment commenced on October 29th, 2003.

Corner pitfall traps were set to catch animals from March 8 to May 12, 2004. Traps were checked every 2 - 3 days, and moist moss was placed in the bottom of each trap to prevent desiccation of captured salamanders. Marked juveniles were identified and weighed in the field, and were taken back to the lab for measuring and mark verification. Juveniles were released in the forest surrounding their natal pond, where they were initially captured for the experiment. Since animals were removed as they were captured, the density of juveniles within the enclosure decreased over time. Any unmarked juvenile northwestern salamanders that were captured, and any other amphibian species, were removed from the enclosures. The number of salamanders recaptured in each enclosure was recorded as a percentage of the number released into the enclosure (proportional survival). Captures of animals after May 12, 2004 were used in calculating proportional survival. A relative growth metric was computed for each salamander captured between March 8 and May 12, 2004 using its weight at the beginning and end of the experiment (equation 1):

$$\text{Weight change} = \frac{\text{Final weight - Initial weight}}{\text{Initial weight}} \qquad (1)$$

The snout-vent-length measurements and head width measurements were not used as they were deemed less reliable than the weight measurements: since animals moved around considerably when snout-vent-length and head widths were measured, it was difficult to obtain consistently accurate measurements.

Adult Experiment

Adults were released into the enclosures on May 5th, 2004. Any adult northwestern salamanders in the enclosures that were encountered while trapping juveniles were removed prior to the experiment. The feeding treatment commenced on May 12th, 2004.

Pitfall traps were set to catch adults at the end of the experiment from August 27th to November 24th, 2004. Traps were checked every 2 – 3 days, and moist moss was placed in each pitfall trap to prevent salamander desiccation. Most adults were not captured in pitfall traps: they were often found at the edge of the pitfall trap or under the cover boards (especially in forest sites). Captured adults were identified, weighed and measured (SVL and head width), and were released back into their enclosures to prevent a change in density over the trapping period. Any other amphibian species that were encountered were removed from the enclosures. On November 24th, all captured animals were released from the enclosures. A weight change metric, using equation (1), was computed for each animal recaptured between August 27th and November 24th; for animals that were recaptured multiple times throughout the trapping period, the final weight of the animal used was that on the last trapping date.

Since many animals were not captured between August 27th and November 24th, enclosures were left intact over the winter; the food addition treatment ended on November 17th, 2004. Manual searches of the enclosures were done on two days at the beginning of February 2005 and two days at the beginning of April 2005. Since spring is the breeding season for this species, we reasoned that any animals remaining in the enclosures would be near the surface trying to leave the enclosures to migrate to the breeding pond. Manual searches, which involved searching under all logs and ferns and in the duff layer at the bases of trees, took one person-hour per enclosure to complete, and were done on days following rainfall to increase the likelihood that salamanders would be close to, or on, the surface. Captured salamanders were identified, weighed and measured. The number of salamanders recovered from each enclosure during the fall trapping and the manual searches were tallied; the

proportional survival was calculated as a percentage of recovered salamanders. All captured animals were released. Holes were cut in the walls of the enclosures in early April 2005 to allow any remaining animals to leave the enclosures.

Invertebrate Sampling

To obtain an estimate of the natural invertebrate community in each enclosure while preventing removal of invertebrates within enclosures, four invertebrate pitfall traps were installed ~1.6 m outside of each enclosure, each separated by ~2 m (Figure 2). Pitfalls consisted of a beer cup (~9 cm diameter) buried flush to the ground, with an ice cream bucket lid suspended with sticks 10 – 15 cm above to shield the trap from rain. Invertebrate pitfalls were set twice during each experiment: samples were collected on December 3rd, 2003 and February 16th, 2004 of the juvenile experiment, and on June 18th, 2004 and August 20th, 2004 of the adult experiment. The pitfall traps were set by removing all debris from the cup and adding ~2 cm of propylene glycol; the traps were left open for one week before collection. Samples for all four traps at each enclosure were pooled together upon collecting to give one sample for each enclosure on each date. Most samples were put into 70% ethanol solution in the laboratory; the June 18th, 2004 sample was put in formalin.

Invertebrate samples were washed over a 1 mm sieve and over a 0.63 μm sieve, and were examined using a dissecting microscope. Invertebrates in the 1 mm fraction were separated from debris and were identified to Order; the number of individuals in each Order was counted for each sample. The 0.63 μm fraction was also separated from debris, and all the invertebrates in the sample were pooled together without identification. For each sample, the dry weight of each Order and the 0.63 μm fraction were obtained by drying them on filter papers in a drying oven (60°C) for a minimum 24 hours (>48 hours for larger insects).

Environmental Variables

Temperature data loggers that recorded temperature every 2.5 hours were placed in one enclosure of each pair during both experiments. Each logger was placed

on the ground under a log so that it was not exposed to direct sunlight; the loggers were in locations that would be used by salamanders on the surface. Air temperature and precipitation data were obtained from a weather station located in the southern portion of MKRF.

A soil sample to determine soil moisture content was collected from one enclosure of each pair once in July, once in August, and once in September of the adult experiment (n=12 for each month). No soil samples were taken during the juvenile experiment: moisture was likely not limiting during winter, as the soil was likely near saturation. The soil samples were taken from holes 20 cm in depth in representative areas of the enclosures. Soil was packed into pre-weighed, small metal containers with tight fitting lids, and the samples were re-weighed. In the laboratory, the containers, without lids, were placed in the drying oven (60°C) for a minimum of 3 days. Samples were re-weighed immediately upon being removed from the oven. Soil moisture content (M.C.) was calculated using equation (2):

$$\text{M.C.} = \frac{\text{filled container wet weight - filled container dry weight}}{\text{filled container dry weight - empty container weight}} \times 100\% \qquad (2)$$

Physical characteristics of each enclosure were quantified in fall and winter 2004/2005. Percent ground cover of each vegetation species in each enclosure was recorded, as well as a measure of the cumulative vegetation cover (all species), and the percent cover of each vegetation type (e.g. tree, shrub, herb, moss). The percent canopy cover in the forest enclosures, and the percentage of uncovered ground (e.g. not covered by vegetation or downed wood) in each enclosure was also recorded (Appendix 1). Photos were taken of each enclosure from standardized locations to enable estimation of the percent cover of downed wood.

Data Analysis

For both experiments, an analysis of variance was done to test for differences between clearcut and forest, food added and ambient food, and any interactions on the weight change of animals and on the proportional survival for each enclosure. For the juvenile experiment, an analysis of variance was also done to test for differences between forest type, food treatment, and interactions on the number of animals recaptured in the wrong enclosure (e.g., opposite side of enclosure pair from where animal was originally released) at the end of the experiment. For the adult experiment, an analysis of variance was also done to test for differences between forest type, food treatment, and interactions on the number of enclosures without recaptures at the end of the experiment. Both the juvenile and the adult experiment were analyzed as a randomized split-plot block design with subsampling. A block contained one replicate of each forest type, and was treated as a random variable. Forest type (clearcut, forest) was the main factor, and food treatment was the split plot; both forest type and food were treated as fixed factors. For the weight change analysis, data from individuals in enclosures were used rather than a mean for each enclosure, as the normality assumption was not met when using means. However, the error term from individuals was not used as the error term for F-tests (Schabenberger and Pierce 2002). Since recaptures were not obtained in some enclosures at the end of the experiment, the weight change data were unbalanced for both experiments. Since the design had both random and fixed factors, and was unbalanced, the MIXED procedure was selected for both the weight change and proportional survival analyses (Spilke et al. 2005). We used the Kenward-Roger method for approximating the degrees of freedom (Spilke et al. 2005). This method, which was created for situations with small sample sizes, incorporates a correction to the more general Satterthwaite method to reduce bias in the estimated covariance matrix of fixed effects (Kenward and Roger 1997, Spilke et al. 2005). Consequently, the denominator degrees of freedom are often non-integer. Proportional survival was arcsine square-root transformed prior to analysis. All analyses were done with SAS version 9.1, and all graphing was done with SigmaPlot. All analysis of variance assumptions were met (e.g., normality, homogeneity of error

variances, etc.). An alpha level of 0.05 was used to determine statistical significance for all tests.

The invertebrate community composition in clearcut and forest sites was compared on the two sampling dates for each experiment using correspondence analysis (CANOCO, Centre for Biometry, Waginengen, the Netherlands). The total biomass and total number of insects captured at each enclosure on the two sampling dates for each experiment were analyzed using a multivariate analysis of covariance (MANOVA) to determine if insect biomass and/or number differed by forest type (clearcut/forest) and by sampling date.

Weather data (maximum and minimum temperatures, precipitation) were summarized for each week of each experiment. Soil moisture was analysed using analysis of variance (MIXED) to test for differences between clearcut and forest and the effect of sampling date. Soil moisture percentages were arcsine square-root transformed prior to analysis.

RESULTS

Environmental Variables

Juvenile Experiment

Temperature loggers in enclosure pairs collected surface temperature data between October 21^{st,} 2003 and April 21st, 2004. Maximum and minimum weekly temperatures were similar for forest and clearcut enclosures between October 21st, 2003 and February 2nd, 2004 (Figure 5a). From February 3rd to April 21st, the clearcut maximum weekly temperature was higher than that of the forest, while minimum temperatures for both forest types remained similar. The highest surface temperature recorded throughout the experiment was 21.7 °C in a clearcut enclosure (week of April 6th to 12th; Figure 5a). During the same week, the highest temperature was recorded in

a forest enclosure (14.4 °C; Figure 5a). The lowest surface temperature was recorded in a forest enclosure (-5.8 °C; week of December 30th to January 5th). The lowest temperature in a clearcut enclosure, -5.2 °C, was also recorded that week.

Maximum air temperatures were higher, and minimum air temperatures were lower, than surface temperatures recorded in enclosures (Figure 5b). The highest air temperature recorded throughout the experiment was 26 °C in the weeks of April 6th to 12th and April 27th to May 3rd. The lowest temperature was recorded in the week of December 30th to January 5th, and was –11.5 °C.

Precipitation varied widely from week-to-week throughout the experiment (Figure 6). Maximum weekly precipitation was 112 mm in the week of March 2nd to 8th, 2004. Two weeks with no precipitation occurred during the experiment: April 6th to 12th, and May 11th to 12th. Most of the precipitation was attributed to rainfall; snow fell on 6 days between December 27th and January 24th.

Adult Experiment

Temperature loggers in enclosure pairs collected surface temperature data between May 6th, 2003 and November 24th, 2004. The clearcut maximum weekly temperature was higher than that of the forest throughout the experiment, while the minimum weekly temperatures for both forest types were similar (Figure 7a). The difference in maximum temperature between the clearcut and the forest between May 6th and November 3rd, 2004 was 4.2 °C ± 0.2 °C (S.E.). The highest surface temperature recorded throughout the experiment was 29.0 °C in a clearcut enclosure (week of July 22nd to 28th; Figure 7a). During the same week, the highest temperature was recorded in a forest enclosure (24.9 °C; Figure 7a). The lowest surface temperature was recorded in a clearcut enclosure (1.7 °C; week of November 4th to 6th). The lowest temperature in a forest enclosure, 2.1 °C, was recorded that same week.

Maximum air temperatures were higher, and minimum air temperatures were similar or lower, than surface temperatures recorded in enclosures (Figure 7b). The highest air temperature recorded throughout the experiment was 35 °C in the week of July 22nd to 28th. The lowest temperature was recorded in the week of November 18th to 24th, and was –1.0 °C.

Precipitation varied widely from week-to-week throughout the experiment (Figure 8). Maximum weekly precipitation was 118 mm in the week of August 19th to 25th, 2004. Three weeks with no precipitation, and seven weeks with less than 5 mm of precipitation occurred during the experiment. All of the precipitation was attributed to rainfall.

There was a significant effect of sampling date on enclosure soil moisture ($F_{2,29}$ = 9.01, p = 0.0009). Soil moisture was significantly lower in both forest types during the August sampling session (Figure 9a). There were no significant effects of forest type ($F_{1,29}$ = 0.92, p = 0.346), or the interaction between forest type and sampling date ($F_{2,29}$ = 0.60, p = 0.554). There was high variability in soil moisture in both forest types during both the July and September sampling sessions (Figure 9a). When mean percent soil moisture was considered (dashed lines in boxplots), soil moisture was slightly higher in the forest treatment than clearcut treatment during the July sampling session, and was higher in the clearcut treatment than the forest treatment during the August and September sampling sessions.

Mean percent soil moisture varied between-sites in each forest type during all three sampling sessions (Figure 9b). Within–site variability was higher in the July and September sampling sessions than the August sampling session. During all three sampling sessions, the highest mean percent soil moisture in forest sites occurred in the K Forest site, and the highest mean percent soil moisture in clearcut sites occurred in the K Clearcut site (Block 3). The E Forest site (Block 2) had the lowest mean percent soil moisture during the July and August sampling sessions; the M Forest and E Forest sites had a similar mean percent soil moisture during the September sampling

session. The F Clearcut site (Block 1) had the lowest mean percent soil moisture in clearcut sites during all three sampling sessions. Mean percent soil moisture was only higher in the forest treatment than the clearcut treatment during the July sampling of Block 1 and the August sampling of Block 3.

Juvenile Experiment

Proportion Recaptured (Survival)

Fifty percent of the juveniles released into the enclosures were recaptured (Table 3). Some juveniles were recaptured from all but one enclosure pair: no animals were seen or captured throughout the course of the experiment within a forested enclosure pair in the K forest site (Block 3; Table 3). After a severe rain event in late October 2003, a ground-level hole, through which animals could escape, was found in one wall of one enclosure of the pair. A small tree fell over the dividing wall between the enclosures, likely allowing animals to cross from the enclosure with intact walls to the one with the hole in the wall. The hole in the wall was repaired and the tree removed, but it is assumed that all of the animals escaped from both enclosures. Recapture data from these two enclosures were not used in the proportion recaptured analyses.

Several animals were recaptured in the wrong enclosure (e.g., wrong food treatment) of an enclosure pair in clearcut and forest sites (Table 3). There was no significant effect of forest type ($F_{1,6} = 0.34$; $p = 0.580$), food level ($F_{1,6} = 0.04$; $p = 0.852$) or the interaction between forest type and food level ($F_{1,6} = 0.34$; $p = 0.580$) on the number of animals recaptured in the wrong enclosure. In clearcuts, three animals moved from enclosures with supplemental food to enclosures with ambient food, and two animals moved from enclosures with ambient food to enclosures with supplemental food (total = 5). In the forest, three animals from enclosures with supplemental food were recaptured in enclosures with ambient food, and five animals from enclosures with ambient food were recaptured in enclosures with supplemental food (total = 8). It is assumed that these animals crossed between enclosures through tunnels or burrows passing under the dividing wall. Since it was not possible to determine how long these

animals had been exposed to the wrong food treatment prior to capture, they were not used in the analysis of the effect of forest type and food level on proportion recaptured. However, since recapture of these animals does demonstrate survival in the forest type throughout the course of the experiment, a separate analysis was done including these animals. In this analysis, each enclosure pair was treated as one unit (e.g., food treatments were combined), and the numbers of animals recaptured on both sides were tallied (Table 3). An analysis of variance was done to test the effect of forest type on proportion recaptured.

Several marked juveniles were recaptured during the adult experiment (after May 12th, 2004; Table 3). Although recapture of these animals does demonstrate survival in the forest type, they were not exposed to the same food treatment throughout the time they were in the enclosures (food was added to different enclosures in juvenile and adult experiments; *see Methods*). Consequently, these animals were not considered in the analysis of the effects of forest type and food level on proportion of juveniles recaptured at the end of the experiment. These animals were considered in the analysis of proportion recaptured in each enclosure pair (*see above*).

Juveniles recaptured in the correct enclosures

There was no significant effect of forest type ($F_{1,6.4} = 0.34$; $p = 0.579$), food level ($F_{1,6.26} = 1.57$; $p = 0.255$) or the interaction between forest type and food level ($F_{1,6.26} = 0.11$; $p = 0.748$) on the proportion of juveniles recaptured in the correct enclosures between March 8th and May 12th, 2004. There was a trend towards a greater proportion recaptured in enclosures with ambient food compared to enclosures with supplemental food for both forest types (Figure 10a). When mean recapture numbers (dashed lines in box plots; Figure 10a) were considered for each treatment combination, slightly more animals were recaptured in the forest treatment than the clearcut treatment for each food treatment (forest-food = 39% recaptured; clearcut-food = 29% recaptured; forest-ambient = 49% recaptured; clearcut-ambient = 44% recaptured). More animals were recaptured in the clearcut with ambient food treatment than the forest with supplemental food treatment (Figure 10a).

There was high variability in the data for each treatment combination, as shown by the spread between the 5^{th} and 95^{th} percentiles (Figure 10a). The mean proportion recaptured in each food treatment at each site was examined to determine the source of this variability (Figure 10b). There was high between-site variability, but low within-site variability, in proportion recaptured for the forest with supplemental food and forest with ambient food treatments. In the clearcut with supplemental food treatment, there was high within-site and low between-site variability in proportion recaptured. In the clearcut with ambient food treatment, there was high within-site and between-site variability.

The effect of the food treatment on proportion recaptured varied at individual forest sites, but was consistent at individual clearcut sites (Figure 10b). In forest sites, there was a trend of higher proportion recaptured in one food treatment at each site, while in clearcut sites, there was a consistent trend of higher proportion recaptured in the ambient food treatment than the supplemental food treatment at each site.

There were no consistent trends between blocks in proportion recaptured (Figure 10b). In Block 1 (B1), there were higher mean proportions of juveniles recaptured in enclosures with ambient food in both forest types. In Blocks 2 and 3 (B2, B3), there was a trend towards an interaction between the food and forest treatments in mean proportion of juveniles recaptured, with higher proportion recaptured in the forest with supplemental food treatment compared to the forest with ambient food treatment, and in the clearcut with ambient food treatment compared to the clearcut with supplemental food treatment.

Juveniles recaptured in enclosure pairs

There was no significant effect of forest type on proportion recaptured when all recaptures within an enclosure pair were considered ($F_{1,3.31} = 0.64$; $p = 0.477$). There was a trend towards a higher proportion of recaptured juveniles in the forest treatment compared to the clearcut treatment (Figure 11a).

The mean proportion recaptured in each site was examined to determine the sources of variability in the data (Figure 11b). There was high within- and between-site variability in the proportion of juveniles recaptured in enclosure pairs in the forest and clearcut treatments. There were no consistent trends between blocks in proportion recaptured in the two forest treatments (Figure 11b).

Weight Change (Growth)

Juveniles recaptured in the correct enclosure between March 8th and May 12th, 2004 were used in the analysis of the effects of forest type and food level on juvenile weight change between the beginning and end of the experiment (Table 4). There were no significant effects of forest type ($F_{1,3.59} = 5.84$; $p = 0.081$), food level ($F_{1,109} = 2.61$; $p = 0.109$), or the interaction between forest type and food level ($F_{1,109} = 3.07$; $p = 0.0827$) on the weight change of juvenile northwestern salamanders. Forest type and the interaction between forest type and food level had a nearly significant effect on juvenile weight change.

On average, animals lost weight throughout the experiment in each forest type – food level combination (mean < 0; Figure 12a). When mean weight change was considered for each treatment combination (dashed lines in box plots; Figure 12a), animals in the clearcut with supplemental food tended to lose less weight than animals in the other treatments (clearcut-food = 0.7% mean weight loss; forest-food = 10.2% mean weight loss; forest-ambient = 9.6% mean weight loss; clearcut-ambient = 7.8% mean weight loss). There was little difference between the mean weight change of animals in the forest with supplemental food and the forest with ambient food treatments.

Mean weight change in each food treatment at each site was examined to determine sources of variability in the data (Figure 12b). There was between-site variability in mean weight change in all forest type – food level combinations. In most of the sites, some animals in each food treatment gained weight throughout the course

of the experiment (Table 4; Figure 12b). The exception was the K Clearcut site with ambient food, where all 9 recaptured animals lost weight throughout the experiment (Table 4). The F Clearcut site with supplemental food was the only site and food treatment where animals had a mean weight gain throughout the experiment (Figure 12b).

There were no consistent trends in weight change between blocks (Figure 12b). In Blocks 1 (B1) and 2 (B2), animals had the highest mean weight loss in both forest food treatments, and the lowest mean weight loss in the clearcut with supplemental food treatment. In Block 3 (B3), animals had the lowest mean weight loss in the supplemental food treatment in the forest and clearcut, and the highest mean weight loss in the forest with ambient food treatment.

Effects of density on weight change

Weight change results were contrasted with the proportion of juveniles recaptured in each treatment combination and site to determine if there was an effect of density on weight change. The lowest mean weight loss was obtained in the treatment combination with the lowest mean proportion recaptured (clearcut-food; Figure 10a and Figure 12a). There were no consistent trends between weight change and proportion recaptured when food treatments were considered for each site (Figure 10b and Figure 12b). In forest enclosures with supplemental food, the highest mean weight loss and the highest mean proportion recaptured were observed in the same site (E Forest). In contrast, in forest enclosures with ambient food and in clearcut enclosures with supplemental food, the lowest mean weight loss and the highest mean proportion recaptured were obtained in the same site (K Forest and F Clearcut). In clearcut enclosures with ambient food, the lowest mean weight loss and the lowest mean proportion recaptured were obtained in the K10 Clearcut site.

Adult Experiment

Proportion Recaptured (Survival)

Thirty-six percent of the adults released into the enclosures were recaptured (Table 6). In four enclosure pairs, adults were recaptured on both sides of the enclosure pair at the end of the experiment (Table 6). In eight enclosure pairs (3 in forest, 5 in clearcut), no adults were recaptured at the end of the experiment in at least one of the enclosures (Table 6). There was no significant effect of forest type ($F_{1,8}$ = 1.00; p = 0.347), food level ($F_{1,8}$ = 1.00; p = 0.347) or the interaction between forest type and food level ($F_{1,8}$ = 1.00; p = 0.347) on the number of enclosures with zero recaptures between August 27th and November 24th, 2004. Adults were not captured or observed in these enclosures after May 31, 2004 (~3 weeks after start of experiment), and in two cases, adults were not captured or observed in either side of an enclosure pair after May 31, 2004 (1 forest, 1 clearcut enclosure pair; Table 6). In all other cases where there were no recaptures in an enclosure, adults were captured or observed in one enclosure of an enclosure pair, but not the other. Since it was not possible to determine whether a lack of recaptures was due to a treatment effect or whether it was due to escapes from the enclosures (possibly through underground tunnels), the analyses of proportion recaptured were done in two different ways: first, using data from every enclosure, and second, using data from enclosures from which at least one animal was recaptured at the end of the experiment (omission of enclosures from which animals were not observed or recaptured between August 27th and November 24th, 2004; Table 6).

In contrast to the juvenile experiment, recapture of an adult in the wrong enclosure at the end of the experiment occurred only once in a clearcut enclosure pair and three times in forest enclosure pairs (Table 6). In three cases, an animal moved from an enclosure with ambient food to one with supplemental food (once in clearcut treatment and twice in forest treatment), and in one case, the animal moved from an enclosure with supplemental food to one with ambient food (forest treatment). These animals were not used in the analyses of the effects of forest type and food level on proportion

recaptured. However, since recapture of these animals does demonstrate survival in the forest type throughout the course of the experiment, a separate analysis was done for each enclosure pair to include these animals (see *Juvenile Experiment* above).

Several adults were found during manual searches of the enclosures at the beginning of February and April 2005. In forest enclosures, nine animals were found that had been captured at some point in fall 2004, but were not removed from the enclosures at the end of the experiment. No animals that had been captured in fall 2004 were found during manual searches in clearcut enclosures. Five animals were found in forest enclosures, and four animals were found in clearcut enclosures, that had not been captured between August 27th and November 24th, 2004 (Table 6). These animals survived longer than the duration of the experiment, and demonstrated survival in the forest type. However, since they were not exposed to the food treatment for the duration of their time in the enclosure (the food treatment ended on November 24th, 2004), these animals were only included in the proportion recaptured analysis for enclosure pairs (*see above*).

Adults recaptured in the correct enclosure: all enclosures

There was a significant effect of forest type on the proportion of adults recaptured in all enclosures between August 27th and November 24th, 2004 ($F_{1,20}$ = 5.01; p = 0.037). Significantly more animals were recaptured in the forest treatment (mean = 45% recaptured) than the clearcut treatment (mean = 13% recaptured). There were no significant effects of food level ($F_{1,20}$ = 0.20; p = 0.662), or the interaction between forest type and food level ($F_{1,20}$ = 0.25; p = 0.622) on the proportion of adults recaptured. When mean recaptures were examined for each treatment combination (dashed lines in box plots; Figure 13a), an equal proportion were recaptured in the forest with supplemental food and ambient food treatments (45% recaptured), and there was a trend of a higher proportion recaptured in clearcut enclosures with supplemental food (16% recaptured) compared to ambient food (10% recaptured).

There was high variability in data for each treatment combination due to the number of enclosures with zero recaptures at the end of the experiment (Figure 13a). No animals were recaptured from the E Forest and K Forest sites with supplemental food, the M Forest and E Forest sites with ambient food, the F Clearcut and K Clearcut sites with supplemental food, and the F Clearcut and K Clearcut sites with ambient food (Figure 13b).

Adults recaptured in the correct enclosure: enclosures with ≥ 1 animal recaptured

When enclosures with zero recaptures between August 27th and November 24th, 2004 were omitted from the analysis, there were significantly more animals recaptured in the forest enclosures than the clearcut enclosures ($F_{1,10} = 23.83$; $p < 0.001$; Figure 14a), and no significant effect of food level ($F_{1,10} = 0.06$; $p = 0.806$), or the interaction between forest type and food level ($F_{1,10} = 0.01$; $p = 0.932$) on proportion of adults recaptured. When mean recaptures were examined for each treatment combination (dashed lines in box plots; Figure 14a), there was a trend of a slightly higher proportion recaptured in clearcuts with the ambient food treatment (29% recaptured) compared to the supplemental food treatment (25% recaptured). The same mean proportions of animals were recaptured from each food treatment in the forest (68% recaptured).

Comparisons of within-site variability were not possible after omitting enclosures with <1 recapture, as means for food treatments could not be calculated for most sites (Figure 14b). This also precluded comparisons of mean weight change between blocks. However, if the proportion recaptured in each site – food treatment for each block are compared (using mean proportion recaptured when possible), there was a consistent trend across all blocks of higher proportion recaptured in forest sites. There were no consistent trends in proportion recaptured in the different food treatments in each block (Figure 14b): in some cases, a higher proportion of animals were recaptured in ambient food enclosures (Block 1 clearcut, Block 2 forest), while in others, a higher proportion were recaptured in supplemental food enclosures (e.g., Block 1 forest, Block 2 clearcut, Block 3 forest and clearcut).

Adults recaptured in enclosure pairs

There was a significant effect of forest type on proportion of adults recaptured when all recaptures within an enclosure pair were considered ($F_{1,8}$ = 8.35; p = 0.020), with a significantly higher proportion of adults recaptured in the forest treatment (63% recaptured) than the clearcut treatment (23% recaptured; Figure 15a). There was high between-site variability in proportion recaptured for both forest types (Figure 15b), and high within-site variability for some sites (e.g., K Forest).

Mean proportions recaptured in enclosure pairs were compared for the forest treatments in each block (Figure 15b). In all three blocks, a higher proportion of adults were recaptured in the forest treatment than the clearcut treatment.

Weight Change (Growth)

Adults recaptured in the correct enclosure between August 27th and November 24th, 2004 were used in the analysis of effects of forest type and food level on adult weight change between the beginning and end of the experiment (Table 7). There were no significant effects of forest type ($F_{1,6.67}$ = 1.57; p = 0.253), food level ($F_{1,5.78}$ = 0.00; p = 0.951), or the interaction between forest type and food level ($F_{1,5.78}$ = 1.92; p = 0.217) on the weight change of adult northwestern salamanders.

Most adults experienced a mean weight loss throughout the experiment. When the mean weight change was considered for each treatment combination (dashed lines in box plots; Figure 16a), animals in the clearcut with supplemental food treatment had the highest mean weight loss (21.4%), while those in the forest with supplemental food treatment had a slight (1.5%) mean weight gain throughout the experiment. Mean weight loss was similar for animals in the forest with ambient food (11.2% mean weight loss) and clearcut with ambient food (9.3% mean weight loss) treatments.

There was high variability in data for some of the treatment combinations, as shown by the spread between the 10th and 90th percentiles (e.g., Forest-food, Clearcut-ambient; Figure 16a). Mean weight change in each food treatment at each site was

examined to determine the sources of this variability (Figure 16b). In all forest type – food treatment combinations, there was high between-site variability in mean weight change. In forest sites with supplemental food, there were differences in the number of animals from each site that gained weight throughout the experiment: in the M Forest site, only one of the 9 recaptured animals lost weight throughout the experiment, while in the K Forest site, all recaptured animals lost weight (Table 7). In the forest with ambient food treatment, and in both food treatments in clearcuts, most animals lost weight, but there was high variability in the amount of weight they lost (Table 7). Sample sizes were very low for clearcut sites, which contributed to high variability.

Mean weight change was compared between the forest and food treatments within each block to determine whether trends were consistent within blocks (Figure 16b). In Blocks 1 (B1) and 2 (B2), animals had the lowest mean weight loss (or a mean weight gain) in forest enclosures with supplemental food, and a mean weight loss in all other enclosures. The highest mean weight loss in these blocks occurred in clearcut with supplemental food treatment. In Block 3 (B3), mean weight loss was slightly higher in forest enclosures with supplemental food compared to forest enclosures with ambient food, and was highest in clearcut enclosures with ambient food. Mean weight loss was similar for animals in forest enclosures with ambient food and clearcut enclosures with supplemental food.

Effects of density on weight change

Weight change results were contrasted with the proportion of adults recaptured (enclosures with ≥1 recapture only) to determine if there was an effect of density on weight change. A mean weight gain was obtained in the treatment combination with a high mean proportion of adults recaptured (forest-food; Figure 13a and Figure 16a). The highest weight loss was obtained in the treatment combination with a low proportion recaptured (clearcut-food). There was an opposite relationship between weight change and proportion recaptured in forest and clearcut sites (Figure 13b and Figure 16b): in forest sites, the lowest weight loss (or weight gain) was observed in the forest sites with the lowest proportion recaptured (M Forest Food, M Forest Ambient),

while in clearcut sites, the lowest mean weight loss was observed in sites with a high proportion recaptured (K Clearcut Food, F Clearcut Ambient).

Invertebrate Sampling

Juvenile Experiment

Number of Trapped Invertebrates

There were no significant effects of forest type ($F_{1,40}$ = 0.05, p = 0.832), sampling session ($F_{1,40}$ = 0.68, p = 0.413), or the interaction between forest type and sampling session ($F_{1,40}$ = 0.96, p = 0.333) on the number of invertebrates trapped (all Orders) during the juvenile experiment. When mean numbers of trapped invertebrates were considered (dashed lines in box plots; Figure 17a), there was a trend of a higher mean number of invertebrates trapped in the forest treatment than the clearcut treatment in December, and a higher mean number of invertebrates trapped in the clearcut than the forest in February. There was high variability in the data for both forest types during the February sampling session.

Mean number of invertebrates trapped in each site during each sampling session was examined to determine the sources of variability in the data (Figure 17b). There was low between-site variability in mean number of invertebrates trapped in the forest treatment when compared to the clearcut treatment during the December sampling session. During the February sampling session, there was high within- and between-site variability in mean number of invertebrates trapped in both forest types.

Trends in mean number of invertebrates trapped were consistent within blocks for both sampling sessions, but were different between blocks (Figure 17b). In Block 1 (B1), there was a higher mean number of trapped invertebrates in the clearcut treatment than the forest treatment during both sampling sessions. In Blocks 2 (B2) and 3 (B3), there were higher mean numbers of trapped invertebrates in the forest treatment than the clearcut treatment during both sampling sessions.

Correspondence analysis of the number of invertebrates captured during the juvenile experiment showed that there was a lot of overlap in samples from both forest types, but there was some separation of samples by sampling date (Figure 18a). When the invertebrate Orders were considered, it appears that a higher number of Collembola and Gastropoda were captured during the February sampling session, while a higher number of Haplotaxida, Acari, Isoptera, Coleoptera, Lepidoptera, and Diptera were captured during the December sampling session (Figure 18b).

Biomass of Trapped Invertebrates

There was a significant effect of the interaction between forest type and sampling session ($F_{1,40} = 5.11$, $p = 0.029$) on biomass of invertebrates trapped (all Orders) during the juvenile experiment. There was a significantly higher biomass of trapped invertebrates in the forest treatment than the clearcut treatment during the December sampling session, and a higher biomass of trapped invertebrates in the clearcut treatment than the forest treatment in the February sampling session (Figure 19a). There were no significant effects of forest type ($F_{1,40} = 0.20$, $p = 0.653$) or sampling session ($F_{1,40} = 0.17$, $p = 0.686$) on the biomass of trapped invertebrates. There was high variability in the data for the forest treatment during the December sampling session and for the clearcut treatment during the February sampling session (Figure 19a).

Trends in invertebrate biomass between sites within forest types were consistent across sampling sessions (Figure 19b). In the forest treatment, the highest biomass of trapped invertebrates was obtained in the M Forest site, and the lowest in the K Forest site, for both sampling sessions. In the clearcut treatment, the highest biomass was obtained in the F Clearcut site, and the lowest in the K Clearcut site, for both sampling sessions.

There were some consistent trends in mean biomass of trapped invertebrates within- and between blocks for the two sampling sessions (Figure 19b). In Block 1 (B1) and Block 2 (B2), there was a higher biomass of trapped invertebrates in the forest

treatment than the clearcut treatment during the December sampling session, and a higher biomass in the clearcut treatment than the forest treatment in the February sampling session. In Block 3 (B3), there was a higher biomass of trapped invertebrates in the forest treatment than the clearcut treatment during both sampling sessions. The biomass of trapped invertebrates was higher in Block 1 than Blocks 2 or 3 for both forest types and sampling sessions.

Correspondence analysis of the biomass of invertebrates captured during the juvenile experiment showed that there was a lot of overlap in samples from both forest types and sampling sessions (Figure 20a). Consequently, no trends in biomass of Orders in the different forest types or sampling sessions can be determined (Figure 20b).

Trends in Number and Biomass of Invertebrates

Trends in mean number of trapped invertebrates and mean biomass of trapped invertebrates were similar for each forest type and sampling session (Figure 17a and Figure 19a). A higher mean number and mean biomass of trapped invertebrates was obtained in the forest treatment during the December sampling session, and in the clearcut treatment during the February sampling session. However, when individual sites were considered, this relationship between high number captured and high biomass did not always hold (Figure 17b and Figure 19b). For example, in forest sites sampled during December, the lowest mean number and highest mean biomass of trapped invertebrates was obtained in the M Forest site.

Although the invertebrate samples differed in number of captured invertebrates for the two sampling sessions (Figure 18a), the samples did not differ in biomass of captured invertebrates on the two sampling sessions (Figure 20a). This indicates that, although there might have been fewer invertebrates captured in one of the sampling sessions, the Orders that were captured had high biomass. In the other sampling session, a higher number of invertebrates were captured, but the Orders that were captured had lower biomass.

Adult Experiment

Number of Trapped Invertebrates

There was a significant effect of sampling session on the number of invertebrates (all Orders) trapped during the adult experiment ($F_{1,40} = 4.81$, $p = 0.034$). A significantly greater number of invertebrates were trapped in both forest types during the first sampling session (June; mean number trapped in forest = 84.7, clearcut = 91.5) than the second sampling session (August; mean number trapped in forest = 66.1, clearcut = 62.8) (Figure 21a). There were no significant effects of forest type ($F_{1,40} = 0.03$, $p = 0.873$) or the interaction between forest type and session ($F_{1,40} = 0.22$, $p = 0.642$) on the number of trapped invertebrates. The mean number of trapped invertebrates was similar between forest and clearcut treatments in each sampling session (dashed lines in box plots; Figure 21a). There was high variability in the data from the clearcut treatment during the June sampling session.

Mean number of invertebrates trapped in each site during each sampling session was examined to determine the sources of variability in the data (Figure 21b). There was higher between-site variability in mean number of trapped invertebrates in the clearcut treatment compared to the forest treatment during the June sampling session. There was high within-site variability in mean number of trapped invertebrates in the K10 Clearcut site during the June sampling session. During the August sampling session, there was between-site variability in both forest types.

There were some consistent trends in mean number of trapped invertebrates within- and between blocks for the two sampling sessions (Figure 21b). In Block 1 (B1) and Block 2 (B2), a higher mean number of trapped invertebrates were obtained in the clearcut treatment than the forest treatment during both sampling sessions. Conversely, in Block 3 (B3), a higher mean number of trapped invertebrates was obtained in the forest treatment than the clearcut treatment during both sampling sessions.

Correspondence analysis of the number of invertebrates captured during the adult experiment showed some separation of the forest types and the sampling sessions (Figure 22a). When the invertebrate Orders were considered, a higher number of Diplopoda, Collembola, Acari, Lepidoptera and Coleoptera were captured in forest sites, while more Chilopoda, Diptera, Isoptera, Araneae, Gastropoda, Haplotaxida and Hymenoptera were captured in clearcut sites (Figure 22b). In addition, more Lepidoptera, Orthoptera, and Chilopoda were captured during the August sampling session, while more Collembola, Pulmonata, Acari and Hymenoptera were captured during the June sampling session (Figure 22b).

Biomass of Trapped Invertebrates

There was a significant effect of forest type ($F_{1,40}$ = 19.18, $p < 0.0001$) on the biomass of invertebrates (all Orders) trapped during the adult experiment. There was a significantly lower biomass of trapped invertebrates obtained in the clearcut treatment than the forest treatment during both sampling sessions (Figure 23a). There were no significant effects of sampling session ($F_{1,40}$ = 0.48, $p = 0.500$) or the interaction between forest type and sampling session ($F_{1,40}$ = 1.84, $p = 0.182$) on the biomass of trapped invertebrates. There was high variability in the data for both forest types sampled in June, and for the forest treatment sampled in August.

There were some trends within- and between blocks in mean biomass of trapped invertebrates (Figure 23b). In all three blocks, there were higher mean biomasses of trapped invertebrates in the forest treatment than the clearcut treatment during both sampling sessions. During the June sampling session, the mean biomass of trapped invertebrates was higher in Block 1 than Blocks 2 or 3 for both forest types; during the August sampling session, the mean biomass of trapped invertebrates was higher in Block 3 than Blocks 1 or 2.

Correspondence analysis of the biomass of invertebrates captured during the adult experiment showed some separation of the forest types, but overlap of sampling sessions (Figure 24a). When the invertebrate Orders were considered, a higher

biomass of Orthoptera, Collembola, Lepidoptera and Coleoptera were captured in forest sites, while a higher biomass of Gastropoda, Haplotaxida, Hymenoptera, Araneae, Diptera, Ispotera and Chilopoda were captured in clearcut sites (Figure 24b).

Trends in Number and Biomass of Invertebrates

There were no consistent trends in mean number and mean biomass of trapped invertebrates for each forest type and sampling session (Figure 21a and Figure 23a). The mean numbers of trapped invertebrates were similar for both forest types in each sampling session, while the biomass was significantly lower in the clearcut than the forest for both sampling sessions. In some cases, the number and biomass of invertebrates captured corresponded (e.g., K Clearcut – June sampling session; K Forest – August sampling session; Figure 21b and Figure 23b). In other cases, the highest biomass and lowest number of invertebrates (or vice versa) were obtained in the same site (e.g., M Forest – June sampling session; K Forest – June sampling session; K Clearcut – August sampling session; Figure 21b and Figure 23b).

Although the invertebrate samples differed in number of captured invertebrates for the two sampling sessions and the two forest types (Figure 22a), the samples did not differ in biomass of captured invertebrates for the two sampling sessions (Figure 24a). As with the juvenile experiment, this indicates that, although there might have been fewer invertebrates captured in one of the sampling sessions, the Orders that were captured had high biomass.

DISCUSSION

We found a significant effect of forest type on the survival of adult northwestern salamanders, with significantly lower survival in clearcut enclosures. This result suggests that mortality of adult northwestern salamanders in clearcuts in summer is significantly higher than in forested areas, which could have long-term implications for the species' population viability in clearcut habitats. Neither forest type nor food

supplementation affected the growth or survival of juvenile northwestern salamanders throughout the experiment. Forest type and food supplementation also did not significantly affect the growth of adults throughout the experiment.

Juvenile Experiment – Winter Conditions

Harvested areas are frequently considered challenging environments for amphibians due to increased soil and surface temperatures and decreased soil and air moisture, which results in high evaporative water loss of amphibians (Heatwole and Lim 1961, Jaeger 1971, Rothermel and Semlitsch 2002, Mazerolle and Desrochers 2005). These environmental conditions do not apply to harvested areas during winter (December – March) in the Pacific Northwest, which is when the juvenile experiment took place. Although minimum surface temperatures do drop below 0°C at times during Pacific Northwest winters, prolonged periods of temperatures below 0°C are uncommon. Rain is frequent during fall, winter, and spring in the Pacific Northwest. Snowfall is relatively rare during winter. Consequently, during periods of activity (e.g., when temperature permits), amphibians are not at risk of evaporative water loss in harvested areas in fall, winter or spring in the Pacific Northwest. Therefore, harvested areas may not have provided a physiologically unsuitable habitat for juveniles throughout this experiment, resulting in no effect of forest type on survival or growth of juveniles.

Since this experiment took place during winter, it is possible that many individuals were relatively inactive for much of the experiment. In fall, juvenile northwestern salamanders move away from breeding ponds and settle in forested areas, where they over-winter in underground burrows. Winter is a time of relative inactivity for many temperate amphibian species. Air temperatures, especially in northern areas (e.g., Pacific Northwest), typically reach low levels in winter (≤1°C), and may often be below the "activity temperature range" of many ectotherms (Pough 1980). No juveniles were observed on the surface for several weeks in late December and early January when minimum surface temperatures dropped well below 0 °C. Observations of juveniles

increased with increasing temperature, with juveniles regularly observed when maximum temperatures in the forest and clearcut approached close to 10 °C.

Oxygen consumption and metabolic demands of inactive amphibians are low (Duellman and Trueb 1994). If low metabolic demands and inactivity during cold weather periods prevented surface activity for a high proportion of juveniles for several months of the experiment, many juveniles may not have accessed the supplemental food added weekly to feeding trays. Most mealworms on feeding trays did disappear between weekly food additions, but it is possible that other organisms in the enclosures (e.g., deer mice, possibly banana slugs) consumed them. Juveniles may have fed on prey encountered in burrows and under logs, which would have been equivalent in supplemental food and ambient food enclosures. This could have resulted in no perceived effect of food supplementation on survival or growth of juveniles.

Adult Experiment – Summer Conditions

In summer, amphibians in harvested areas may experience high evaporative water loss due to the increased surface and soil temperatures and decreased soil and air moisture associated with canopy removal (Heatwole and Lim 1961, Jaeger 1971, Rothermel and Semlitsch 2002, Mazerolle and Desrochers 2005). This may lead to desiccation and mortality of amphibians in harvested areas. During the adult experiment, maximum weekly surface temperatures (daytime temperatures) between May and September were 4 - 6°C higher in clearcut enclosures than forest enclosures. Minimum weekly surface temperatures (night-time temperatures) were approximately equal in clearcut and forest enclosures, and were as much as 15°C cooler than maximum weekly temperatures. How temperature stabilized with increasing depth underground, and how deep salamanders had to burrow to avoid high surface temperatures, is not known. Salamanders in clearcuts may have had to move to deeper burrows during daytime to avoid the higher surface temperatures. This may have resulted in greater energy expenditure for salamanders in clearcuts compared to those in forest sites if longer daily movements were required to ensure exposure to suitable temperatures.

No significant differences were observed in soil moisture between clearcut and forest enclosures on any sampling date, but there were trends towards higher mean soil moisture in clearcut enclosures than in forest enclosures during the August and September sampling sessions. Clearcut enclosures had a higher percentage of shrub and downed wood cover than forest enclosures, which may have minimized soil moisture loss. If soil moisture was similar in both forest types, salamanders foraging on the surface at night, when temperatures in the two forest types were similar, may not have experienced greater evaporative water loss in clearcut than forest enclosures. Therefore, desiccation stress does not appear to explain the significant effect of forest type on survival of adults.

The dry surface conditions during summer in both forest types may have reduced salamander surface activity for much of the experiment. Dry conditions may force individuals to depend on underground, moist refugia, which may reduce foraging time (Jaeger 1980a, Dupuis et al. 1995). In summer, salamanders in both forest types may have been dependent on precipitation for surface movements due to dry conditions (Dupuis et al. 1995, Johnston and Frid 2002). There were low amounts of rainfall between mid-June and mid-August (<20 mm per week; 6 weeks with <5 mm), which may have negatively affected foraging ability. Consequently, salamanders in both forest types may not have accessed the supplemental food often enough throughout the experiment, which may have resulted in no significant effect of food supplementation on survival or growth of adults.

Due to the reduced survival of adults in clearcut enclosures, the density of animals in clearcut enclosures would have been lower than that in forest enclosures. If conditions (food availability and ability to forage effectively) were similar in forest and clearcut enclosures, then this reduced density in clearcut enclosures might have been expected to result in better performance (e.g., lower weight loss or greater weight gain) for surviving animals in clearcut enclosures. Since this was not the case, there is

evidence that clearcut enclosures in summer did not provide equivalent habitat to forest enclosures.

Relation to Invertebrate Sampling Results

During the juvenile experiment, there was a significant effect of the interaction between sampling date and forest type on invertebrate biomass, with a higher biomass of invertebrates captured in the clearcut treatment compared to the forest treatment during the February sampling session. However, this higher biomass of captured invertebrates in clearcuts late in the juvenile experiment, at a time of year when juveniles are expected to have been active above-ground, did not affect growth of juveniles. This could indicate that ambient invertebrate biomasses in both forest types were below the threshold required to affect growth of juvenile salamanders. In other words, juvenile salamanders may have been food limited in both forest types. Alternatively, it could indicate that juveniles were not food limited in either forest type in winter: food may have been so abundant in both forest types that the higher biomass of invertebrates in clearcuts late in the experiment did not have any effect on juvenile growth.

The most likely explanation for the lack of relationship between the invertebrate sampling results and the juvenile growth results is that the invertebrate sampling data does not reflect available prey for juvenile northwestern salamanders. Some invertebrate Orders, or life stages of Orders, were likely undersampled due to the movement bias inherent in pitfall trapping. There has been little research on the diet of terrestrial northwestern salamanders, although they are assumed to eat a wide variety of terrestrial invertebrates (Nussbaum et al. 1983). Other ambystomatid salamanders have been documented consuming snails, adult beetles and invertebrate larvae (Bellocq et al. 2000). It is possible that northwestern salamanders primarily feed on soft-bodied invertebrates such as slugs, worms, and larvae that they encounter in and around burrows and downed wood. No larval invertebrates were found in any of the invertebrate pitfall samples, indicating that such organisms were not sampled adequately. Therefore, it is possible that there was no difference between clearcuts and

forest in the biomass of prey items preferred by juvenile northwestern salamanders, which resulted in no effect of forest type on growth of juveniles.

The biomass of invertebrates captured in clearcut sites during the adult experiment was significantly lower than in forest sites, although numbers were not significantly different. This indicates that smaller invertebrate species were captured in the clearcuts. The results of our correspondence analysis generally supports this, with heavier species such as Coleoptera, Lepidoptera and Orthoptera captured in forest sites.

There are a number of possible explanations for why the lower biomass of invertebrates in clearcuts did not result in increased weight loss of salamanders in that forest type. As above, it is possible that adult salamanders were not food limited in forest or clearcut sites. It is also possible that adults were food limited in clearcuts, and that those individuals unable to compete adequately for food resources perished. The subsequent reduction in density in the clearcut enclosures may have meant that remaining salamanders had equivalent food resources to salamanders in the forest treatment. However, as above, the most likely explanation for the lack of relationship between the invertebrate sampling results and the adult growth results is that the pitfall traps did not sample some invertebrate Orders, or life stages of Orders, that adult northwestern salamanders consume. Few slugs, and no larval invertebrates, were found in any of the invertebrate pitfall samples collected during the adult experiment.

Comparisons with Previous Studies

Few studies have examined the effects of harvested areas on amphibians during the winter. Many studies in eastern North America (Pough et al. 1987, Petranka et al. 1993, Petranka et al. 1994, deMaynadier and Hunter 1998, Harpole and Haas 1999, Cromer et al. 2002, Knapp et al. 2003) and western North America (Dupuis et al. 1995, Cole et al. 1997, Davis 1998, Naughton et al. 2000, Matsuda and Richardson 2005), sampled amphibians during the summer, sometimes in addition to fall and spring sampling. A negative effect of harvested areas on amphibian abundance and diversity

was found for all studies that included summer sampling. Sampling for our juvenile experiment was limited to the spring, and we found no effects of harvested areas on juvenile survival. Other studies in the Pacific Northwest in which sampling did not occur in summer (sampling in fall and/or spring) have had mixed results. Several studies found negative effects of forest harvesting on amphibian abundance and diversity (Bury 1983, Aubry 2000, Grialou et al. 2000), while others found no effect (Maxcy 2000, Biek et al. 2002). The reduced abundance (survival) of adults in clearcut enclosures in our experiment appears to agree with previously published studies in which sampling was conducted in summer.

One hypothesis for the observed reduced abundance and diversity of amphibians in harvested areas in many studies is that amphibians move out of clearcuts due to a reduction in habitat suitability (emigration hypothesis). Therefore, it might be argued that retaining animals in field enclosures prevents a natural response to harvested areas (Chazal and Niewiarowski 1998). Although microhabitat preferences and selection by amphibians have been documented (Taub 1961, Jaeger 1971, 1980b, Davis 1998, Bille 2000, Grover and Wilbur 2002), it is not known if amphibians respond to distant habitat cues from nearby suitable habitat (Rothermel 2004). Radio-tagged coastal giant salamanders (*Dicamptodon tenebrosus*) responded to clearcuts by spending more time underground, reducing home range size, and restricting movement to precipitation events, but they did not appear to move out of clearcuts to adjacent forest (Johnston and Frid 2002). Maxcy (2000) found that movement distances and movement rates of northwestern salamanders and ensatinas in clearcut and forest sites were not significantly different, and there were no trends of animals in clearcuts moving in the direction of the forest. Therefore, we would argue that salamanders in the Pacific Northwest do not respond to clearcuts by moving to adjacent forest, and that salamanders in our field enclosures responded to clearcuts in a similar way as free-ranging salamanders.

Field enclosures have been used before to study of the effects of forest harvesting on ambystomatid salamanders. Chazal and Niewiarowski (1998) used field enclosures

in one clearcut and one forest site to study the effects of forest harvesting on juvenile mole salamanders (*Ambystoma talpoideum*) in a dry loblolly pine-dominated stand in the southeastern United States. As in our juvenile experiment, they found no significant differences between forest treatments for apparent salamander survival rates or final body mass (Chazal and Niewiarowski 1998). Differences in moisture level and temperature between clearcuts and forest are likely more pronounced in the southeastern United States when compared to the Pacific Northwest. However, both experiments took place during winter, when temperature and moisture differences between clearcuts and forest were not as extreme as during summer, even in the southeastern United States (Chazal and Niewiarowski 1998).

Many studies in the eastern United States that have reported a negative effect of harvesting on amphibians have focussed on salamanders from the family Plethodontidae (Petranka et al. 1993, Petranka et al. 1994, Ash 1997, Harpole and Haas 1999, Knapp et al. 2003). It is possible that plethodontids may be more sensitive than some other amphibian taxa to habitat changes associated with harvesting due to their small home ranges and limited dispersal ability (Welsh Jr. and Droege 2001). In a review of 15 studies, deMaynadier and Hunter (1995) found that plethodontids were captured a median of 5 times more often in control stands than clearcut stands. In comparison, anurans were captured a median of 1.7 times more often in control stands (9 studies) (deMaynadier and Hunter 1995). Therefore, the results of our experiments should be extrapolated to other salamander families with caution (*see Management Implications*).

Unanswered Questions and Limitations

In the juvenile experiment, there was no significant effect of forest type or food treatment on survival, although there was a trend of higher survival in ambient food treatments in both forest types. This result might have been an artefact of the trapping methods used (pitfall traps and cover boards). Captures under cover boards and in pitfall traps are biased towards animals that are moving around on the surface. In ambient food treatments, it is possible that animals had a higher frequency or longer

distance of movement while foraging, resulting in them being captured in pitfall traps and under cover boards more frequently. Rohr et al. (2004) found that food limitation caused increased activity of larval streamside salamanders (*Ambystoma barbouri*). However, if this trend were due to a movement bias, then we would have expected to capture more juveniles during the adult experiment in the enclosures that had supplemental food during the juvenile experiment. However, during the adult experiment, equal numbers of juveniles were recaptured in both food treatments in the forest treatment (supplemental food = 7 animals; ambient food = 7 animals), and roughly equivalent numbers were recaptured in both food treatments in the clearcut treatment (supplemental food = 12 animals; ambient food = 9 animals). Therefore, the trend of a lower apparent survival rate of juveniles in the supplemental food treatments does not appear to be an artefact of the trapping method.

The significant effect of forest type on adult survival could have also been an artefact of the trapping methods used. Few adults in clearcut or forest enclosures were captured in corner pitfall traps at the end of the experiment; most were captured under cover boards at feeding stations, or under the cover board of corner pitfall traps. Animals that have been in the enclosures for an extended period of time may learn the locations of pitfall traps, and not fall in them as often. If there is ample natural cover available in the enclosure (e.g., in clearcuts), frequency of use of cover boards might be expected to be lower than in areas with little natural cover. Therefore, even if salamanders were equally active aboveground in both clearcut and forest enclosures, they might be captured more often under cover boards in forest enclosures due to lower percentages of downed wood and shrub cover available for refuge. It is possible that this same effect was not observed during the juvenile experiment due to the absence of heat and evaporative stressors during winter.

Alternatively, movement behaviour of adult salamanders in clearcut and forest enclosures may have differed, which may have affected capture rates. Adult salamanders in clearcut enclosures may not have moved as far from underground refugia as salamanders in forest enclosures, and therefore didn't use the cover boards

as often. Such a difference in movement behaviour between the two forest types could have been caused by two factors. First, it is possible that resources (food, suitable moist refugia) were sufficiently abundant in clearcuts that salamanders didn't have to travel as far to meet their needs. Since our invertebrate sampling may have undersampled important prey items for northwestern salamanders (e.g., larval invertebrates), the invertebrate sampling results cannot be used to predict differences in movement behaviour between the forest types. Environmental variables don't appear to predict any differences in movement behaviour between the forest types. While it is possible that clearcuts had more abundant moist surface refugia than forest enclosures due to the higher downed wood and vegetation cover, there were no significant differences in soil moisture between clearcut and forest enclosures. Second, it is possible that movement behaviour was affected by intraspecific competition for moist refugia. Salamanders in clearcut enclosures may have faced less competition for moist refugia than salamanders in forest enclosures due to an abundance of naturally occurring cover, and therefore did not move around as often.

Although it is difficult to determine the cause for the difference in proportion of adults recaptured in clearcut and forest enclosures, we attempted to eliminate the possibility that the result was an artefact of the sampling method or movement differences in the two forest types by conducting manual ground searches for adults the spring following the experiment. Litter, downed wood, small mammal runways, and vegetation were moved and searched by hand. Since adults migrate to breeding ponds during early spring, they should have been attempting to escape the enclosures, and should have been near the surface. However, despite extensive search effort, only four new salamanders were found in clearcut enclosures. In contrast, five new salamanders and nine previously captured salamanders were found in forest enclosures. Therefore, we are confident that there was an actual difference in salamander abundance in clearcut and forest enclosures at the end of the experiment, and that the result was not an artefact of the trapping method or differences in movement behaviour between the forest types.

Adult northwestern salamanders in clearcut enclosures in summer may have been exposed to a higher density of predators than salamanders in forest enclosures. There are 3 species of garter snakes in southwestern British Columbia, all of which hibernate in winter, but are active between spring and fall: the western terrestrial garter snake (*Thamnophis elegans*), the northwestern garter snake (*Thamnophis ordinoides*), and the common garter snake (*Thamnophis sirtalis*). Although both *T. ordinoides* and *T. sirtalis* use moist meadows, grassland, shrublands and forest clearings as habitat, and can be found in clearcuts away from water (P.T. Gregory, Univ. of Victoria, Canada – pers. comm.), only the latter consumes amphibians, including salamanders (Gregory 1984, Gregory and Campbell 1984). Remains of northwestern salamanders have been found in the guts of *T. sirtalis* on Vancouver Island (Gregory 1984). Northwestern salamanders do contain a toxin, which is released from granular glands concentrated in the parotoid and tail areas as a form of anti-predator defence. *T. sirtalis* is probably unaffected by the toxin (P.T. Gregory, Univ. of Victoria, Canada – pers. comm.), as it also feeds on *Taricha granulosa* (rough-skinned newt), a species that makes both *T. elegans* and *T. ordinoides* on Vancouver Island ill (Macartney and Gregory 1981).

Shrews (*Sorex* spp.) may also have been a predator of adult northwestern salamanders in clearcut enclosures. During invertebrate sampling in June, a higher number of shrews were captured around clearcut enclosures than forest enclosures (clearcut = 27; forest = 8), indicating a higher number of shrews in clearcut sites. Terrestrial shrews and salamanders both use small mammal runways and tunnels, and likely encounter each other frequently. Shrews have a very high metabolism, and can eat up to twice their own body weight every day (Whitaker 1994). Although shrew diets are mainly composed of invertebrates, plants and fungi, they have been noted to consume small mammals and amphibians as well (Whitaker 1994). Madison and Farrand (1998) found frequent predation of radio-implanted adult tiger salamanders (average mass = 30 g) in small-mammal runways, and concluded that predation was most likely by short-tailed shrews (*Blarina brevicauda*; average mass = 22g; (Ballenger 2000). Some terrestrial shrew species in the Pacific Northwest do reach up to 9 g (e.g., *Sorex cinereus, Sorex trowbridgii*, and *Sorex vagrans*) (Whitaker 1994), and may be

able to consume adult northwestern salamanders (average mass = 15.5 g in this experiment), providing they could capture them. It is not known if the toxin contained by northwestern salamanders is a deterrent to shrews.

It is possible that garter snakes and shrews entered clearcut enclosures more often than forest enclosures and consumed some of the adult salamanders, which may have contributed to the reduced survival of adults in clearcuts. However, garter snakes were not observed in any of the clearcut or forest sites during the adult experiment, and shrews were never captured in pitfall traps in enclosures in either forest type. It is also not known if these species commonly consume adult northwestern salamanders, which would represent relatively large prey items. It is more likely that these species would opportunistically consume smaller amphibians, such as juvenile northwestern salamanders and plethodontid salamanders. Therefore, while there may have been occasional predation of adult northwestern salamanders by garter snakes and shrews during the experiment, we do not feel that predation explains the reduced survival of adult northwestern salamanders in clearcut enclosures.

Management Implications

Results of our study indicate that survival of northwestern salamanders in clearcuts in the Pacific Northwest is reduced during summer, but not during winter. Northwestern salamanders are a relatively mobile species, capable of breeding migrations of at least 1 km (Maxcy 2000), and likely encounter clearcuts frequently during their migrations. Migrations from breeding ponds to terrestrial habitat often happen during late spring (adults) and fall (juveniles). There is some risk that adult and juvenile northwestern salamanders may settle in clearcuts in spring and fall, times of year when clearcuts may not be unsuitable for salamanders based on the results of our juvenile experiment. Adults that settle in clearcuts in late spring may remain in these clearcuts during summer: dry surface conditions may prohibit or slow movements out of the clearcut during summer, and/or salamanders may be unable to respond to distant habitat cues from nearby suitable habitat once the habitat quality in the clearcut deteriorates (Rothermel 2004). Juveniles mature in the terrestrial environment for more

than 1 year after emerging from breeding ponds, and may remain in these clearcuts until the following summer, when they too are prevented from moving to suitable habitat for the above reasons. In these cases, clearcuts might become population sinks, and may have negative effects on the local northwestern salamander population.

The reason for the unsuitability of clearcuts in summer remains unclear, making it difficult to suggest ways to improve habitat in clearcuts for northwestern salamanders. We did not find significant differences in soil moisture between clearcut and forest sites, and although surface temperatures were higher in clearcuts than forest sites during summer, maximum temperatures were only about 5 °C warmer in clearcuts. Also, our experiment suggests that food limitation is not a factor in clearcuts.

Further investigations into microclimate conditions in clearcuts in summer in the Pacific Northwest are warranted. It is important that microclimate in habitats that are relevant to the amphibian species in question be considered. For instance, for species such as northwestern salamanders that use underground burrows, soil moisture at 20 cm depth may not be as relevant as moisture at 0.5 m depth. In addition, since this species likely spends little time above ground, surface temperatures may not be that important. For other species that use habitat closer to the surface (e.g., plethodontid salamanders, frogs), measurements of moisture and temperature closer to the surface may be more relevant. In addition, soil moisture may vary considerably depending on surface cover (e.g., downed wood; shrub cover). Since amphibians also use areas under surface cover, soil sampling should take surface cover types into consideration through adequate stratification.

Further investigations into amphibian food availability in clearcuts in the Pacific Northwest are also warranted. It is important that the Orders and life stages of invertebrates that are important food sources for the amphibian species in question be sampled adequately. This requires knowledge of the diet of the amphibian species, and especially, of the diet that maximizes fitness. This information will allow tailoring of the invertebrate sampling scheme to ensure that those invertebrate species and life

stages are adequately sampled in various habitats. It is also important that invertebrate sampling occur in amphibian habitats, to ensure that sampled invertebrates can be considered "available" to the amphibian species. For instance, since many amphibian species forage under downed wood, it may be necessary to sample invertebrates in these areas rather than in open areas.

Although our experiment only tested the response of one salamander species to clearcuts, we feel that it is possible to extrapolate our results to other amphibian species in the Pacific Northwest with some caution. Since northwestern salamanders use underground burrows where they are removed from surface conditions, and since they are capable of long distance movements, one might assume that they are less sensitive than some other amphibian species (e.g., ensatina, western red-backed salamanders, tailed frogs) that are more restricted in their movements and use habitat closer to the surface (e.g., decayed wood). Therefore, the reduced survival of northwestern salamanders in clearcuts in our experiment is likely a conservative estimate of what might happen to other amphibian species in Pacific Northwest clearcuts during summer.

Table 1. General description of the forest and clearcut sites in each block.

	Block 1		Block 2		Block 3	
	M Forest	F Clearcut	E Forest	K10 Clearcut	K Forest	K Clearcut
Aspect	South	South	Southeast	Southeast	East	East
Elevation (m)	275	225	300	300	310	310
Forest age (yrs)	141	5	96	6	81	6
Forest Patch Size (ha)	27	n/a	7	n/a	26	n/a
Clearcut size (ha)	n/a	8.7	n/a	2.0	n/a	1.2

Table 2. Total biomass (g) and mean initial mass (g) of animals in each enclosure in the juvenile experiment. Standard error of means provided (±1 S.E).

Experiment	Block	Site	Enclosure Pair	Food Treatment	Total Biomass (g)	Mean Initial Mass (g)	S.E. (g)
Juvenile (n=14 animals/ enclosure at start of exp't)	1	M Forest	1	Food	75.61	5.40	0.43
				Ambient	68.52	4.89	0.28
			2	Food	65.98	4.71	0.20
				Ambient	67.93	4.85	0.46
		F Clearcut	1	Food	71.72	5.12	0.26
				Ambient	71.21	5.09	0.29
			2	Food	66.42	4.74	0.26
				Ambient	64.19	4.59	0.25
	2	E Forest	1	Food	69.35	4.95	0.38
				Ambient	69.49	4.96	0.33
			2	Food	73.74	5.27	0.33
				Ambient	67.39	4.81	0.23
		K10 Clearcut	1	Food	65.48	4.68	0.40
				Ambient	77.15	5.51	0.31
			2	Food	73.97	5.28	0.34
				Ambient	70.25	5.02	0.37
	3	K Forest	1	Food	66.87	4.78	0.31
				Ambient	65.05	4.65	0.29
			2	Food	77.39	5.53	0.31
				Ambient	74.09	5.29	0.30
		K Clearcut	1	Food	68.24	4.87	0.18
				Ambient	65.41	4.67	0.22
			2	Food	73.74	5.27	0.37
				Ambient	69.93	5.00	0.21
				Overall:	**1679.12**	**5.00**	**0.06**

Table 3. Sample sizes for juvenile experiment analyses. The 'Recaptures in Wrong Enclosure' column shows which food treatment the animal(s) moved *out of*: the animal was recaptured in the other food treatment. Enclosure pair sample size includes animals recaptured in the wrong enclosures, and those captured after May 12th, 2004. Some animals captured after May 12th, 2004 were also recaptured in the wrong enclosure, so columns may not tally correctly to provide enclosure pair sample size. Sample size is lower for weight change analysis than enclosure sample size due to omission of animals with incorrect marks (unable to determine animal's initial weight).

					Proportion Recaptured Analyses				
Experiment	**Block**	**Site**	**Enclosure Pair**	**Food Treatment**	**Enclosure *n***	**Recaptures in Wrong Enclosure**	**Recaptures after May 12th, 2004**	**Enclosure Pair *n***	**Weight Change Analysis *n***
Juvenile (n=14 animals/ enclosure at start of exp't; n_{total} = 336 animals)	1	M Forest	1	Food	3	1	0	15	3
				Ambient	10	0	1		9
			2	Food	4	1	0	17	4
				Ambient	11	0	1		11
		F Clearcut	1	Food	3	2	1	18	3
				Ambient	12	0	0		11
			2	Food	7	0	3	17	6
				Ambient	5	0	2		4
	2	E Forest	1	Food	9	0	4	23	9
				Ambient	5	4	1		5
			2	Food	7	1	1	17	7
				Ambient	5	1	2		5
		K10 Clearcut	1	Food	2	1	1	8	2
				Ambient	4	1	0		4
			2	Food	5	0	4	17	4
				Ambient	7	1	1		6
	3	K Forest	1	Food	0	0	0	0	0
				Ambient	0	0	0		0
			2	Food	4	0	2	11	3
				Ambient	3	0	2		3
		K Clearcut	1	Food	3	0	1	11	3
				Ambient	2	0	5		2
			2	Food	4	0	2	14	4
				Ambient	7	0	1		7
				TOTAL:	**122**	**13**	**35**	**168**	**115**

Table 4. Weight change of juveniles recaptured between March 8th and May 12th, 2004. Weight change is calculated as (final weight – initial weight)/(initial weight). Negative values represent animals that lost weight throughout the course of the experiment.

Site	Enclosure Pair	Food Treatment	Individual Juvenile Weight Change										
M Forest	1	Food	-0.1247	-0.0637	0.0692								
		Ambient	-0.0882	-0.2084	-0.1932	0.0221	0.0036	0.0583	-0.0485	-0.0370	-0.1275		
	2	Food	-0.0495	-0.0077	-0.1467	-0.2668							
		Ambient	0.0561	-0.1078	-0.1580	-0.0817	-0.2128	0.1700	-0.0674	-0.0132	-0.1118	-0.2399	-0.1521
F Clearcut	1	Food	-0.0232	-0.0602	-0.1308								
		Ambient	-0.0962	-0.0295	0.0405	-0.0485	-0.1928	-0.0623	-0.0447	0.0065	-0.0310	-0.1189	-0.2353
	2	Food	-0.0064	0.0922	0.3103	-0.0796	0.2135	-0.1178					
		Ambient	-0.3007	-0.0177	-0.0025	-0.0380							
E Forest	1	Food	-0.1407	-0.1098	-0.0660	-0.0979	-0.1093	-0.0897	-0.2892	-0.0902	0.0590		
		Ambient	-0.0935	-0.1594	-0.1797	-0.1570	-0.0823						
	2	Food	-0.0674	-0.0961	-0.1632	-0.1674	-0.2986	-0.1106	-0.1185				
		Ambient	-0.1455	-0.0992	-0.2415	-0.0488	0.0248						
K10 Clearcut	1	Food	0.0556	0.1638									
		Ambient	0.0557	-0.0363	-0.0296	-0.0704							
	2	Food	-0.0725	-0.0387	-0.2406	0.0026							
		Ambient	-0.0792	-0.0763	0.0565	-0.1484	0.1089	-0.2119					
K Forest	1	Food											
		Ambient											
	2	Food	0.0392	-0.0173	-0.1285								
		Ambient	0.0390	-0.1121	-0.3745								
K Clearcut	1	Food	0.0060	0.0165	0.1754								
		Ambient	-0.1000	-0.1425									
	2	Food	-0.1516	0.0482	-0.2629	-0.0699							
		Ambient	-0.0284	-0.0957	-0.0909	-0.1479	-0.1247	-0.1503	-0.1568				

Table 5. Total biomass (g) and mean initial mass (g) of animals in each enclosure in the adult experiment. Standard error of means provided (±1 S.E).

Experiment	Block	Site	Enclosure Pair	Food Treatment	Total Biomass (g)	Mean Initial Mass (g)	S.E. (g)
Adult (n=7 animals/ enclosure at start of exp't)	1	M Forest	1	Food	102.08	14.58	0.39
				Ambient	113.49	16.21	1.10
			2	Food	106.75	15.25	0.96
				Ambient	104.39	14.91	0.88
		F Clearcut	1	Food	109.41	15.63	0.51
				Ambient	104.56	14.94	0.32
			2	Food	104.61	14.94	0.61
				Ambient	110.21	15.74	0.82
	2	E Forest	1	Food	115.04	16.43	0.71
				Ambient	111.56	15.94	0.89
			2	Food	110.95	15.85	1.22
				Ambient	105.59	15.08	0.62
		K10 Clearcut	1	Food	110.16	15.74	0.95
				Ambient	108.87	15.55	0.82
			2	Food	108.93	15.56	0.81
				Ambient	106.63	15.23	0.66
	3	K Forest	1	Food	110.02	15.72	1.16
				Ambient	110.53	15.79	0.69
			2	Food	106.78	15.25	0.72
				Ambient	112.67	16.10	1.23
		K Clearcut	1	Food	102.95	14.71	0.52
				Ambient	108.96	15.57	0.71
			2	Food	114.49	16.36	0.56
				Ambient	109.52	15.65	0.93
				Overall:	**2609.15**	**15.53**	**0.16**

Table 6. Sample sizes for adult experiment analyses. The 'Recaptures in Wrong Enclosure' column shows which food treatment the animal moved *out of*: the animal was recaptured in the other food treatment. 'Recaptures after November 24th, 2004' refers to captures of animals that were not previously captured between August 27th and November 24th, 2004. Enclosure pair sample size includes animals recaptured in the wrong enclosures, and those captured after November 24th, 2004. Some animals captured after November 24th, 2004 were also recaptured in the wrong enclosure, so columns may not tally correctly to provide enclosure pair sample size. Sample size is the same for weight change analysis and proportion recaptured analysis.

					Proportion Recaptured Analyses				
Experiment	**Block**	**Site**	**Enclosure Pair**	**Food Treatment**	**Enclosure *n***	**Recaptures in Wrong Enclosure**	**Recaptures after Nov. 24th, 2004**	**Enclosure Pair *n***	**Weight Change Analysis *n***
Adult (n=7 animals/ enclosure at start of exp't; n_{total} = 168 animals)	1	M Forest	1	Food	4	0	1	6	4
				Ambient	0*	1	0		0
			2	Food	5	0	0	9	5
				Ambient	4	0	0		4
		F Clearcut	1	Food	2	0	1	3	2
				Ambient	0*	0	0		0
			2	Food	0*	0	0	4	0
				Ambient	3	1	0		3
	2	E Forest	1	Food	5	1	0	13	5
				Ambient	6	1	0		6
			2	Food	0*	0	0	omit	0
				Ambient	0*	0	0		0
		K10 Clearcut	1	Food	1	0	0	1	1
				Ambient	0*	0	0		0
			2	Food	2	0	0	2	2
				Ambient	0*	0	0		0
	3	K Forest	1	Food	5	0	1	12	5
				Ambient	6	0	0		6
			2	Food	0*	0	1**	4	0
				Ambient	3	0	0		3
		K Clearcut	1	Food	0*	0	0	omit	0
				Ambient	0*	0	0		0
			2	Food	2	0	2	6	2
				Ambient	1	0	1		1
				TOTAL:	**49**	**4**	**7**	**60**	**49**

* = Enclosures that were omitted from the second proportion recaptured analysis (enclosures with no recaptures at end of experiment). ** This animal was recaptured in February 2005.

Table 7. Weight change of adults recaptured between August 27th and November 24th, 2004. Weight change is calculated as (final weight – initial weight)/(initial weight). Negative values represent animals that lost weight throughout the course of the experiment.

Block	Site	Enclosure Pair	Food Treatment	Individual Adult Weight Change					
1	M Forest	1	Food	0.3703	0.1441	0.1940	0.0014		
			Ambient						
		2	Food	0.2159	-0.0734	0.2962	0.0353	0.1102	
			Ambient	-0.1363	0.1117	-0.1391	-0.0743		
	F Clearcut	1	Food	-0.2786	-0.3222				
			Ambient						
		2	Food						
			Ambient	-0.1210	0.2832	-0.3133			
2	E Forest	1	Food	-0.0285	-0.3001	0.0816	-0.1699	0.1935	
			Ambient	-0.1817	-0.0645	-0.1172	-0.0222	-0.3176	-0.2540
		2	Food						
			Ambient						
	K10 Clearcut	1	Food	-0.0363					
			Ambient						
		2	Food	-0.2813	-0.3293				
			Ambient						
3	K Forest	1	Food	-0.2231	-0.0591	-0.1637	-0.2232	-0.1151	
			Ambient	-0.1461	0.0354	-0.1545	-0.1818	-0.1604	-0.4021
		2	Food						
			Ambient	-0.0155	0.1125	-0.0194			
	K Clearcut	1	Food						
			Ambient						
		2	Food	-0.2336	-0.0158				
			Ambient	-0.2222					

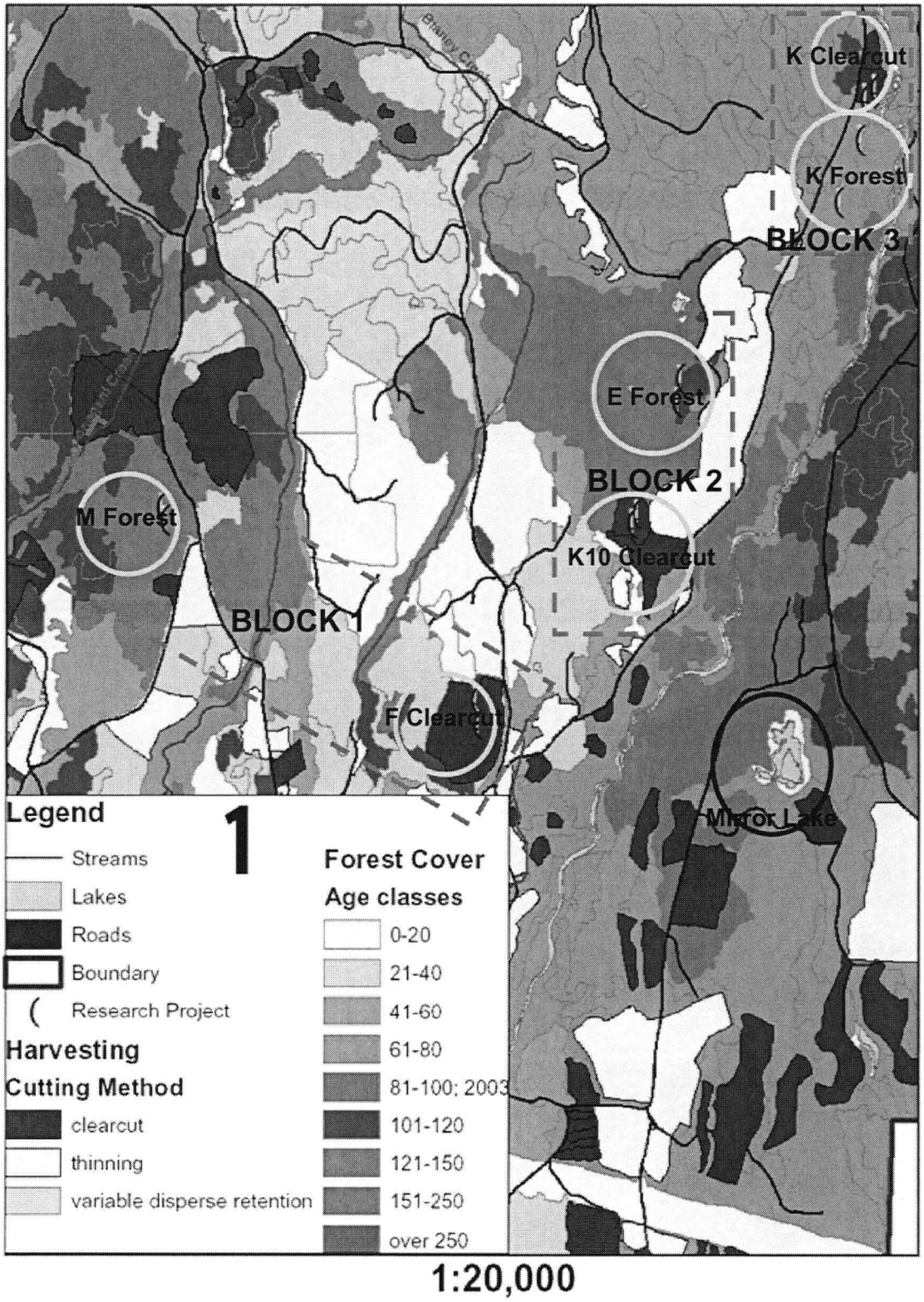


Figure 1. Map of research forest, showing sites where enclosures were located (yellow circles), and grouping of sites into blocks (red dashed line). Two enclosure pairs were built at each site. Size of yellow circles around sites does not reflect site size. Juveniles and adults were captured around the perimeter of Mirror Lake.

Figure 2 – Photograph of enclosure pair in forest.

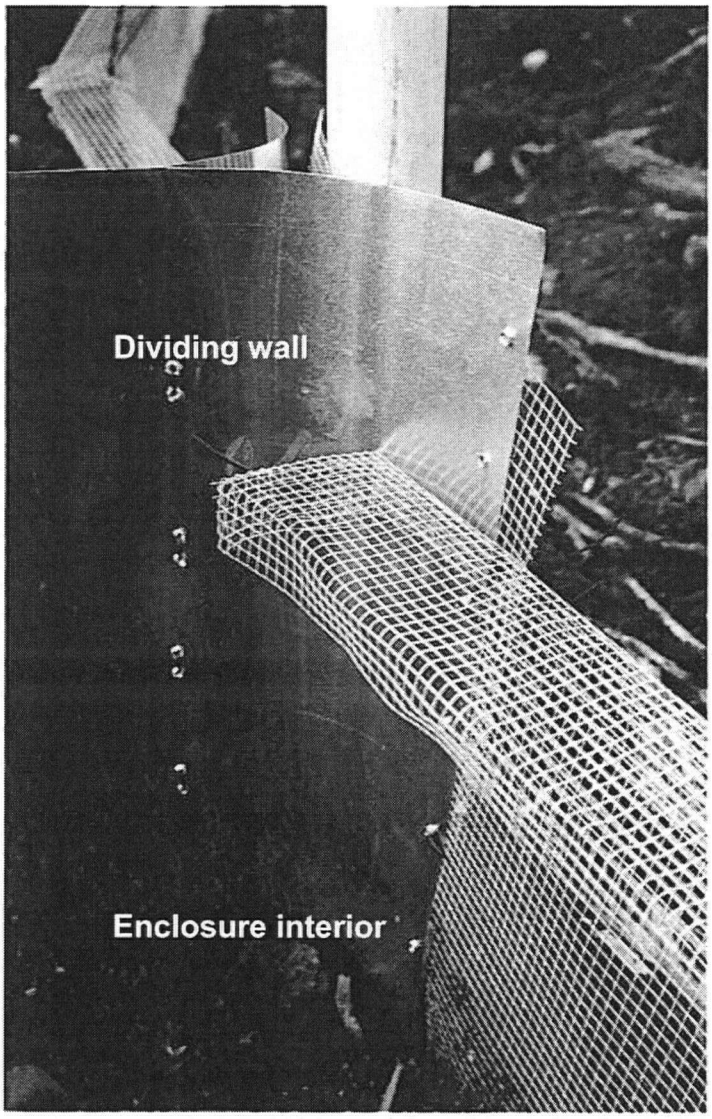
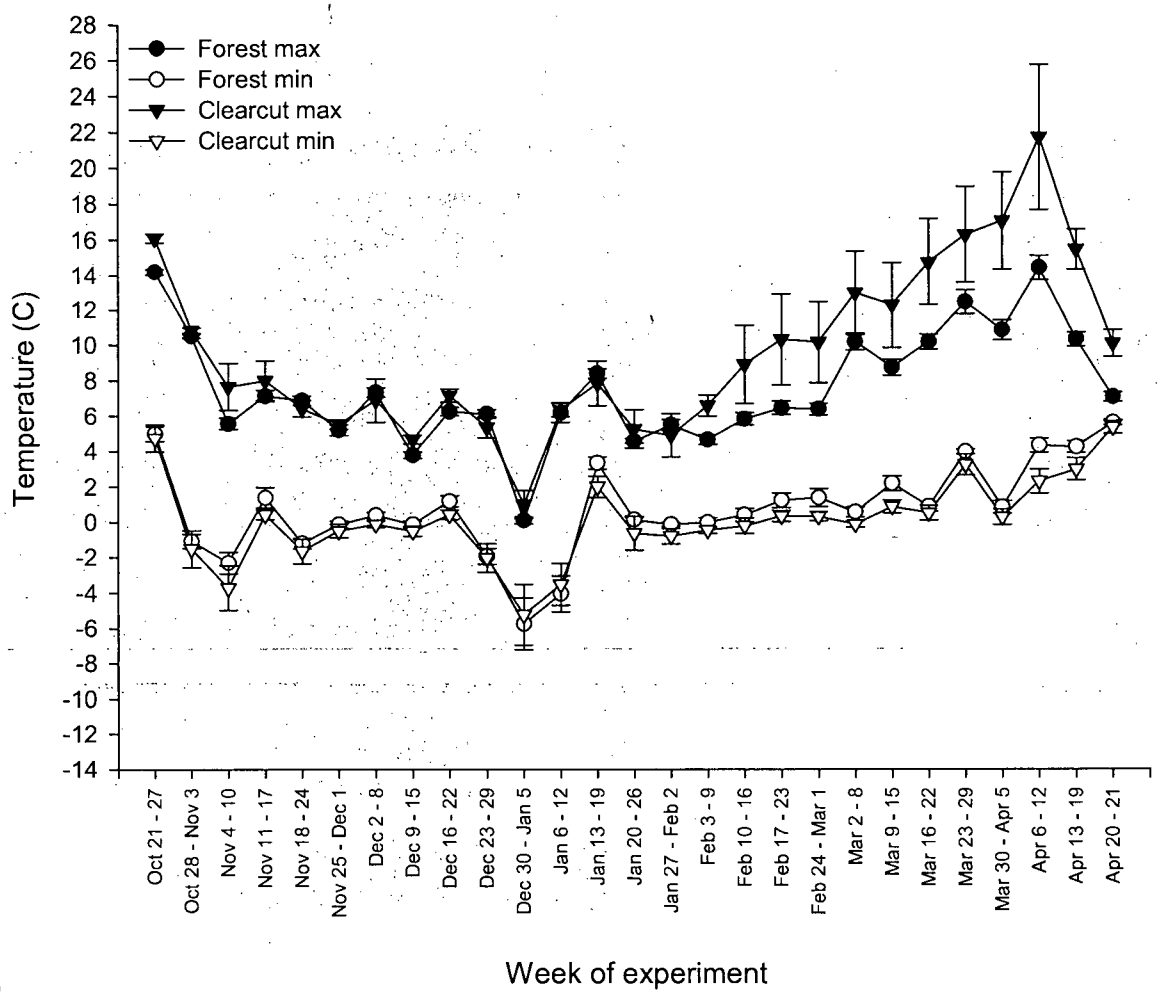


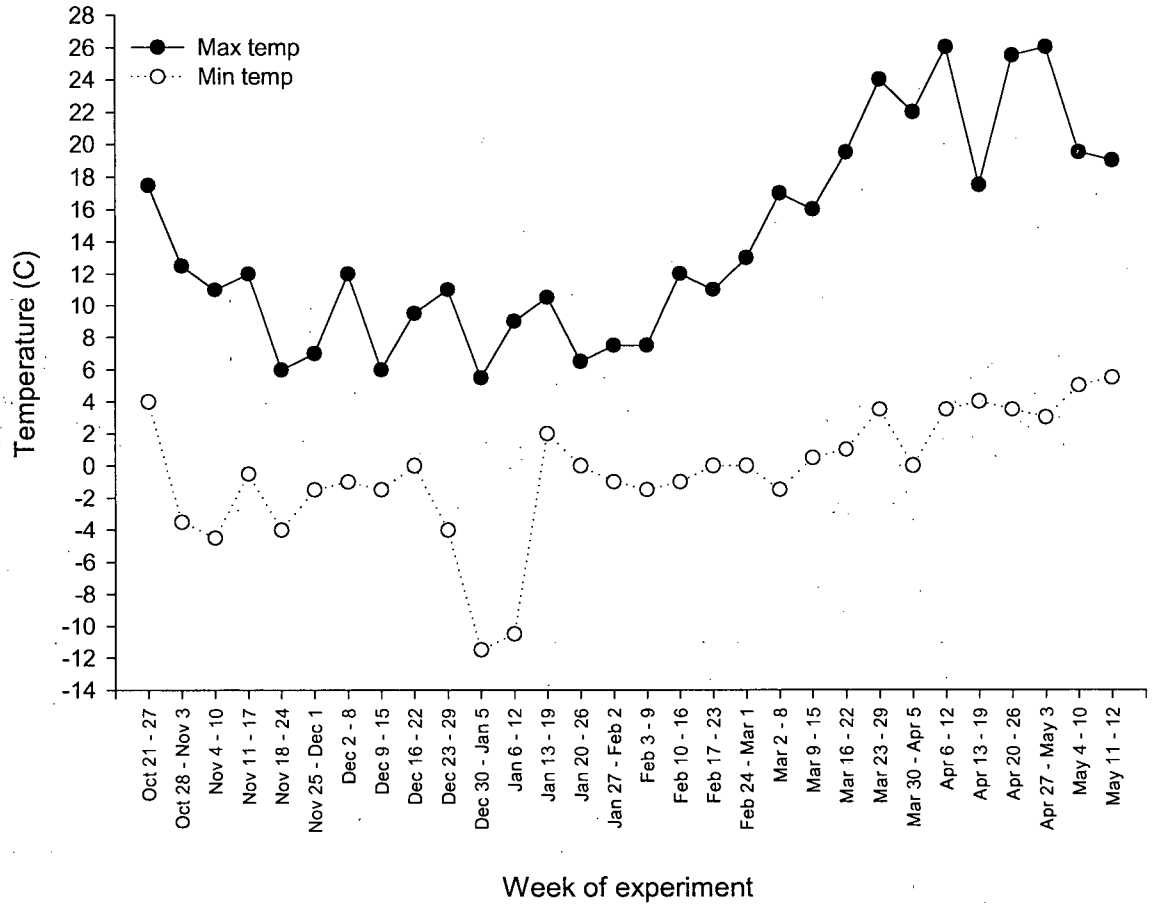
Figure 3 – Photograph of mesh fence of an enclosure showing the double folding at the top of the mesh fence towards the interior of the enclosure to prevent salamanders from climbing out. The aluminum flashing used for the dividing wall is also shown.

Figure 4 – Photograph of an enclosure in a clearcut, showing the aluminum flashing used to build the dividing wall. The small flaps of metal attached to the dividing wall posts were used to prevent animals from climbing the posts.



a)

Figure 5a. Environmental variables for the juvenile experiment: maximum and minimum surface temperatures in each forest type, from temperature loggers in each enclosure pair. Temperature logger data ended on April 21, 2004.



b)

Figure 5b. Environmental variables for the juvenile experiment: maximum and minimum air temperatures, from weather station in Malcolm Knapp Research Forest.

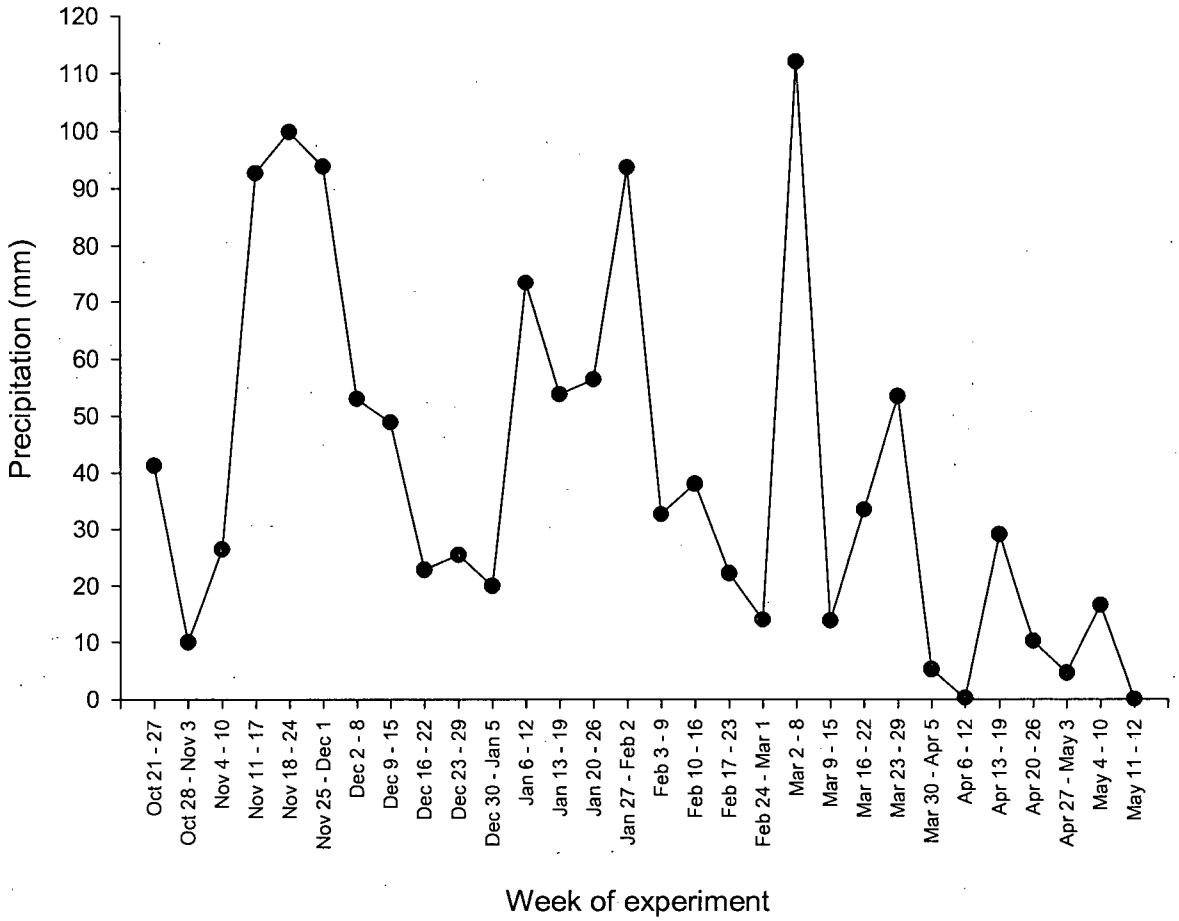
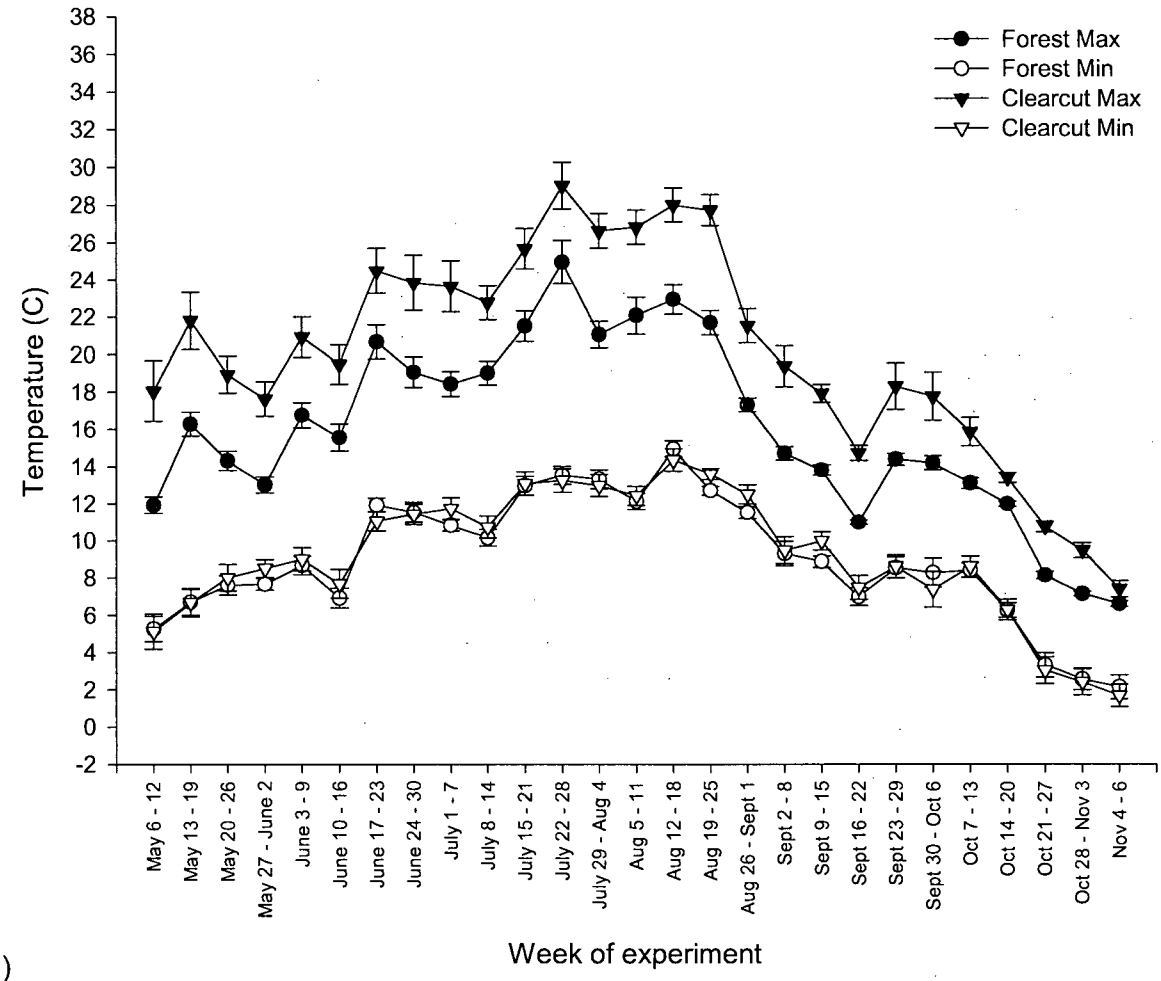
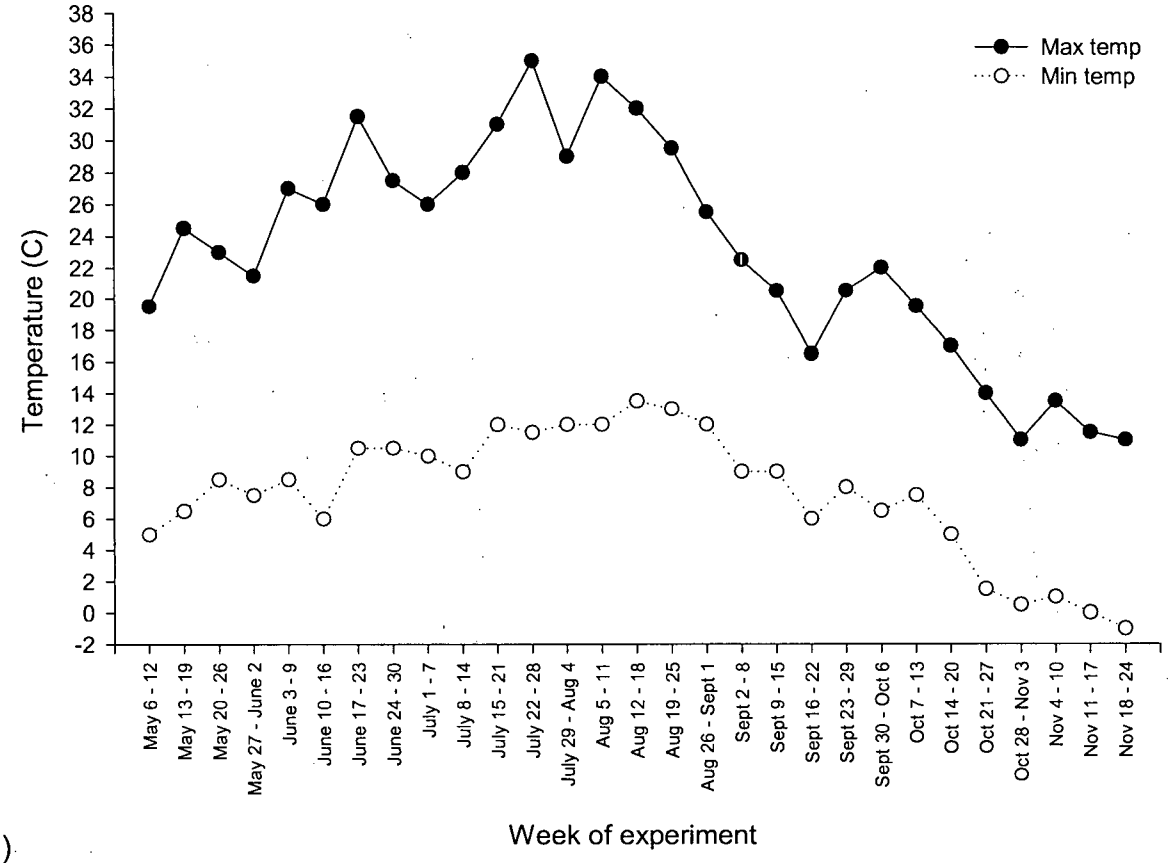


Figure 6. Total precipitation (mm) during each week of the juvenile experiment. Data were collected at a weather station in Malcolm Knapp Research Forest.



a)

Figure 7a. Environmental variables for the adult experiment: maximum and minimum surface temperatures in each forest type, from temperature loggers in each enclosure pair. Temperature logger data ended on November 6, 2004.



b)

Figure 7b. Environmental variables for the adult experiment: maximum and minimum air temperatures, from weather station in Malcolm Knapp Research Forest.

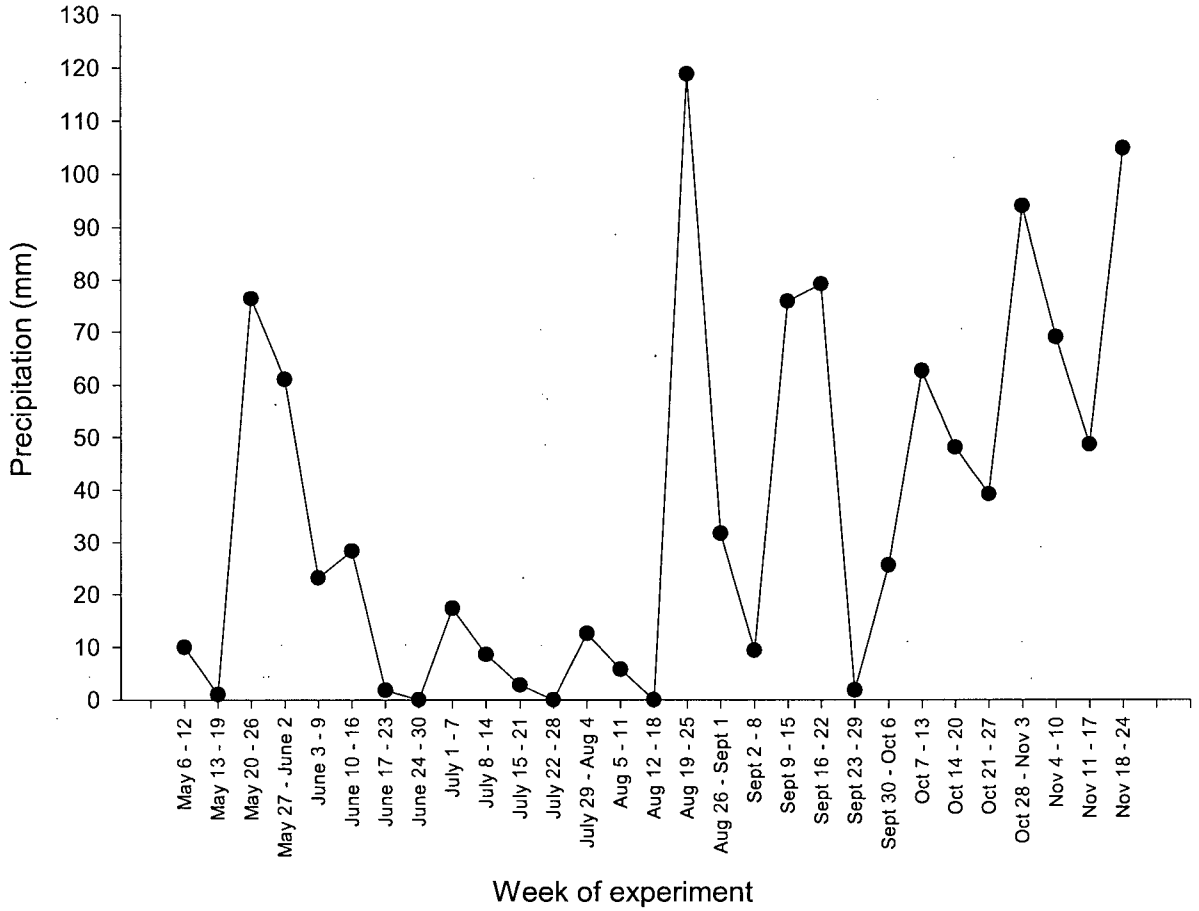
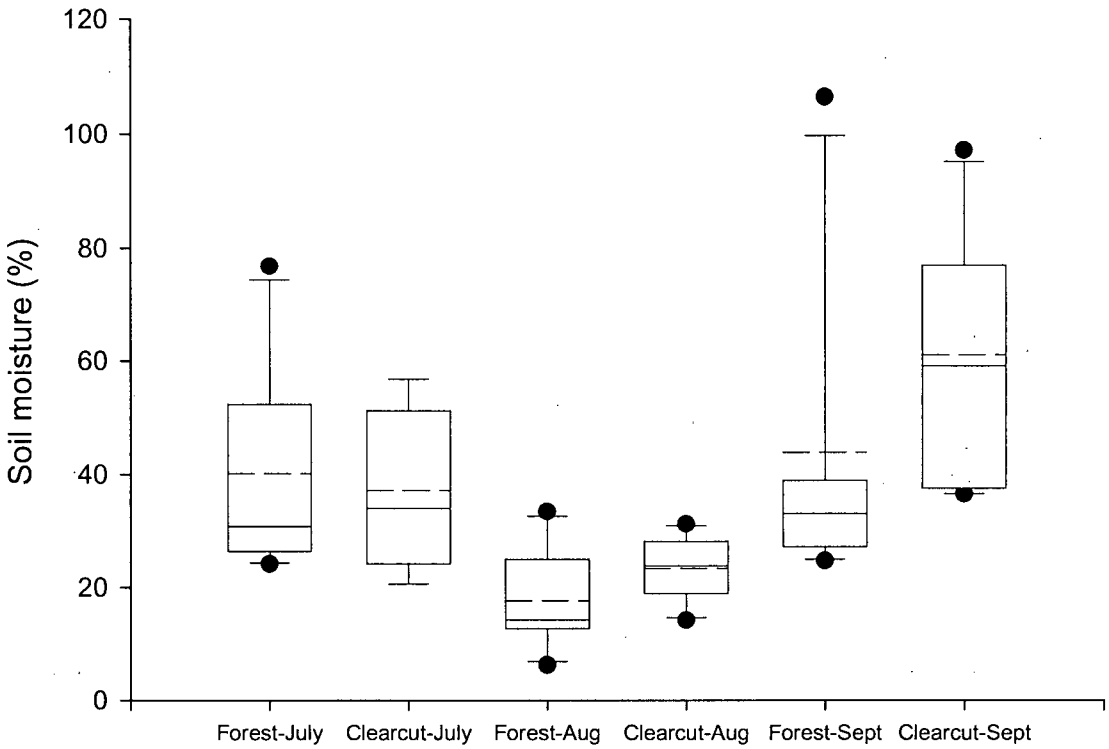
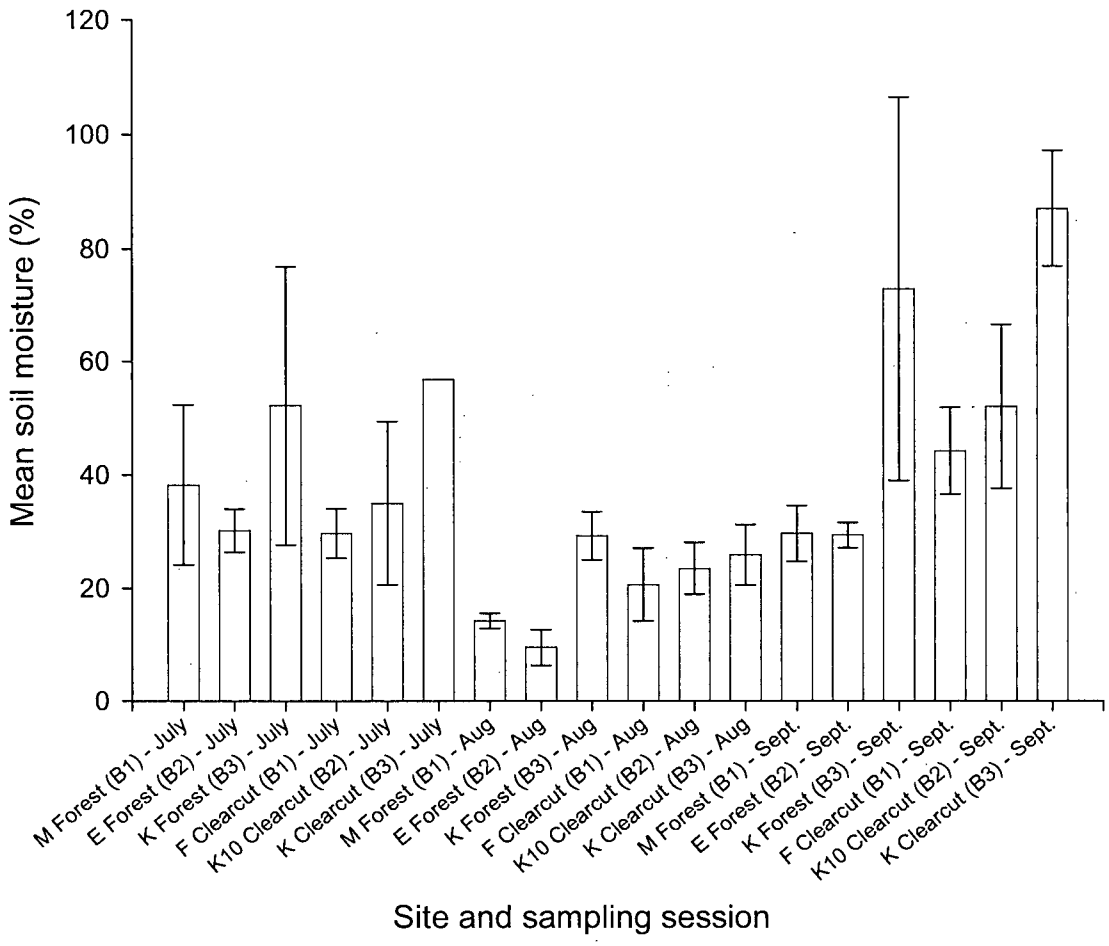


Figure 8. Total precipitation (mm) during each week of the adult experiment. Data were collected at a weather station in Malcolm Knapp Research Forest.



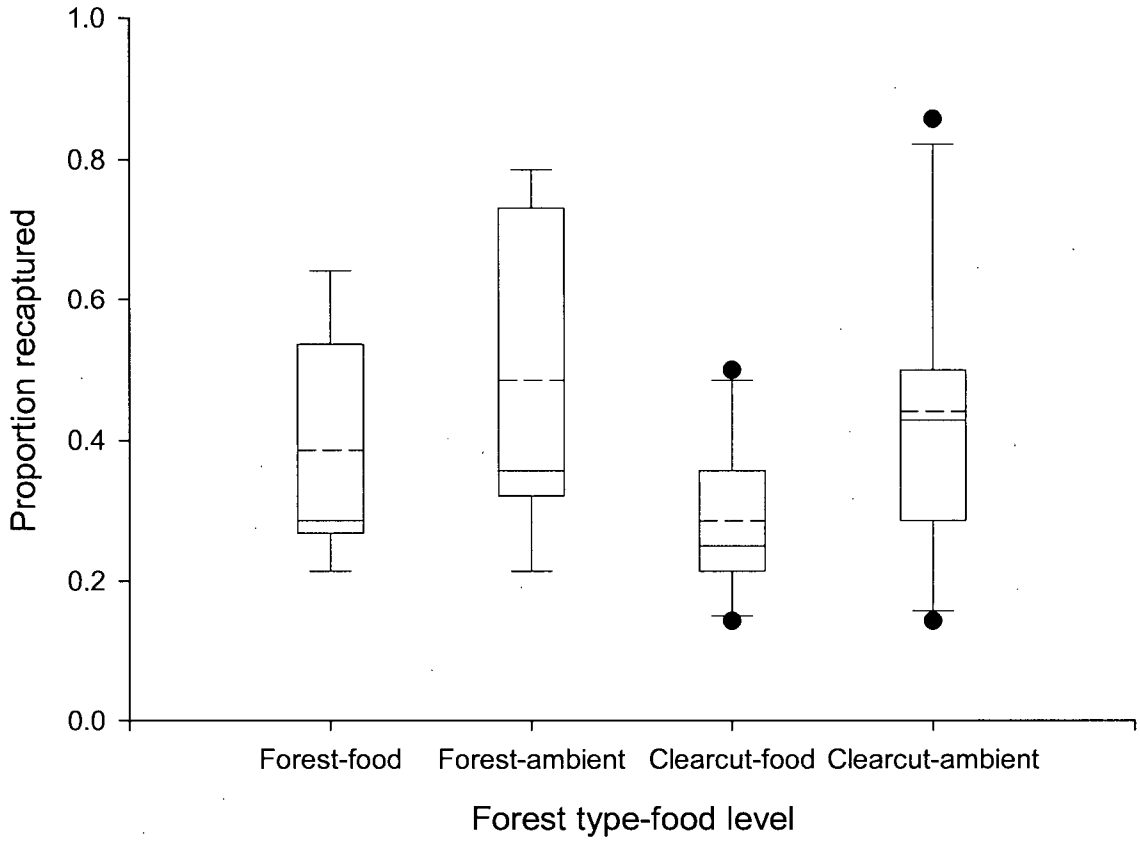
a)

Figure 9a. Enclosure soil moisture (%) during the adult experiment in each forest type on each sampling session. Dashed line in box plots represents the mean, while solid line represents the median. Box plot represents the 10^{th} and 90^{th} percentiles of the data, while whiskers represent the 5^{th} and 95^{th} percentiles of the data.



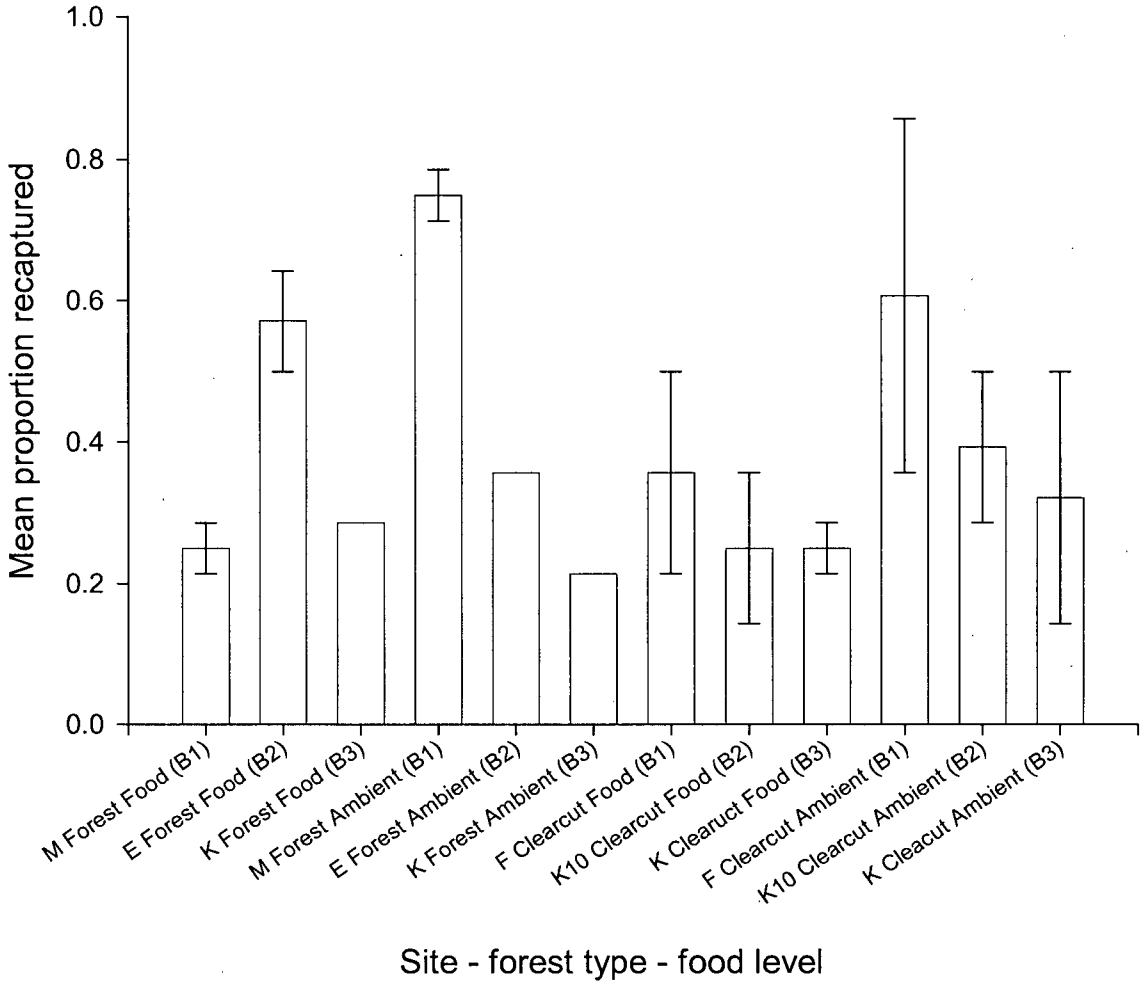
b)

Figure 9b. Enclosure soil moisture (%) during the adult experiment in each site on each sampling session (including standard error bars on the mean). Blocks are listed in brackets (e.g., B1 = Block 1).



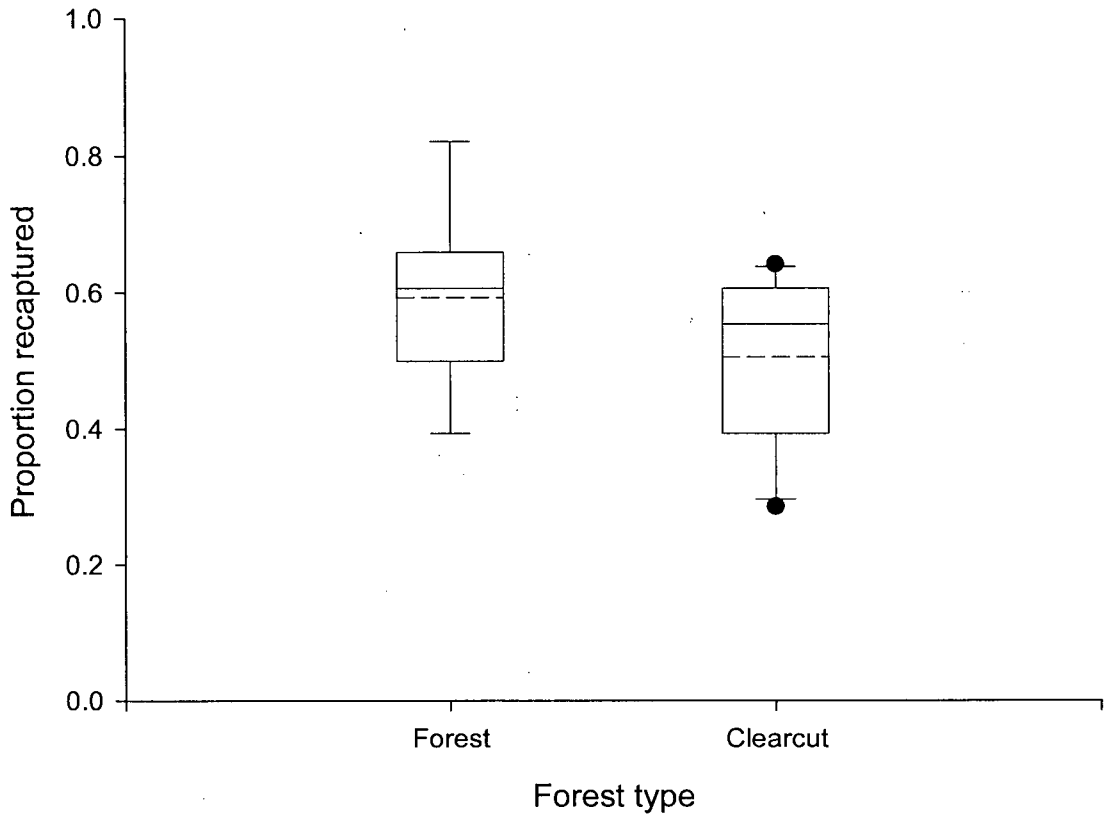
a)

Figure 10a. Proportion of juveniles recaptured in the correct enclosure at the end of the experiment in each forest type and food treatment. Figure conventions follow those used in Figure 9a.



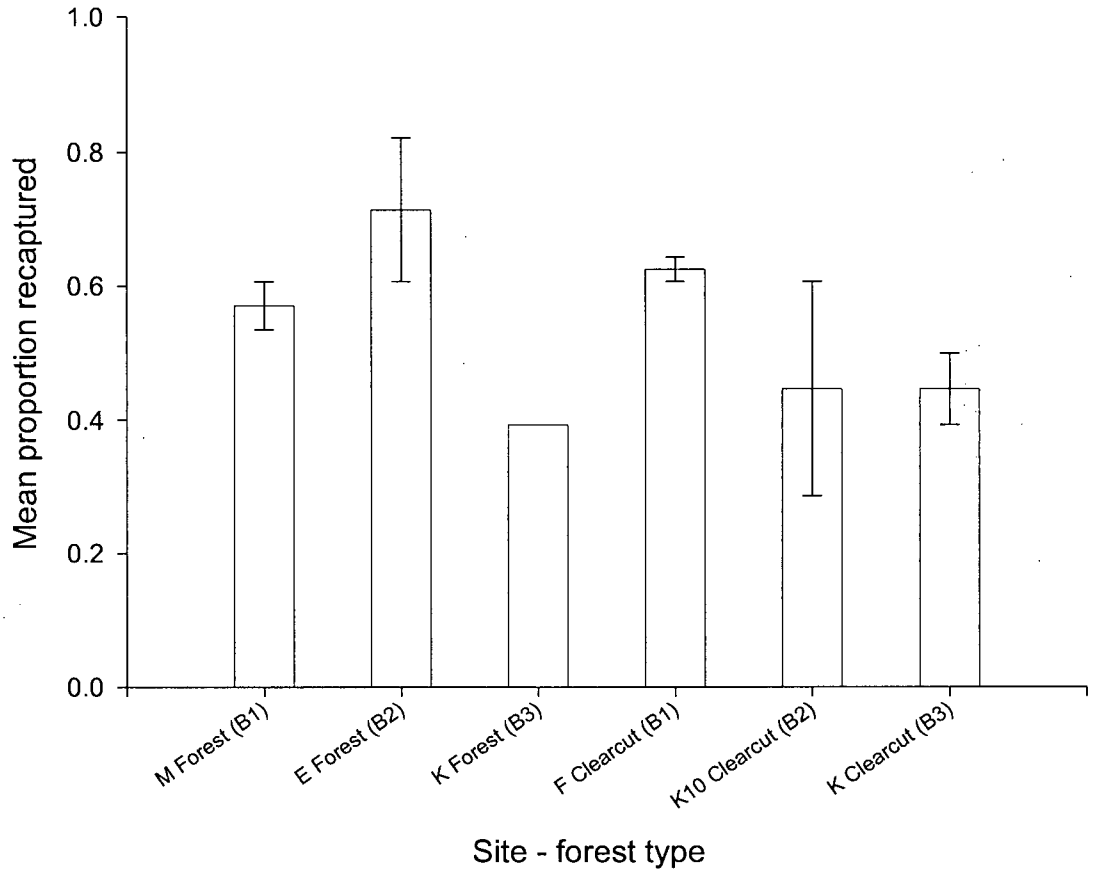
b)

Figure 10b. Proportion of juveniles recaptured in the correct enclosure at the end of the experiment in each food treatment at each site (including standard error bars on the mean). No mean could be calculated for K Forest Food, as data were only available from one enclosure. Figure conventions follow those used in Figure 9b.



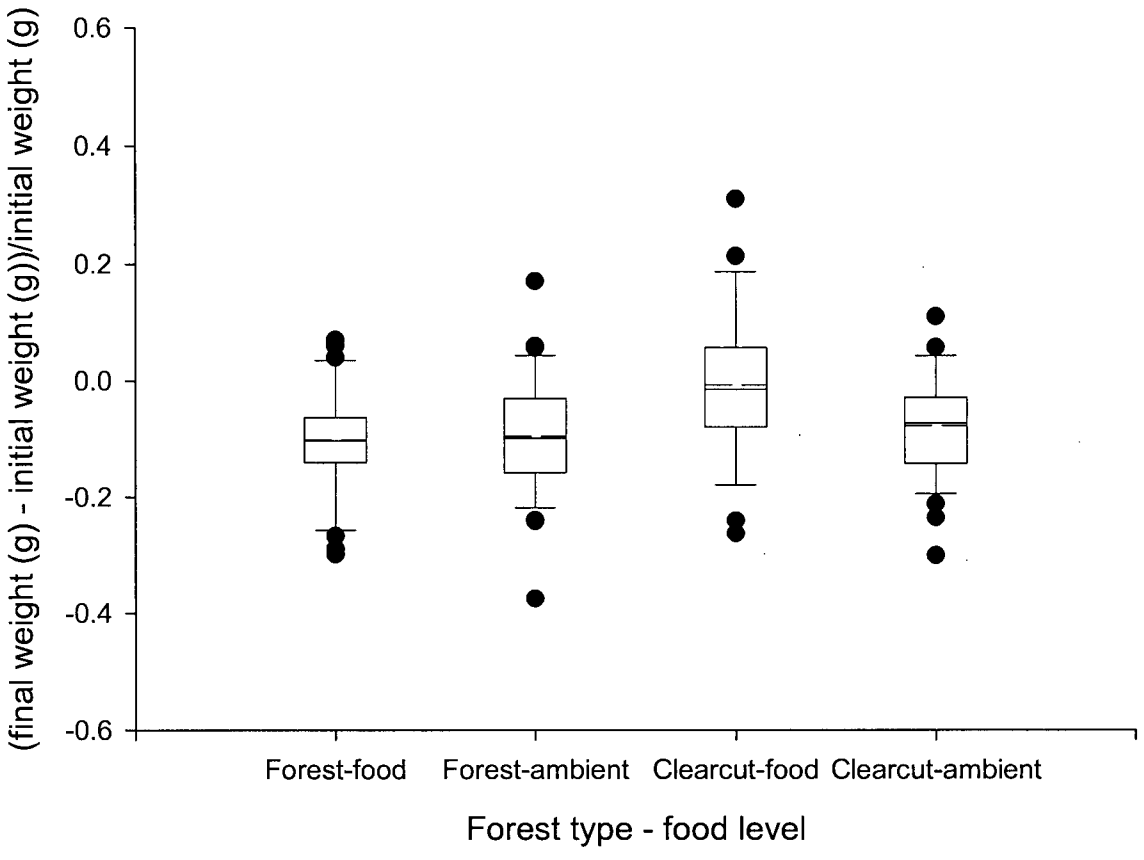
a)

Figure 11a. Proportion of juveniles recaptured in each enclosure pair at the end of the experiment in each forest type. Figure conventions follow those used in Figure 9a.



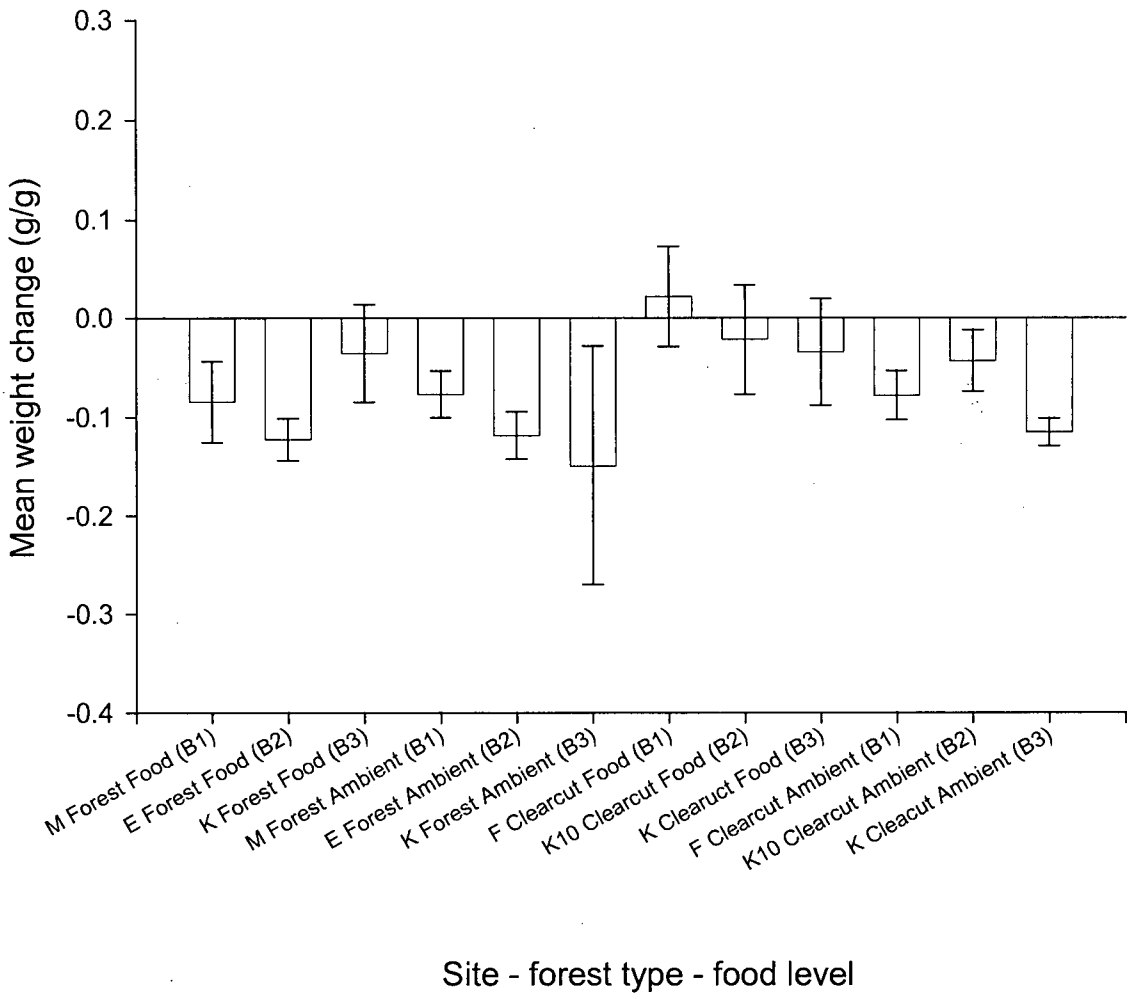
b)

Figure 11b. Proportion of juveniles recaptured in each enclosure pair at the end of the experiment in each site (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



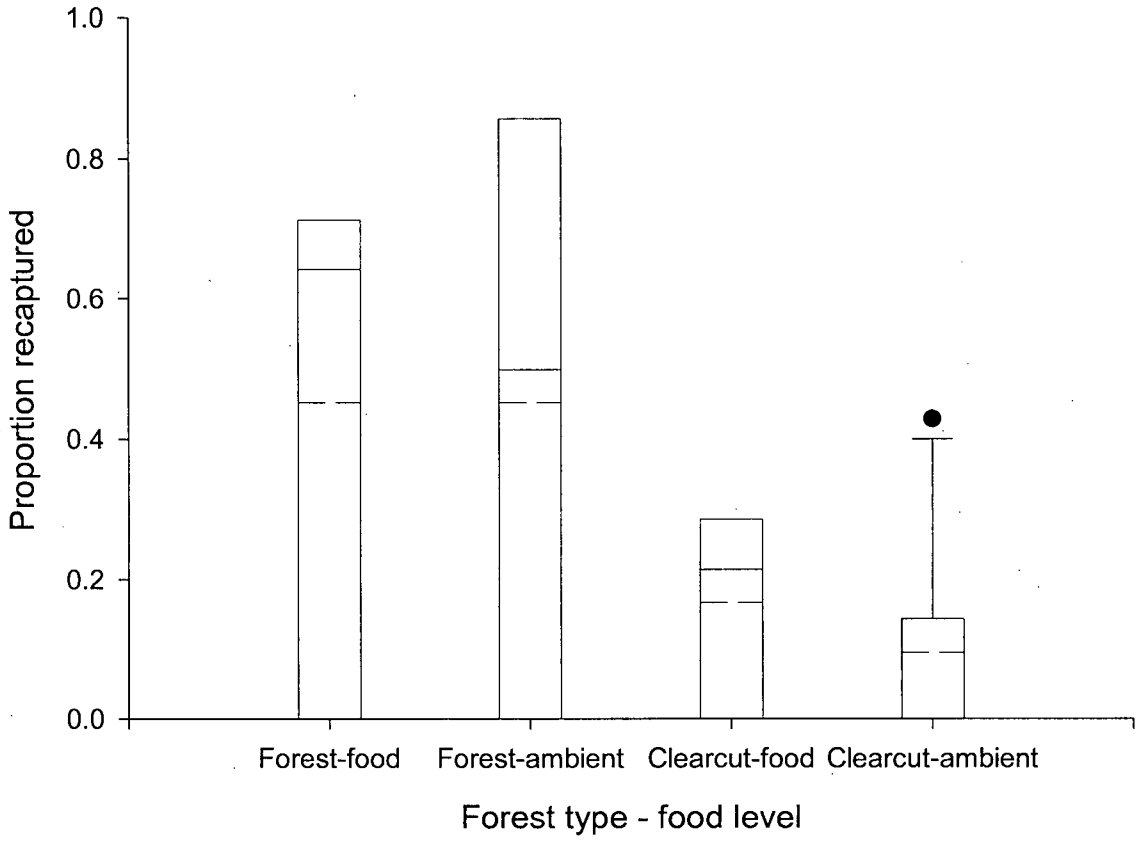
a)

Figure 12a. Weight change of juveniles over the entire experiment in each forest type and food treatment. Figure conventions follow those used in Figure 9a.



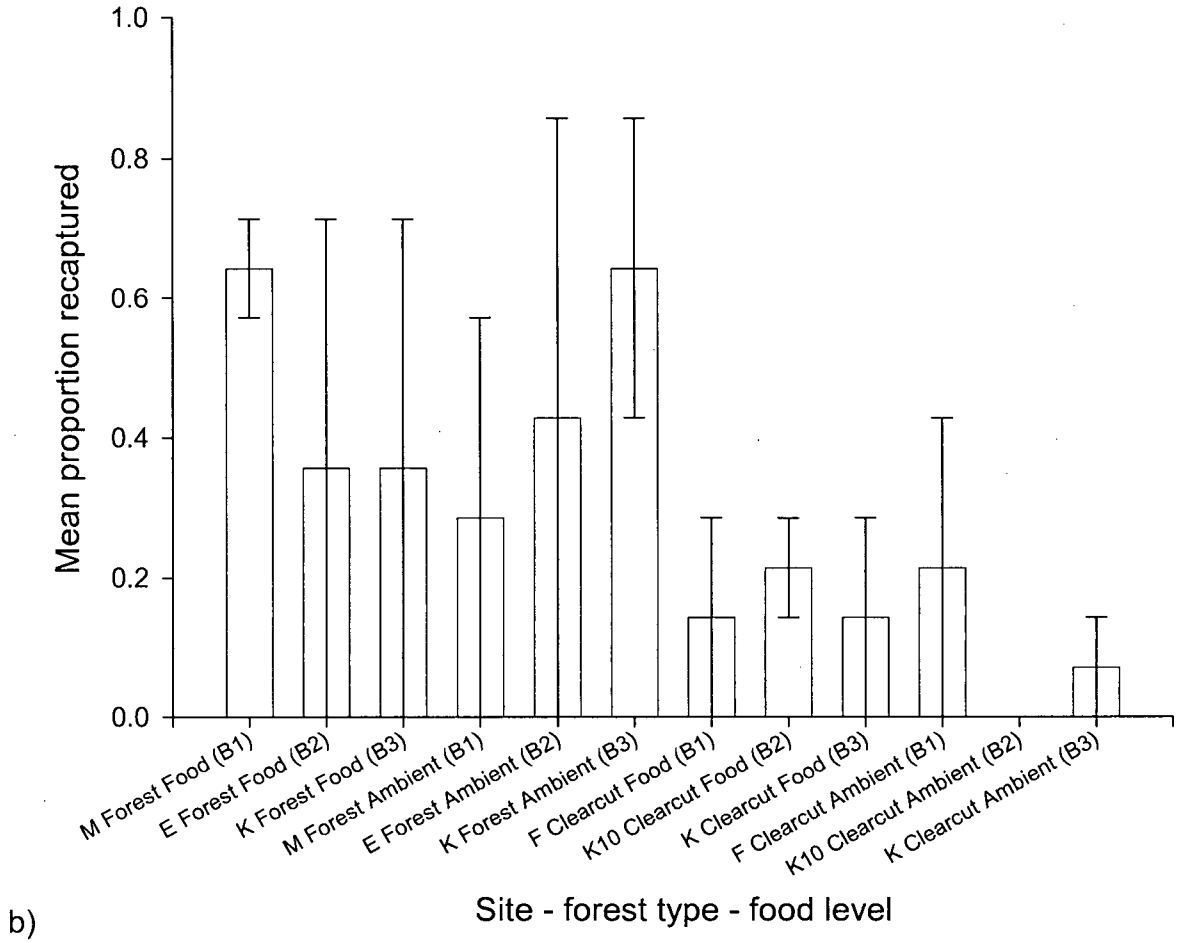
b)

Figure 12b. Weight change of juveniles over the entire experiment in each food treatment at each site (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



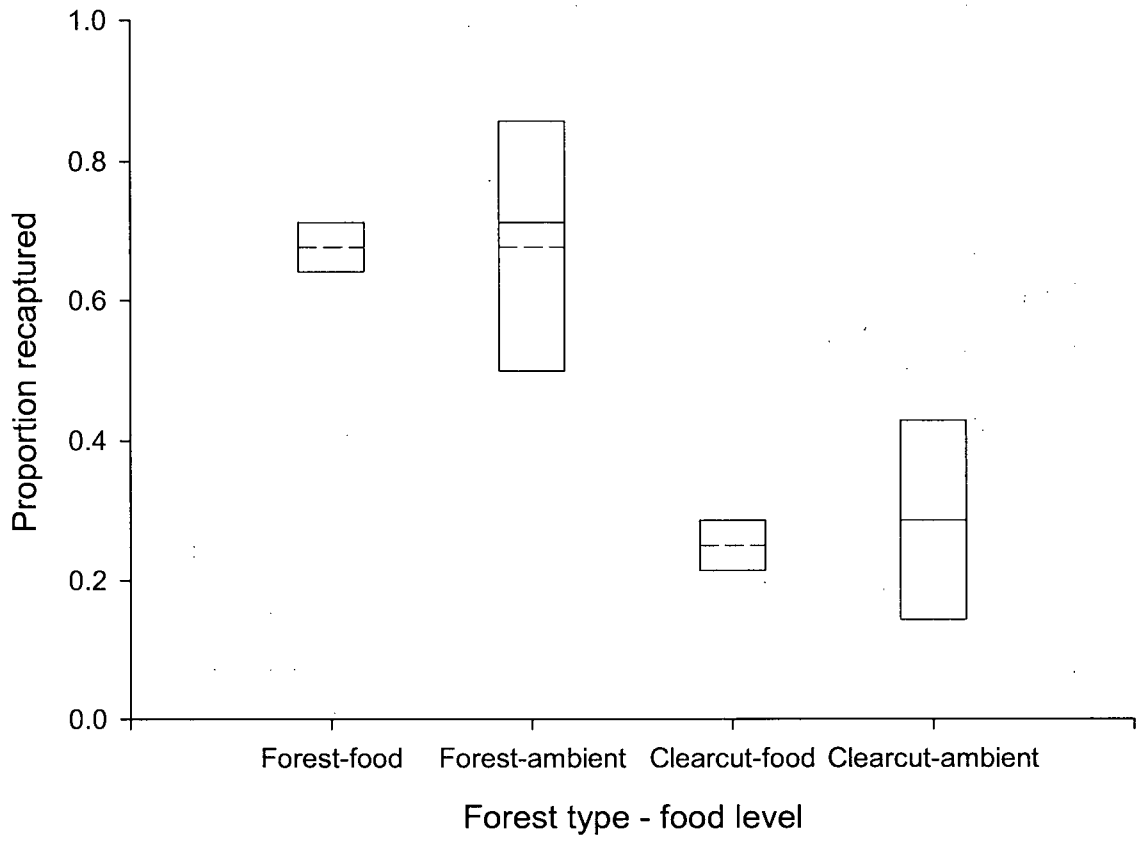
a)

Figure 13a. Proportion of adults recaptured in the correct enclosure at the end of the experiment in each forest type and food treatment. Enclosures with zero recaptures throughout experiment are **included**. Figure conventions follow those used in Figure 9a.



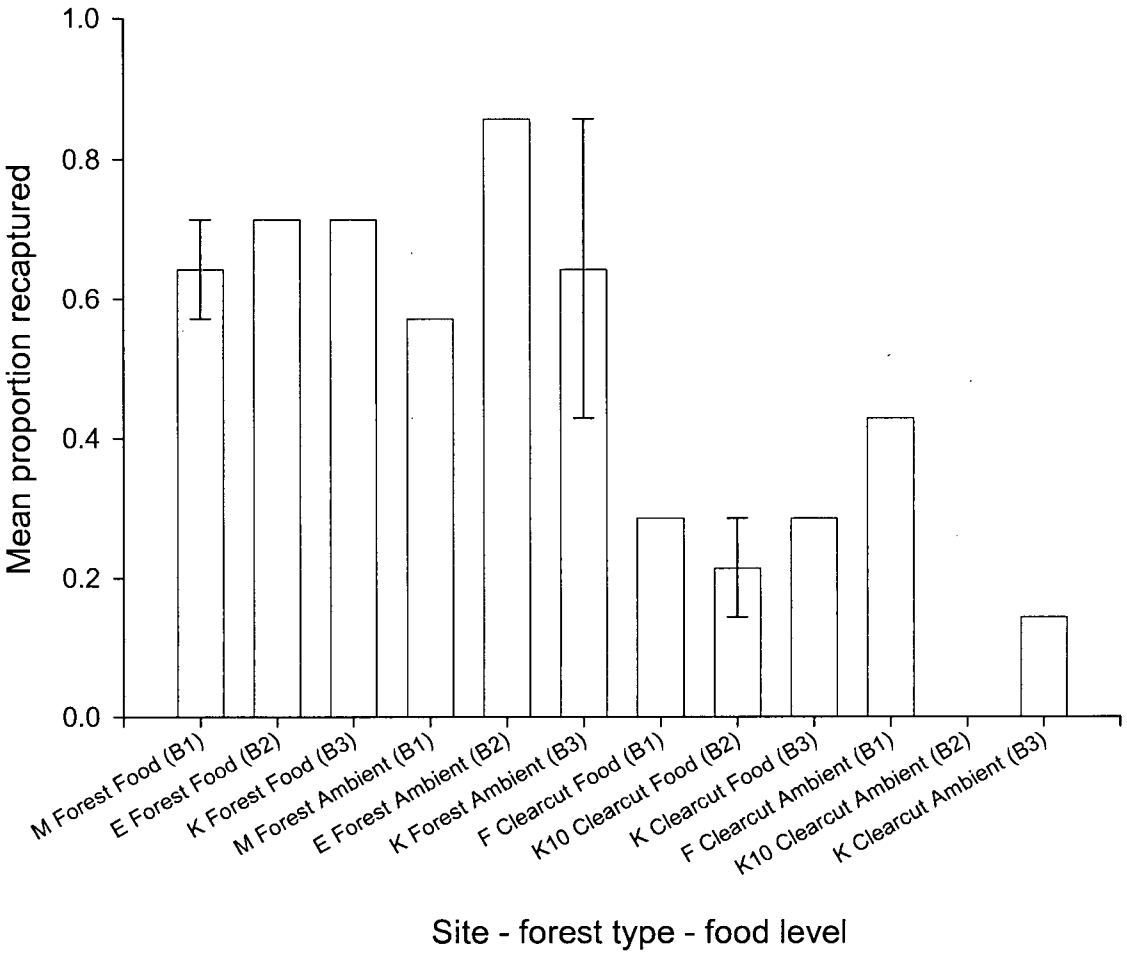
b)

Figure 13b. Proportion of adults recaptured in the correct enclosure at the end of the experiment in each food treatment at each site (including standard error bars on the mean). Enclosures with zero recaptures throughout experiment are **included**. Figure conventions follow those used in Figure 9b.



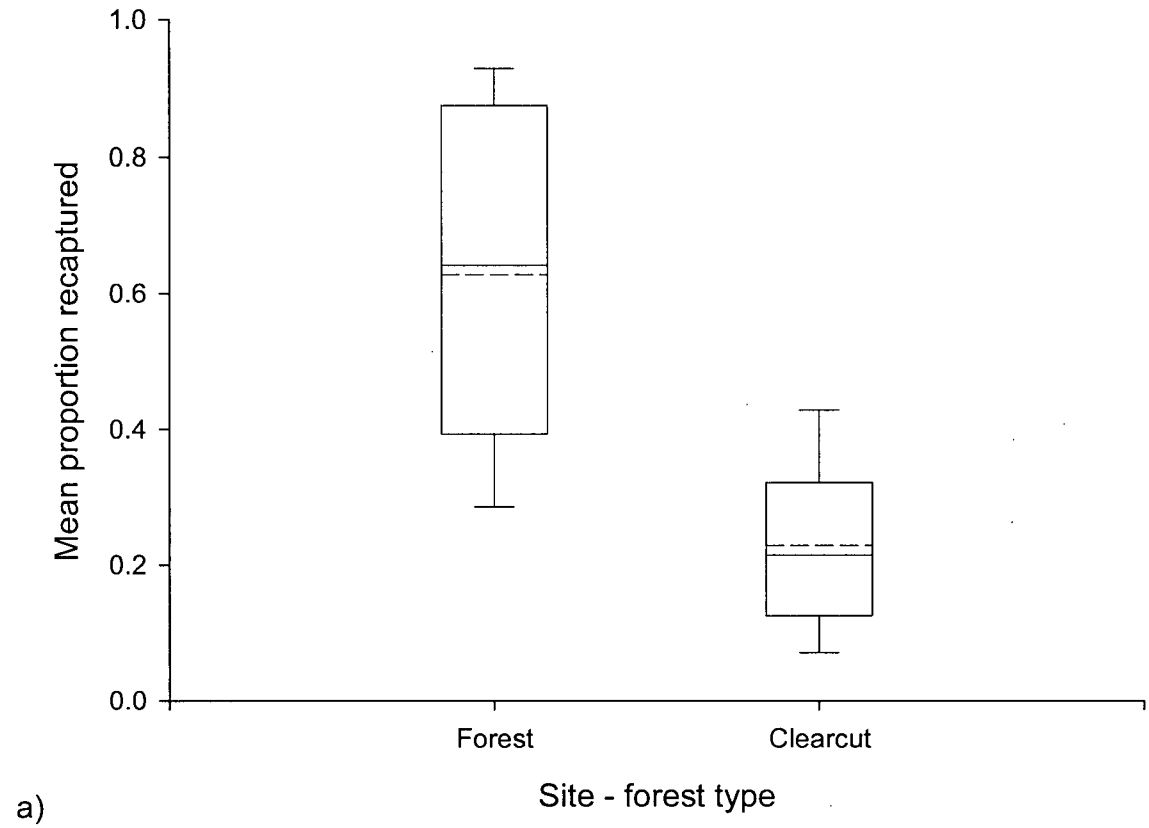
a)

Figure 14a. Proportion of adults recaptured in the correct enclosure at the end of the experiment in each forest type and food treatment. Enclosures with zero recaptures throughout experiment are **omitted**. Figure conventions follow those used in Figure 9a.



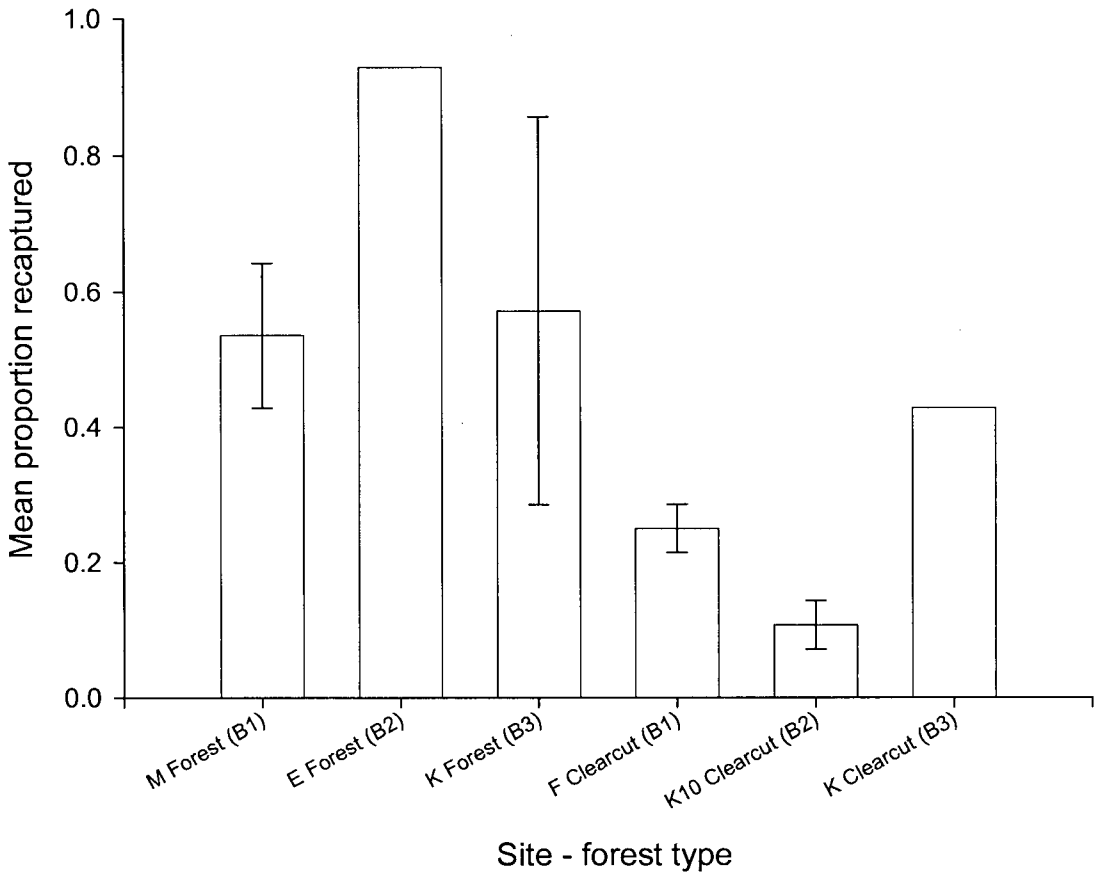
b)

Figure 14b. Proportion of adults recaptured in the correct enclosure at the end of the experiment in each food treatment at each site (including standard error bars on the mean). Enclosures with zero recaptures throughout experiment are **omitted**. Figure conventions follow those used in Figure 9b.



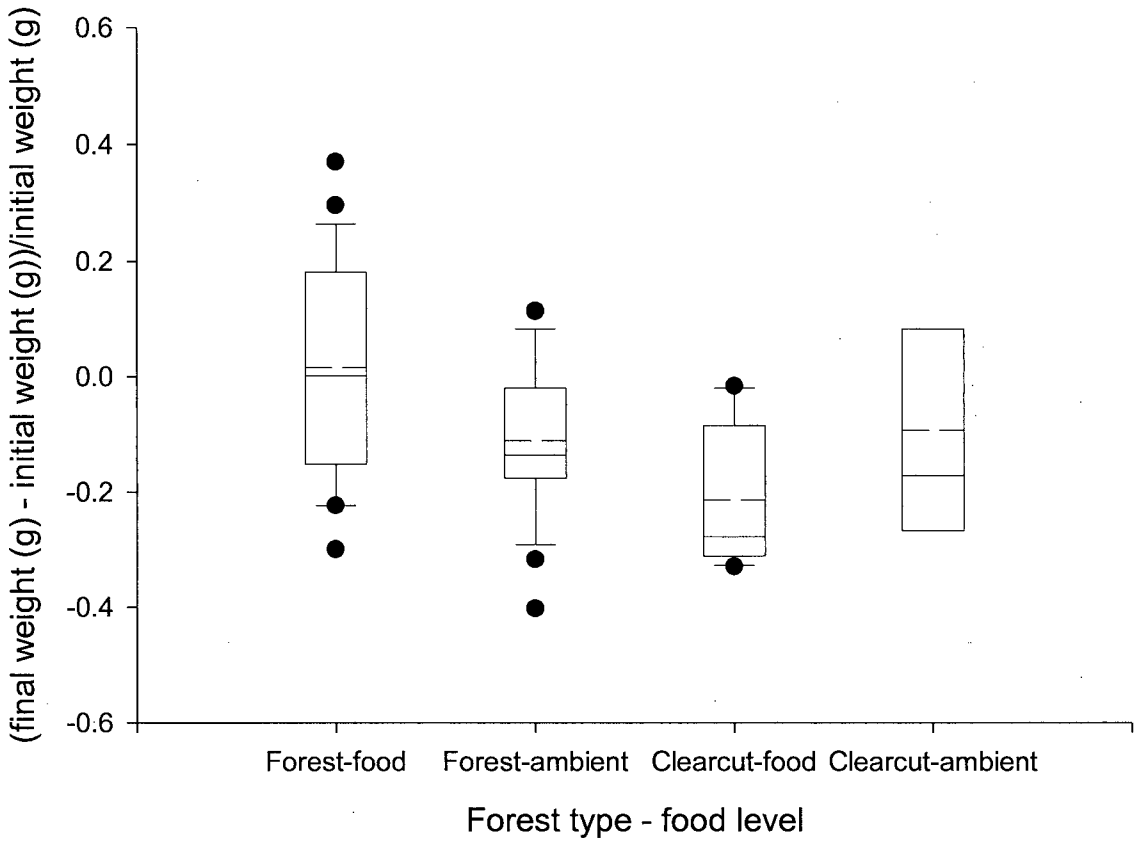
a)

Figure 15a. Proportion of adults recaptured in each enclosure pair at the end of the experiment in each forest type. Figure conventions follow those used in Figure 9a.



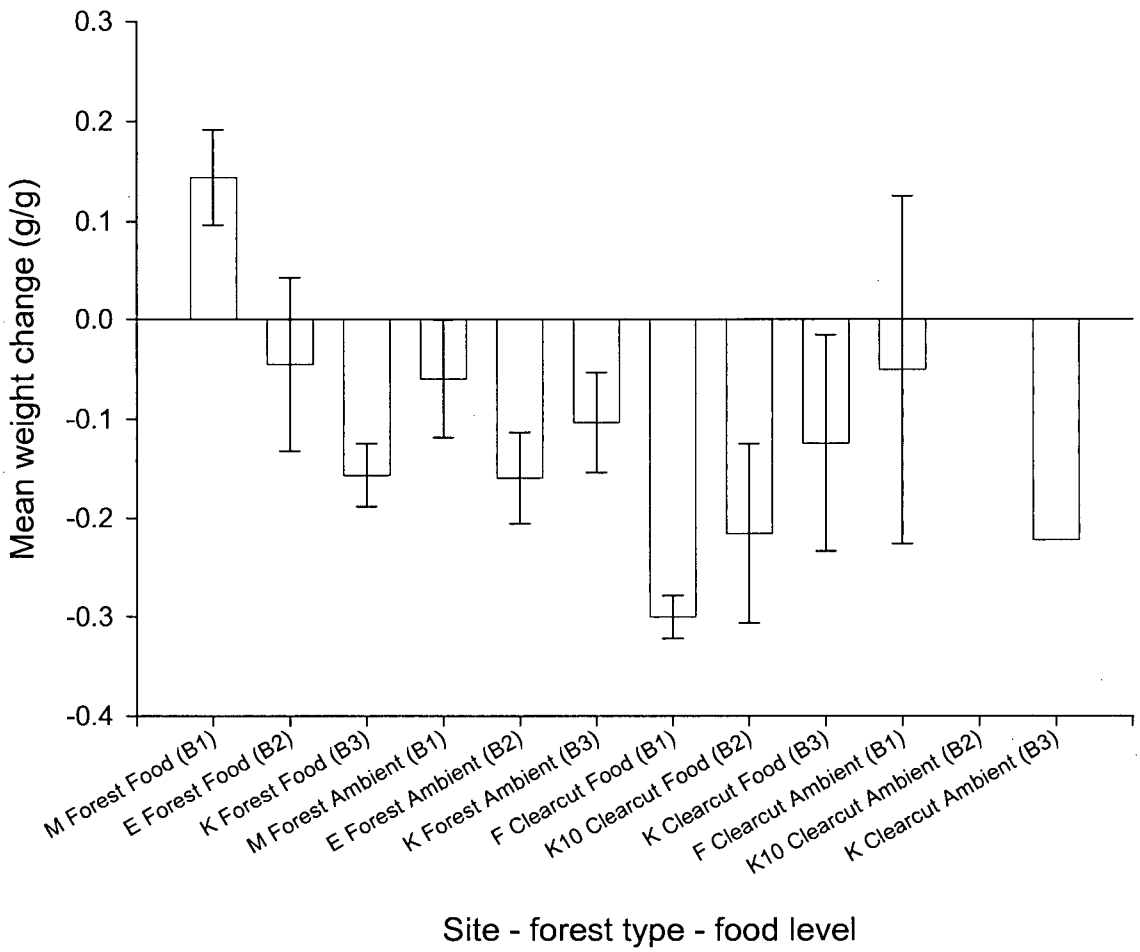
b)

Figure 15b. Proportion of adults recaptured in each enclosure pair at the end of the experiment in each site (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



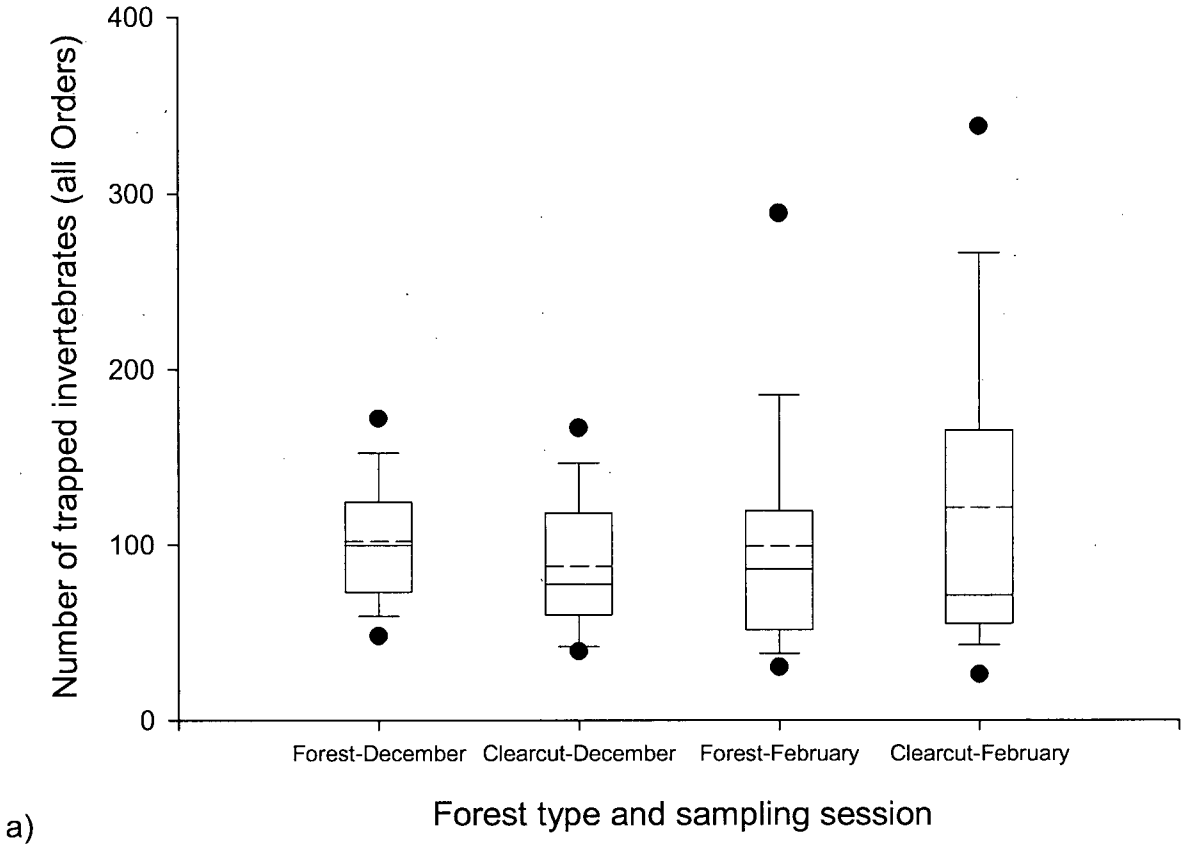
a)

Figure 16a. Weight change of adults over the entire experiment in each forest type and food treatment. Figure conventions follow those used in Figure 9a.



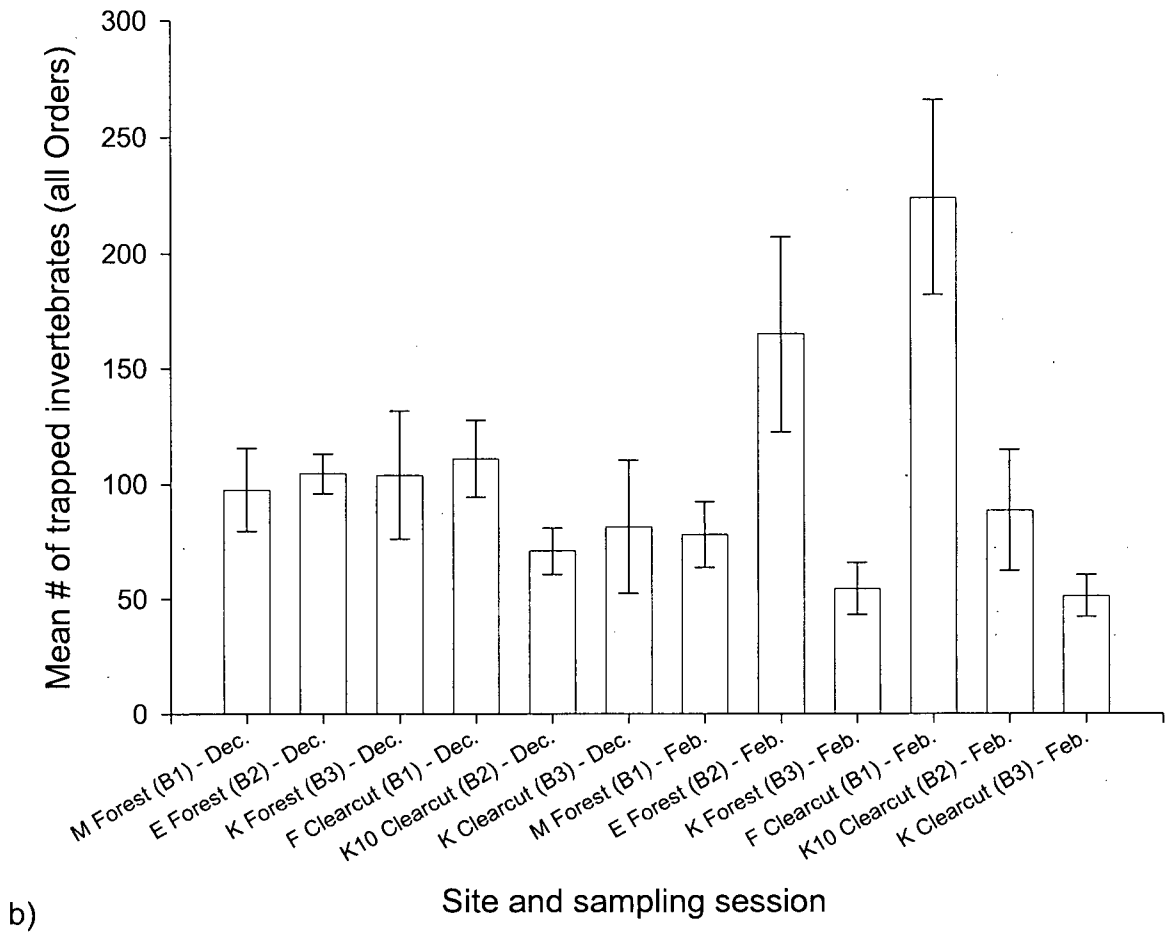
b)

Figure 16b. Weight change of adults over the entire experiment in each food treatment at each site (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



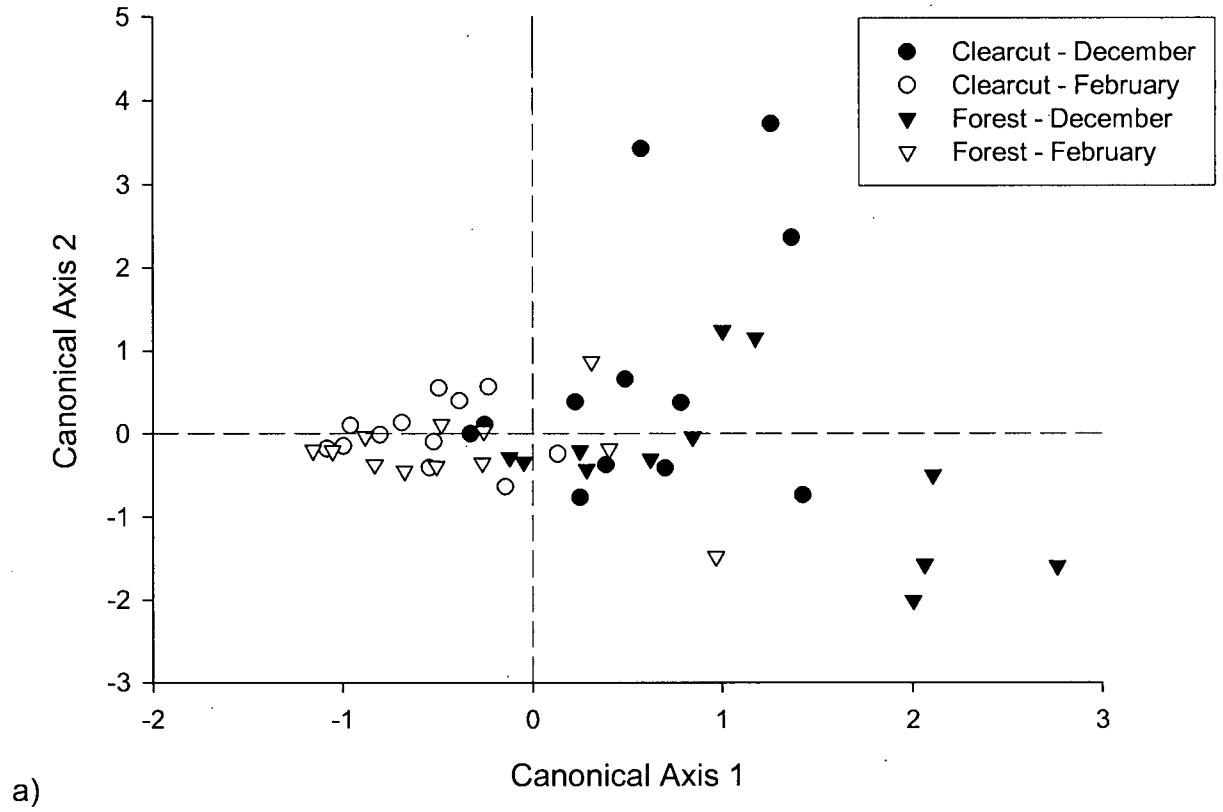
a)

Figure 17a. Invertebrate sampling during the juvenile experiment: number of invertebrates trapped from all Orders in each forest type treatment during each sampling session. Figure conventions follow those used in Figure 9a.



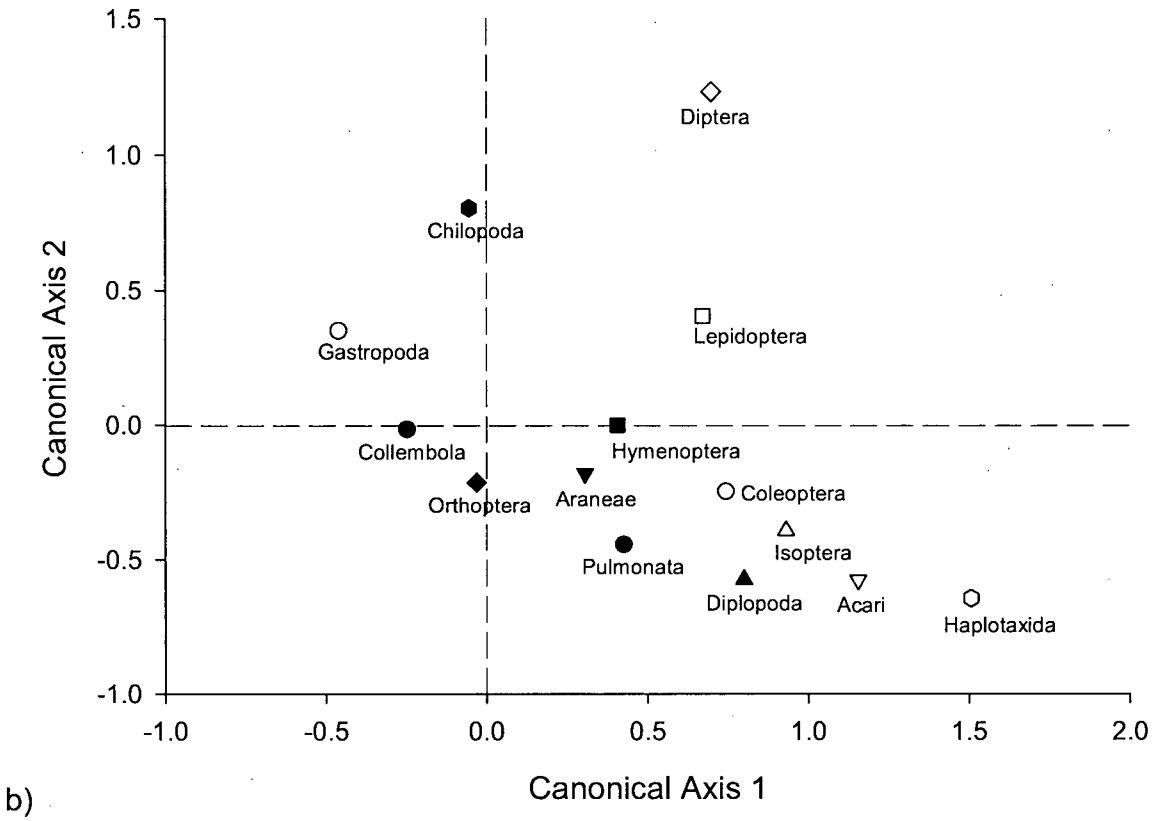
b)

Figure 17b. Invertebrate sampling during the juvenile experiment: mean number of invertebrates trapped (all Orders) in each site during each sampling session (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



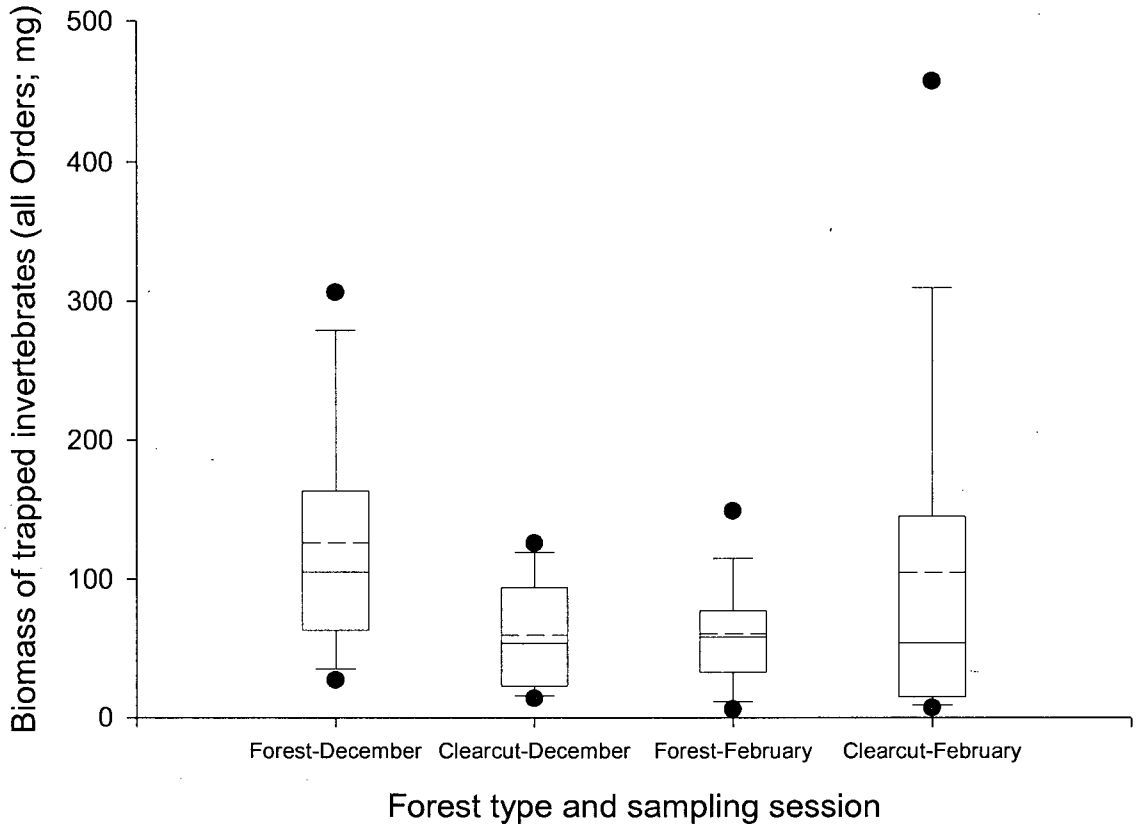
a)

Figure 18a. Correspondence analysis of number of invertebrates captured during the juvenile experiment, with data separated by forest treatment and sample date.



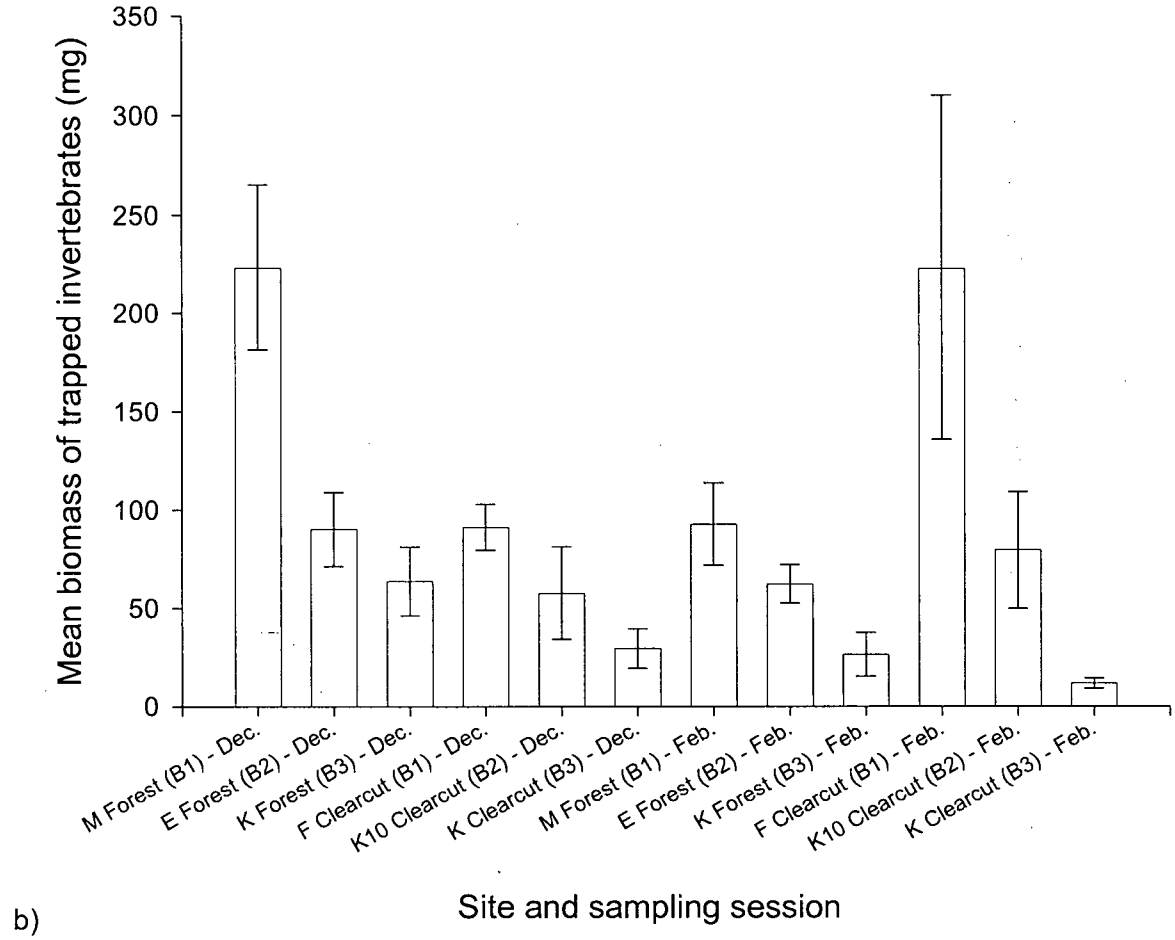
b)

Figure 18b. Correspondence analysis of number of invertebrates captured during the juvenile experiment, with data separated by each invertebrate Order.



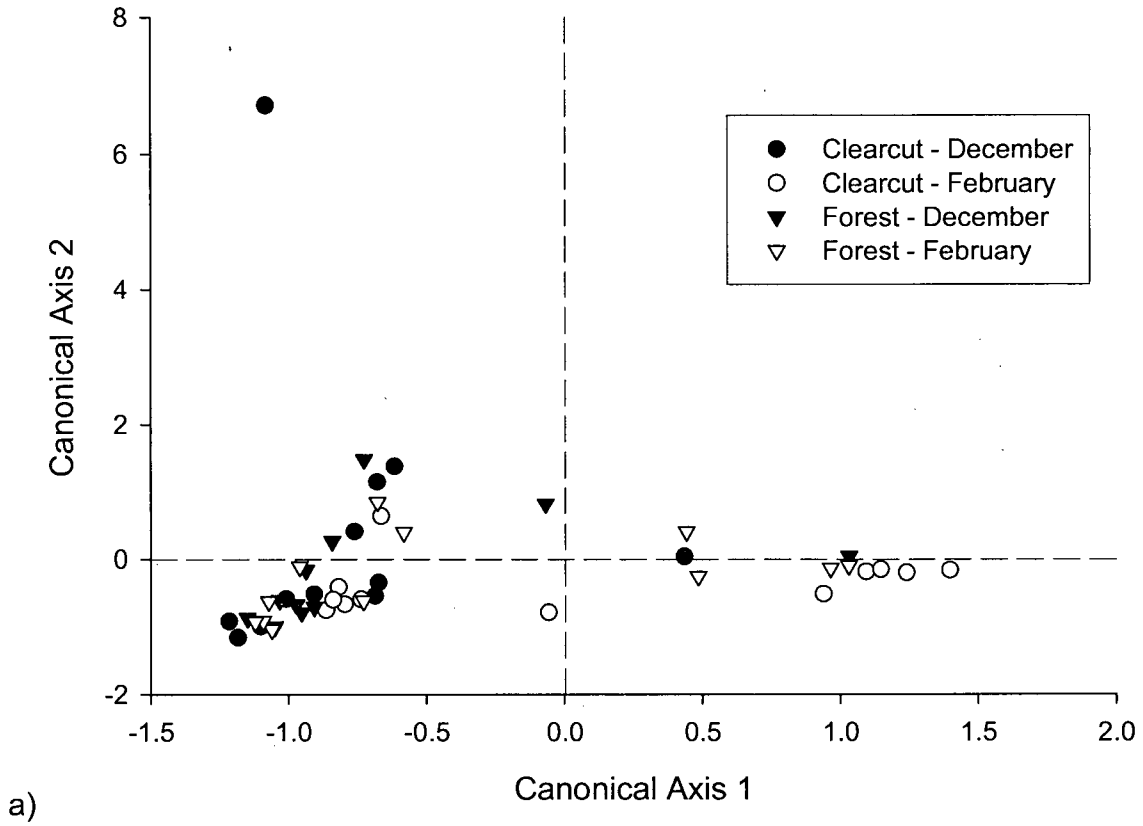
a)

Figure 19a. Invertebrate sampling during the juvenile experiment: biomass (mg) of invertebrates trapped from all Orders in each forest type treatment during each sampling session. Figure conventions follow those used in Figure 9a.



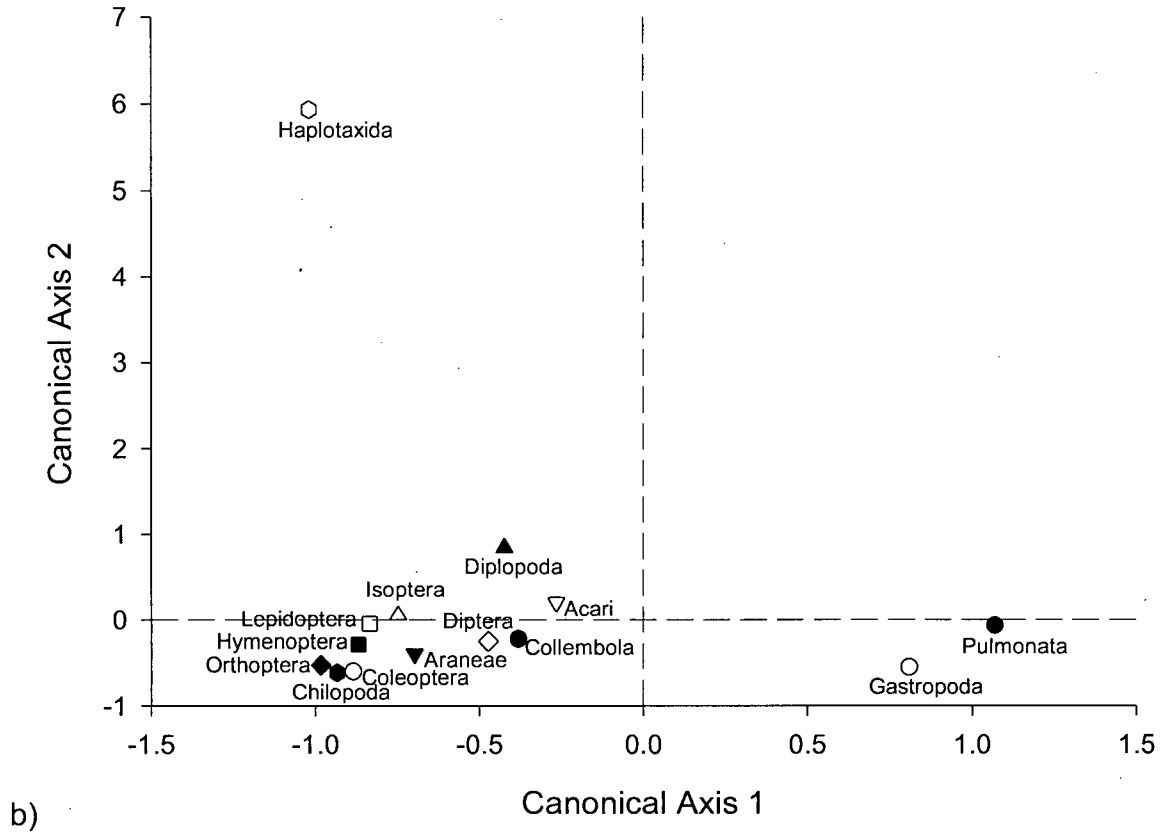
b)

Figure 19b. Invertebrate sampling during the juvenile experiment: mean biomass of invertebrates trapped (all Orders) in each site during each sampling session (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



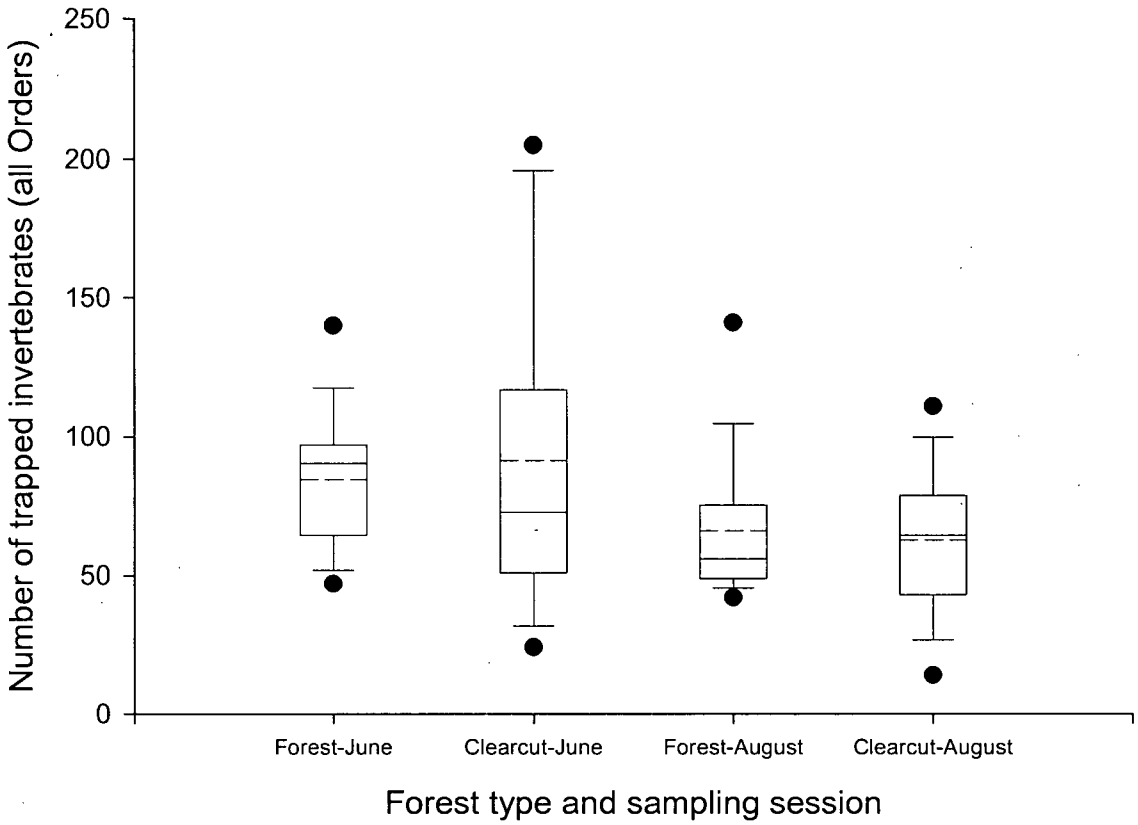
a)

Figure 20a. Correspondence analysis of biomass of invertebrates captured during the juvenile experiment, with data separated by forest treatment and sample date.



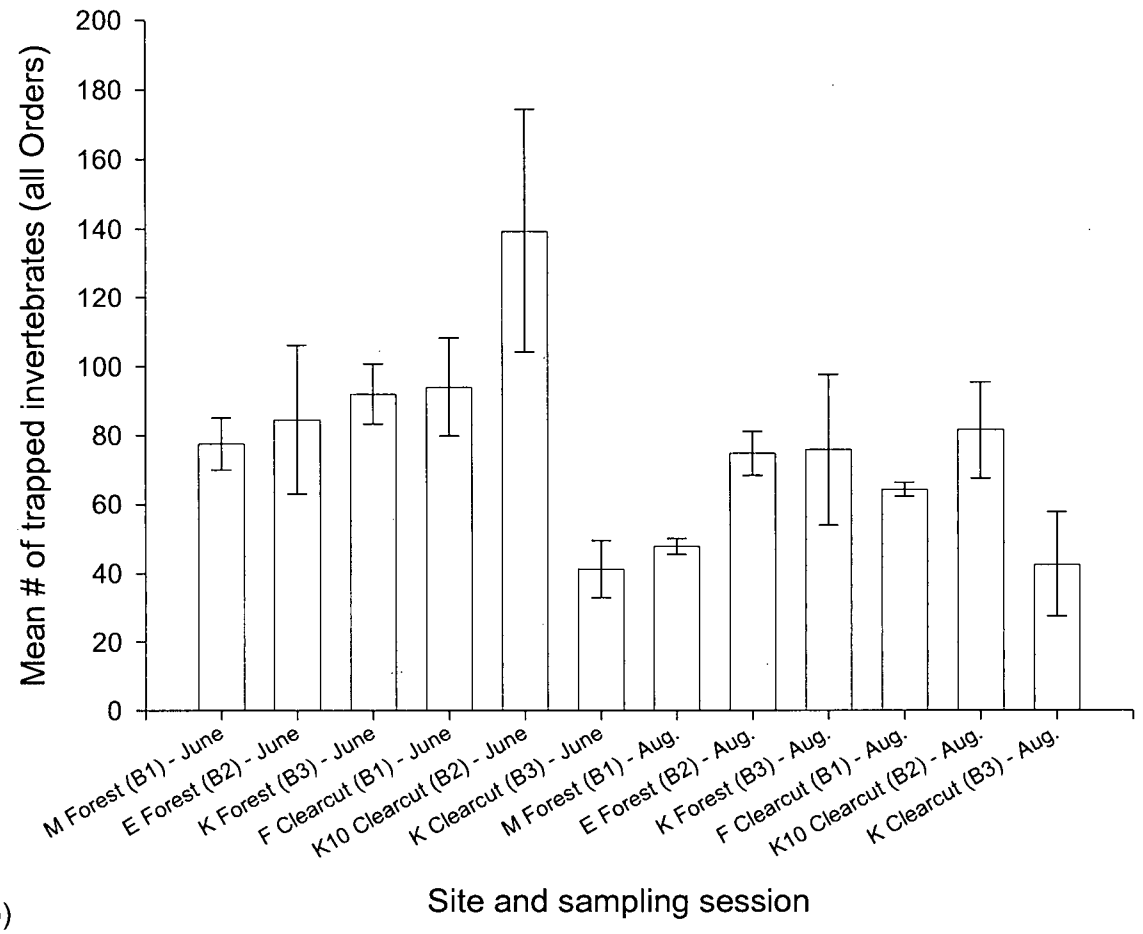
b)

Figure 20b. Correspondence analysis of biomass of invertebrates captured during the juvenile experiment, with data separated by each invertebrate Order.



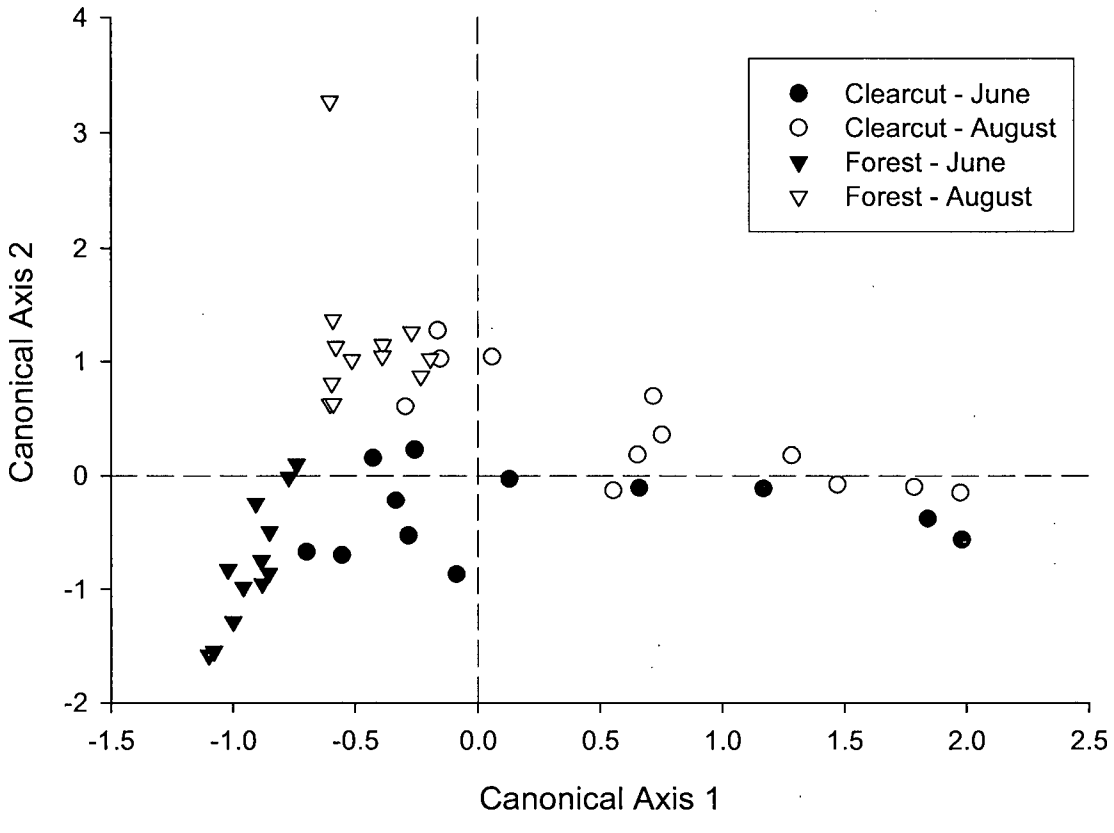
a)

Figure 21a. Invertebrate sampling during the adult experiment: number of invertebrates trapped from all Orders in each forest type treatment during each sampling session. Figure conventions follow those used in Figure 9a.



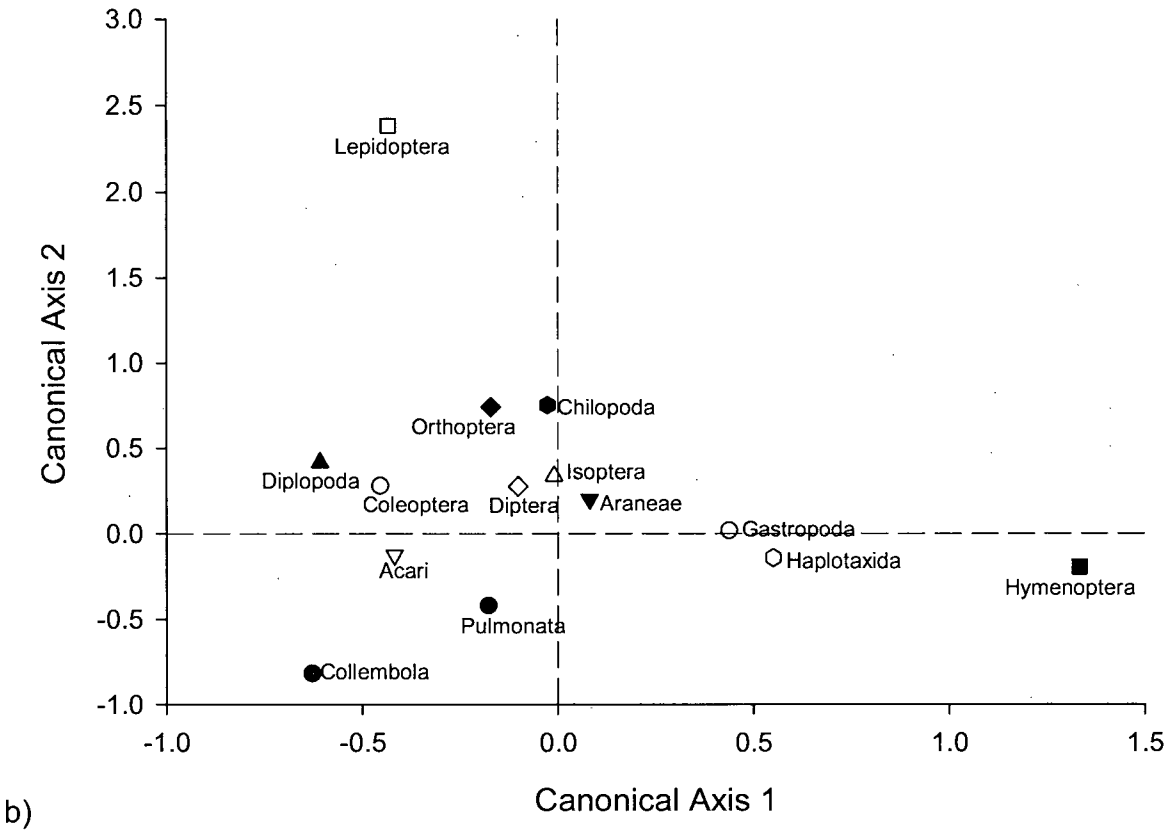
b)

Figure 21b. Invertebrate sampling during the adult experiment: mean number of invertebrates trapped (all Orders) in each site during each sampling session (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



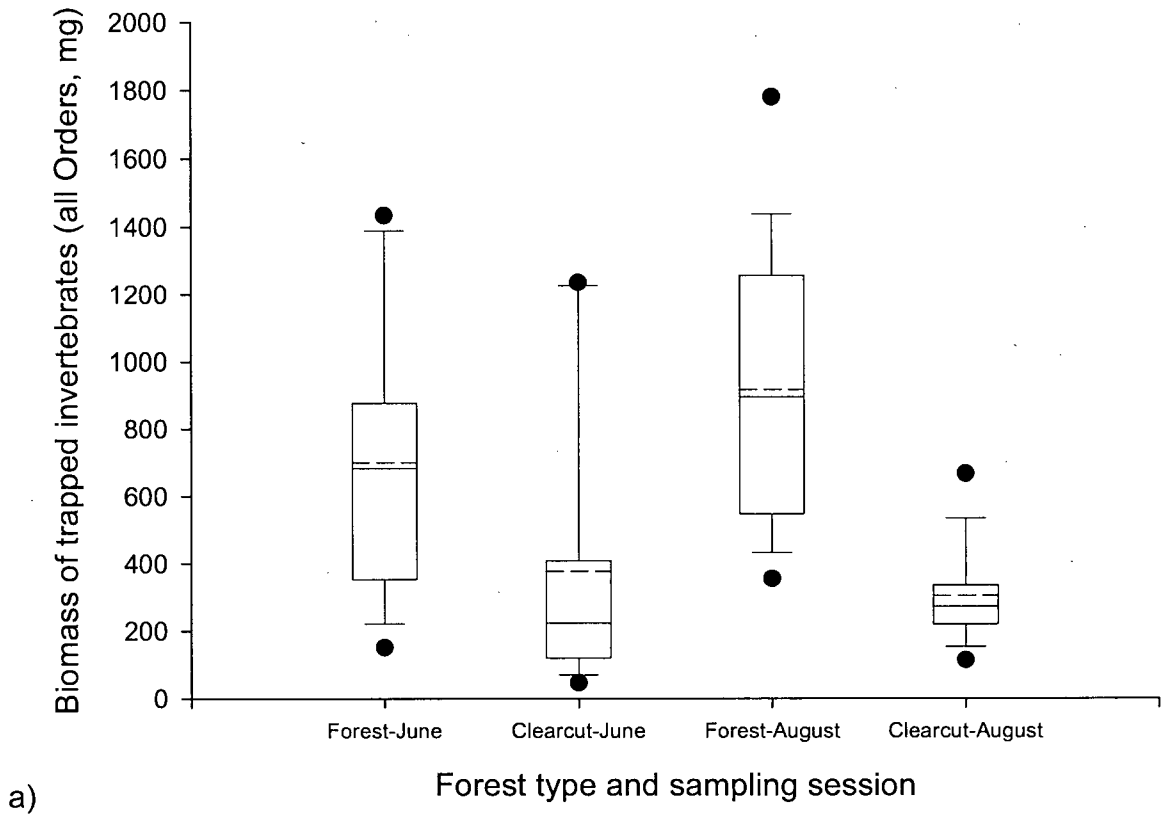
a)

Figure 22a. Correspondence analysis of number of invertebrates captured during the adult experiment, with data separated by forest treatment and sample date.



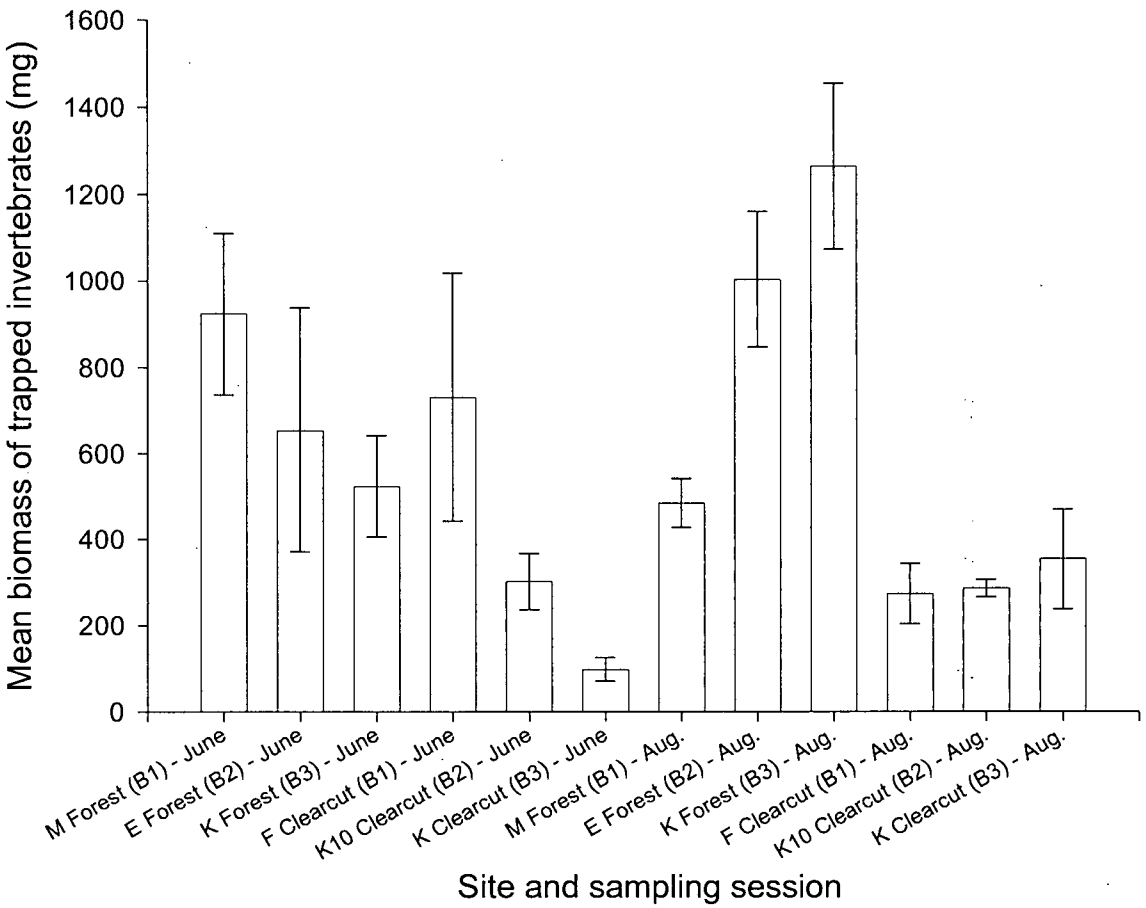
b)

Figure 22b. Correspondence analysis of number of invertebrates captured during the adult experiment, with data separated by each invertebrate Order.



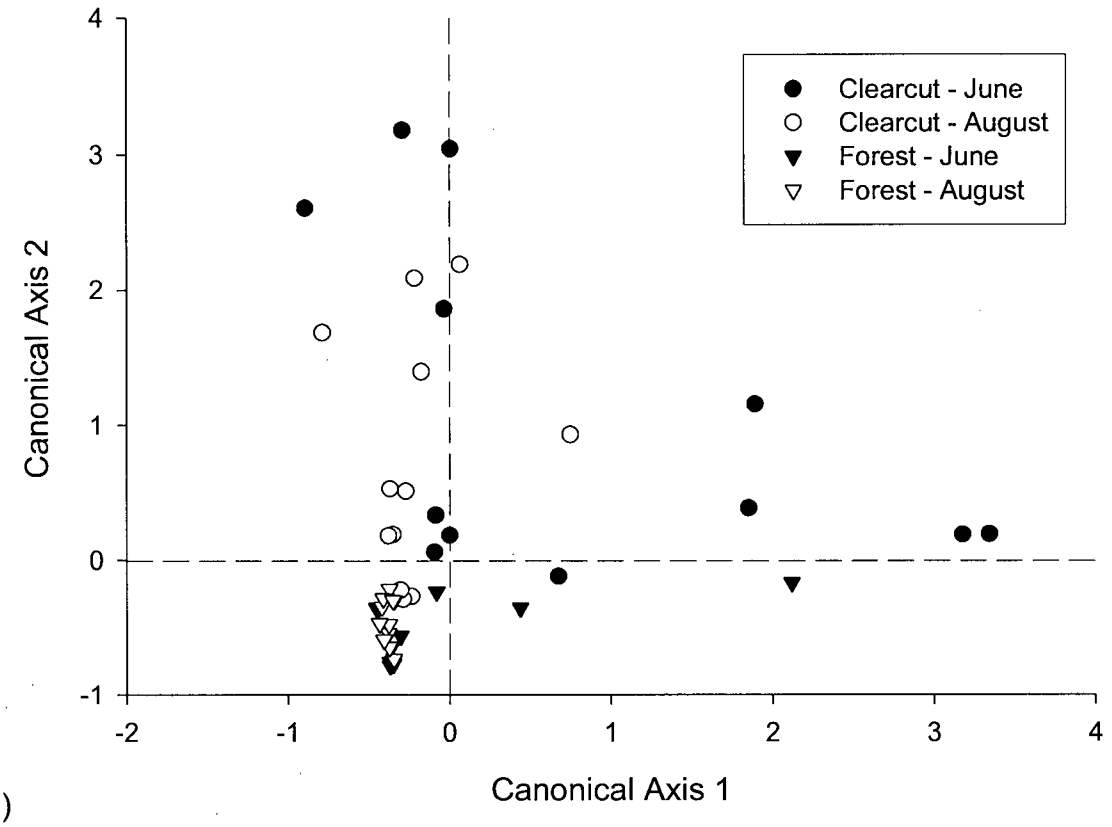
a)

Figure 23a. Invertebrate sampling during the adult experiment: biomass (mg) of invertebrates trapped from all Orders in each forest type treatment during each sampling session. Figure conventions follow those used in Figure 9a.



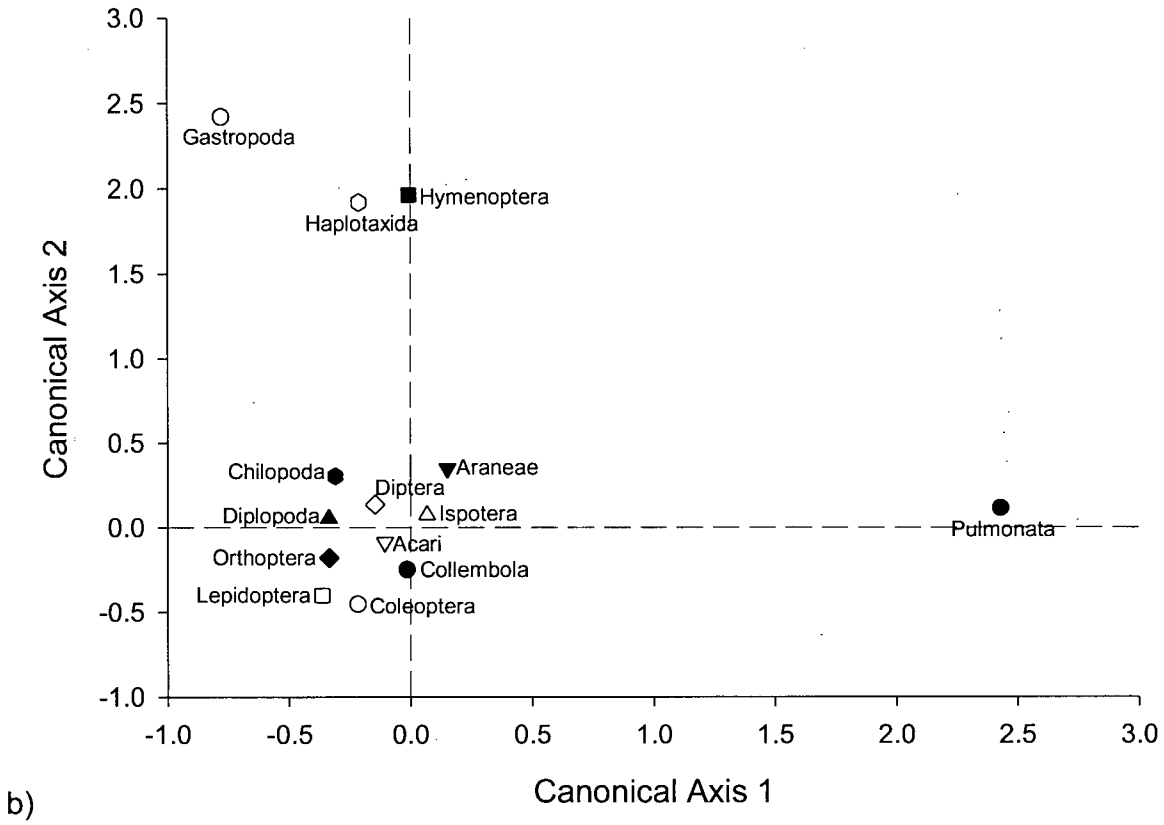
b)

Figure 23b. Invertebrate sampling during the adult experiment: mean biomass of invertebrates trapped (all Orders) in each site during each sampling session (including standard error bars on the mean). Figure conventions follow those used in Figure 9b.



a)

Figure 24a. Correspondence analysis of biomass of invertebrates captured during the adult experiment, with data separated by forest treatment and sample date.



b)

Figure 24b. Correspondence analysis of biomass of invertebrates captured during the adult experiment, with data separated by each invertebrate Order.

LITERATURE CITED

Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology **11**:983-989.

Ash, A. N., and R. C. Bruce. 1994. Impacts of timber harvesting on salamanders. Conservation Biology **8**:300-301.

Aubry, K. B. 2000. Amphibians in managed, second-growth Douglas-fir forests. Journal of Wildlife Management **64**:1041-1052.

Ballenger, L. 2000. Blarina brevicauda *in* University of Michigan Museum of Zoology Animal Diversity Web (On-line). Accessed February 23, 2006. http://animaldiversity.ummz.umich.edu/site/accounts/information/Blarina_brevicauda.html.

Beebee, T. J. C. 1996. Ecology and conservation of amphibians. Chapman & Hall, New York.

Bellocq, M. I., K. Kloosterman, and S. M. Smith. 2000. The diet of coexisting species of amphibians in Canadian jack pine forests. Herpetological Journal **10**:63-68.

Biek, R., L. S. Mills, and R. B. Bury. 2002. Terrestrial and stream amphibians across clearcut-forest interfaces in the Siskiyou Mountains, Oregon. Northwest Science **76**:129-140.

Bille, T. 2000. Microhabitat utilization of the Mexican salamander, *Pseudoeurycea leprosa*. Journal of Herpetology **34**:588-590.

Bird, G. A., and L. Chatarpaul. 1986. Effect of whole tree and conventional forest harvest on soil microarthropods. Canadian Journal of Zoology **64**:1986-1993.

Blaustein, A. R. 1994. Chicken little or Nero's fiddle? A perspective on declining amphibian populations. Herpetologica **50**:85-97.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology **8**:60-71.

Bull, E. L., and B. E. Carter. 1996. Tailed frogs: distribution, ecology, and association with timber harvest in northeastern Oregon. Res. Pap. PNW-RP-497. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Bury, R. B. 1983. Differences in amphibian populations in logged and old growth redwood forest. Northwest Science **57**:167-178.

Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. Pages 11-22 *in* K. Szaro, E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. USDA Forest Service General Technical Report RM-166.

Chazal, A. C., and P. H. Niewiarowski. 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. Ecological Applications **8**:1133-1143.

Chen, J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology **63**:219-237.

Cole, E. C., W. C. McComb, M. Newton, C. L. Chambers, and P. Leeming. 1997. Response of amphibians to clearcutting, burning, and glyphosate application in the Oregon Coast Range. Journal of Wildlife Management **61**:656-664.

Corkran, C. C., and C. Thoms. 1996. Amphibians of Oregon, Washington and British Columbia. Lone Pine Publishing.

Cromer, R. B., J. D. Lanham, and H. H. Hanlin. 2002. Herpetofaunal response to gap and skidder-rut wetland creation in a southern bottomland hardwood forest. Forest Science **48**:407-413.

Currens, C. R., P. H. Niewiarowski, and H. H. Whiteman. 2002. Effects of temperature and time of day on the resting metabolic rates of paedomorphic mole salamanders, *Ambystoma talpoideum*. Copeia **2002**:489-495.

Davis, T. M. 1998. Terrestrial salamander abundance in successional forests of coastal British Columbia. Northwest Science **72**:89-90.

deMaynadier, P. G., and M. L. J. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews **3**:230-261.

deMaynadier, P. G., and M. L. J. Hunter. 1998. Effects of silvicultural edges onthe distrbution and abundance of amphibians in Maine. Conservation Biology **12**:340-352.

Duellman, W. E., and L. Trueb. 1994. Biology of amphibians. Johns Hopkins University Press, Baltimore.

Dupuis, L., J. N. M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology **9**:645-653.

Dupuis, L., and D. Steventon. 1999. Riparian management and the tailed frog in northern coastal forests. Forest Ecology and Management **124**:35-43.

Dyrness, C. T. 1965. Soil surface condition following tractor and high-lead logging in the Oregon Cascades. Journal of Forestry **63**:272-275.

Faccio, S. D. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. Journal of Herpetology **37**:479-489.

Geiger, R. 1971. The climate near the ground. Harvard University Press, Cambridge, Massachusetts.

Gibbons, J. W. 1988. The management of amphibians, reptiles, and small mammals in North America: the need for an environmental attitude adjustment. Pages 4-10 *in* K. Szaro, E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. USDA Forest Service General Technical Report RM-166.

Gregory, P. T. 1984. Habitat, diet, and composition of assemblages of garter snakes (*Thamnophis*) at eight sites on Vancouver Island. Canadian Journal of Zoology **62**:2013-2022.

Gregory, P. T., and R. W. Campbell. 1984. The reptiles of British Columbia. Royal British Columbia Provincial Museum, Victoria, British Columbia.

Grialou, J. A., S. D. West, and R. N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. Journal of Wildlife Management **64**:105-113.

Grover, M. C., and H. M. Wilbur. 2002. Ecology of ecotones: Interactions between salamanders on a complex environmental gradient. Ecology **83**:2112-2123.

Harpole, D. N., and C. A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management **114**:349-356.

Heatwole, H., and K. Lim. 1961. Relation of substrate moisture to absorption and loss of water by the salamander, *Plethodon cinereus*. Ecology **42**:814-819.

Heliola, J., M. Koivula, and J. Niemela. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology **15**:370-377.

Jaeger, R. G. 1971. Moisture as a factor influencing the distributions of two species of terrestrial salamanders. Oecologia (Berlin) **6**:191-207.

Jaeger, R. G. 1980a. Fluctuations in prey availability and food limitation for a terrestrial salamander. Oecologia (Berlin) **44**:335-341.

Jaeger, R. G. 1980b. Microhabitats of a terrestrial forest salamander. Copeia **1980**:265-268.

Johnston, B. 1998. Terrestrial pacific giant salamanders (*Dicamptodon tenebrosus* Good) - natural history and their response to forest practices. Master's Thesis. University of British Columbia, Vancouver.

Johnston, B., and L. Frid. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). Canadian Journal of Zoology **80**:2170-2177.

Kenward, M. G., and J. H. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics **53**:983-997.

Knapp, S. M., C. A. Haas, D. N. Harpole, and R. L. Kirkpatrick. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conservation Biology **17**:752-762.

Macartney, J. M., and P. T. Gregory. 1981. Differential susceptibility of sympatric garter snake species to amphibian skin secretions. American Midland Naturalist **106**:271-281.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology **31**:542-551.

Madison, D. M., and L. Farrand III. 1998. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. Copeia **1998**:402-410.

Matsuda, B. M., and J. S. Richardson. 2005. Movement patterns and relative abundance of coastal tailed frogs in clearcuts and mature forest stands. Canadian Journal of Forest Research **35**:1131-1138.

Maxcy, K. A. 2000. The response of terrestrial salamanders to forest harvesting in southwestern British Columbia. Master's Thesis. University of British Columbia, Vancouver.

Mazerolle, M. J., and A. Desrochers. 2005. Landscape resistance to frog movements. Canadian Journal of Zoology **83**:455-464.

Merchant, H. C. 1970. Estimated energy budget of the red-backed salamander, *Plethodon cinereus*. Ph.D. Dissertation. Rutgers University, New Jersey.

Naughton, G. P., C. B. Henderson, K. R. Foresman, and R. L. McGraw II. 2000. Long-toed salamanders in harvested and intact Douglas-fir forests of western Montana. Ecological Applications **10**:1681-1689.

Niemela, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera:Carabidae) in western Canada. Conservation Biology **7**:551-561.

Nussbaum, R. A., E. D. Brodie Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University Press of Idaho, Moscow.

Pearson, P. G. 1955. Population ecology of the spadefoot toad, *Scaphiopus h. holbrooki* (Harlan). Ecological Monographs **25**:233-267.

Pechmann, J. H. K. 1995. Use of large field enclosures to study the terrestrial ecology of pond-breeding amphibians. Herpetologica **51**:434-450.

Petranka, J. W. 1994. Response to impact of timber harvesting on salamanders. Conservation Biology **8**:302-304.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management **67**:135-147.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology **7**:363-370.

Pough, F. H. 1980. The advantages of ectothermy for tetrapods. The American Naturalist **115**:92-112.

Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management **20**:1-9.

Regosin, J. V., B. S. Windmiller, and J. M. Reed. 2003. Influence of abundance of small-mammal burrows and conspecifics on the density and distribution of spotted salamanders (*Ambystoma maculatum*) in terrestrial habitats. Canadian Journal of Zoology **81**:596-605.

Richardson, J. S., R. J. Naiman, F. J. Swanson, and D. E. Hibbs. 2005. Riparian communities associated with Pacific Northwest headwater streams: assemblages, processes, and uniqueness. Journal of the American Water Resources Association **41**:935-947.

Richardson, J. S., and W. E. Neill. 1998. Headwater amphibians and forestry in British Columbia: Pacific giant salamanders and tailed frogs. Northwest Science **72**:122-123.

Rohr, J. R., A. A. Elskus, B. S. Shepherd, P. H. Crowley, T. M. McCarthy, J. H. Niedzwiecki, T. Sager, A. Sih, and B. D. Palmer. 2004. Multiple stressors and salamanders: effects of an herbicide, food limitation, and hydroperiod. Ecological Applications **14**:1028-1040.

Rothermel, B. B. 2004. Migratory success of juveniles: a potential contraint on connectivity for pond-breeding amphibians. Ecological Applications **14**:1535-1546.

Rothermel, B. B., and R. D. Semlitsch. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology **16**:1324-1332.

Schabenberger, O., and F. J. Pierce. 2002. Contemporary Statistical Models for the Plant and Soil Sciences. CRC Press, Boca Raton, FL.

Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology **59**:315-322.

Semlitsch, R. D. 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Canadian Journal of Zoology **61**:616-620.

Semlitsch, R. D. 2003. Conservation of pond-breeding amphibians. Pages 8-23 *in* R. D. Semlitsch, editor. Amphibian conservation. Smithsonian Institution, Washington.

Shure, D. J., and D. L. Phillips. 1991. Patch size of forest openings and arthropod populations. Oecologia (Berlin) **86**:325-334.

Sidle, R. C., and D. M. Drlica. 1981. Soil compaction from logging with a low-ground pressure skidder in the Oregon Coast Range. Soil Science Society of America Journal **45**:1219-1224.

Southwood, T. R. E. 1988. Tactics, strategies and templets. Oikos **52**:3-18.

Spilke, J., H. P. Piepho, and X. Hu. 2005. Analysis of unbalanced data by mixed linear models using the MIXED procedure of the SAS system. journal of Agronomy and Crop Science **191**:47-54.

Stebbins, R. C., and N. W. Cohen. 1995. A Natural History of Amphibians. Princeton University Press, Princeton, New Jersey.

Taub, F. B. 1961. The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. Ecology **42**:681-698.

Vlug, H., and J. H. Borden. 1973. Soil Acari and Collembola populations affected by logging and slash burning in a coastal British Columbia coniferous forest. Environmental Entomology **2**.

Welsh Jr., H. H., and S. Droege. 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conservation Biology **15**:558-569.

Whitaker, J. O. 1994. National Audobon Society Field Guide to North American Mammals, 10th edition. Alfred A. Knopf, Inc., New York, USA.

APPENDIX 1. Mean percent cover (± 1 S.E.) of understory vegetation, canopy cover, exposed ground and downed wood in each site.

		Block 1		Block 2		Block 3	
		M Forest	F Clearcut	E20 Forest	K10B Clearcut	K Forest	K Clearcut
Total vegetation cover		24.75 (9.39)	81.25 (4.27)	15.25 (5.92)	86.75 (4.01)	35.50 (9.14)	65.00 (3.54)
Total tree cover (understory)		2.00 (1.22)	9.00 (5.05)	0	35.00 (17.68)	1.25 (1.25)	20.00 (4.98)
Total shrub cover		14.75 (3.30)	63.75 (9.44)	0	26.25 (8.00)	6.50 (3.01)	45.00 (7.36)
Total herb cover		8.00 (4.55)	31.25 (11.97)	0	30.00 (8.42)	15.75 (10.96)	13.75 (2.40)
Total moss cover		0.50 (0.50)	1.88 (0.52)	15.25 (5.92)	1.00 (0.41)	12.75 (7.44)	0
Total exposed ground (litter/soil/rock)		49.25 (14.55)	12.00 (2.83)	78 (7.04)	12.00 (3.34)	58.75 (8.57)	14.25 (2.59)
Canopy cover		90.00 (0.00)	0	88.25 (1.18)	0	80 (3.54)	0
Downed wood cover		31.88 (4.75)	34.38 (3.75)	10.00 (5.86)	51.88 (11.62)	13.56 (1.82)	73.02 (9.54)
Common name	**Latin name**						
Amabilis fir	*Abies amabilis*	0	0	0	0	0	0.25 (0.25)
Black cottonwood	*Populus balsamifera*	0	0	0	0.50 (0.50)	0	3.75 (3.75)
Douglas-fir	*Pseudotsuga menziesii*	0	1.25 (0.48)	0	3.25 (2.36)	0	1.50 (0.29)
Paper birch	*Betula papyrifera*	0	0	0	13.75 (8.00)	0	4.00 (0.91)
Western hemlock	*Tsuga heterophylla*	2.00 (1.22)	7.50 (4.79)	0	29.00 (14.50)	0.25 (0.25)	11.75 (6.93)
Western redcedar	*Thuja plicata*	0	0.25 (0.25)	0	3.75 (1.49)	0	0
Alaskan blueberry	*Vaccinium alaskaense*	0	0	0	0	0	3.00 (1.22)
Black huckleberry	*Vaccinium membranaceum*	0	0	0	0.50 (0.50)	0	0
Cascara	*Rhamnus purshiana*	0	0.50 (0.50)	0	0	0	0
Dull oregon-grape	*Mahonia nervosa*	3.50 (2.36)	0	0	0	0	0
Elderberry spp.	*Sambucus spp.*	0	0	0	1.25 (0.75)	0	1.75 (1.03)
Evergreen blackberry	*Rubus laciniatus*	0	2.50 (2.50)	0	1.50 (1.19)	0	0
Hardhack	*Spiraea douglasii*	0	1.75 (0.48)	0	0.75 (0.48)	0	3.00 (2.38)
Holly		0.75 (0.48)	0	0	0	0	0
Oval-leaved blueberry	*Vaccinium ovalifolium*	0	0	0	0	0	1.25 (1.25)
Red huckleberry	*Vaccinium parvifolium*	1.75 (0.75)	0.75 (0.48)	0	1.25 (1.25)	3.25 (2.36)	7.67 (3.84)
Salal	*Gaultheria shallon*	9.00 (5.02)	36.25 (12.14)	0	2.50 (1.44)	0.75 (0.75)	0

		Block 1		Block 2		Block 3	
		M Forest	F Clearcut	E20 Forest	K10B Clearcut	K Forest	K Clearcut
Salmonberry	*Rubus spectabilis*	0.67 (0.29)	7.50 (2.22)	0	18.75 (8.60)	0	12.50 (4.33)
Sticky currant	*Ribes viscosissimum*	0	0.50 (0.29)	0	0	0	0
Thimbleberry	*Rubus parviflorus*	0	1.50 (0.29)	0	1.50 (0.50)	0	15.00 (4.56)
Trailing blackberry	*Rubus ursinus*	0	4.50 (1.55)	0	2.25 (0.25)	0	8.50 (7.19)
Vine maple	*Acer circinatum*	0.75 (0.75)	2.88 (2.40)	0	0	2.50 (2.50)	0
Willow spp.	*Salix spp.*	0	0	0	1.75 (1.75)	0	0.50 (0.29)
Bracken fern	*Pteridium aquilinum*	0	24.50 (12.69)	0	24.75 (7.02)	0.75 (0.75)	4.25 (2.17)
Common foxglove	*Digitalis purpurea*	0	0	0	0	0	0.25 (0.25)
Common rush	*Juncus effusus*	0	1.25 (0.25)	0	0	0	0
Deer fern	*Blechnum spicant*	2.50 (1.66)	0	0	7.25 (1.60)	2.75 (1.31)	3.50 (1.55)
Fireweed	*Epilobium angustifolium*	0	1.75 (0.48)	0	6.75 (4.71)	0	1.25 (0.75)
Grass spp.		0	0	0	0	0	1.25 (1.25)
Great mullein	*Verbascum thapsus*	0	0.25 (0.25)	0	0	0	2.00 (0.41)
Pearly everlasting	*Anaphalis margaritacea*	0	1.63 (1.31)	0	1.00 (0.87)	0	2.00 (1.22)
Sword fern	*Polystichum munitum*	6.25 (3.12)	2.25 (1.03)	0	0	12.50 (9.46)	4.25 (0.75)
Wall lettuce	*Lactuca muralis*	0	0.25 (0.25)	0	0	0	0.25 (0.25)
White clover	*Trifolium repens*	0	0	0	0	0	0.25 (0.25)

APPENDIX 2. Number of invertebrates captured outside each enclosure during the two invertebrate sampling sessions in the juvenile and adult experiments. Invertebrates are presented by Order.

Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Total
MFOR1A	J	1	44	28	4	46	0	3	0	10	3	0	1	0	0	0	0	5	0	0	0	0	144
MFOR1B	J	1	27	10	4	14	0	0	1	1	4	0	2	0	0	1	0	0	0	0	0	0	64
MFOR2A	J	1	27	33	3	7	0	1	0	1	3	0	0	0	0	0	0	0	0	0	0	0	75
MFOR2B	J	1	39	31	2	12	1	0	0	12	7	0	0	0	0	1	1	1	0	0	0	0	107
E201A	J	1	49	23	2	0	0	1	0	16	1	0	0	0	0	0	0	0	0	0	0	0	92
E201B	J	1	65	29	8	0	2	0	0	5	2	0	0	1	0	0	0	0	0	0	0	0	112
E202A	J	1	63	26	5	3	0	2	0	22	1	0	3	0	0	0	0	0	0	0	0	0	125
E202B	J	1	67	14	3	2	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	89
KFOR1A	J	1	26	6	5	3	0	3	1	3	0	0	1	0	0	0	0	0	0	0	0	0	48
KFOR1B	J	1	96	10	3	5	0	5	1	2	0	0	2	0	0	0	0	0	0	0	0	0	124
KFOR2A	J	1	47	11	6	2	0	1	0	3	0	1	0	0	0	0	0	0	0	0	0	0	71
KFOR2B	J	1	117	36	7	4	0	1	0	5	0	1	1	0	0	0	0	0	0	0	0	0	172
FCC1A	J	1	73	10	0	9	1	0	0	2	3	0	1	0	0	0	0	0	0	0	0	0	99
FCC1B*	J	1	56	6.67	0	1.33	0	0	0	4	1.33	0	0	0	0	0	0	0	0	0	0	0	69.3
FCC2A*	J	1	66.7	8	1.33	5.33	0	2.67	0	50.7	1.33	0	0	1.33	0	0	0	0	0	0	0	0	137
FCC2B	J	1	98	7	5	12	0	0	1	14	0	0	0	0	1	0	0	0	0	0	0	0	138
K10B1A*	J	1	53.3	0	0	1.33	0	4	0	26.7	0	0	0	0	0	0	0	0	0	0	0	0	85.3
K10B1B	J	1	56	11	2	2	0	2	0	10	1	0	0	0	0	1	0	1	0	0	0	0	86
K10B2A	J	1	24	2	3	4	0	5	1	3	0	0	0	0	1	0	0	0	0	0	0	0	43
K10B2B	J	1	35	7	4	10	0	7	0	2	2	0	1	0	0	1	0	0	0	0	0	0	69
KCC1A	J	1	39	8	2	4	1	2	0	3	3	0	1	0	1	0	0	0	0	0	0	0	64
KCC1B	J	1	18	6	0	1	1	4	0	9	0	0	0	0	0	0	0	0	0	0	0	0	39
KCC2A	J	1	39	6	1	5	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	56
KCC2B*	J	1	137	10.7	2.67	6.67	0	0	0	8	1.33	0	0	0	0	0	0	0	0	0	0	0	167
MFOR1A	J	2	59	3	0	3	0	1	1	4	1	0	0	0	0	0	1	2	0	0	0	0	75
MFOR1B	J	2	26	3	0	2	0	0	0	3	3	0	0	0	0	0	3	1	0	0	0	0	41
MFOR2A	J	2	49	21	3	4	0	0	0	0	9	0	0	0	0	0	0	1	0	0	0	0	87
MFOR2B	J	2	91	5	4	1	0	0	0	2	4	0	0	0	0	0	0	2	0	0	0	0	109
E201A	J	2	118	7	2	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	130

Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Total
E201B	J	2	276	5	3	1	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	289
E202A	J	2	95	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	99
E202B	J	2	128	5	4	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	141
KFOR1A	J	2	20	3	2	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	30
KFOR1B	J	2	44	4	2	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	54
KFOR2A	J	2	43	4	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	49
KFOR2B	J	2	67	9	3	2	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	85
FCC1A	J	2	148	5	2	2	0	2	0	3	0	0	0	1	0	0	0	1	0	0	0	1	165
FCC1B	J	2	135	10	2	5	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	156
FCC2A*	J	2	221	2.67	5.33	2.67	1.33	0	0	1.33	0	0	0	1.33	0	0	0	0	0	0	0	0	236
FCC2B	J	2	326	4	0	1	0	0	0	2	1	0	0	0	0	0	0	4	0	0	0	0	338
K10B1A	J	2	155	3	2	0	1	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	166
K10B1B	J	2	56	7	0	0	0	1	0	6	0	0	0	0	0	0	0	2	1	0	0	0	73
K10B2A	J	2	43	0	1	2	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	50
K10B2B	J	2	46	3	3	4	0	0	0	4	1	0	0	0	0	0	0	4	0	0	0	0	65
KCC1A	J	2	21	0	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26
KCC1B*	J	2	56	1.33	4	1.33	0	0	0	5.33	1.33	0	0	0	0	0	0	0	0	0	0	0	69.3
KCC2A*	J	2	46.7	0	2.67	1.33	0	1.33	0	4	0	0	0	0	0	0	0	0	0	0	0	0	56
KCC2B	J	2	45	3	2	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	54
MFOR1A	A	1	39	12	5	19	2	0	1	1	5	0	0	0	1	0	1	4	0	0	0	0	90
MFOR1B	A	1	26	11	2	12	1	0	5	1	7	0	0	0	0	0	0	0	0	1	0	0	66
MFOR2A	A	1	20	17	5	32	0	0	0	1	15	0	0	0	0	0	0	1	0	0	0	0	91
MFOR2B	A	1	12	16	5	16	1	2	1	0	6	0	0	2	0	1	0	1	0	0	0	0	63
E201A	A	1	13	21	1	0	1	0	4	4	2	0	0	0	0	0	0	1	0	0	0	0	47
E201B	A	1	66	35	7	19	2	0	5	5	1	0	0	0	0	0	0	0	0	0	0	0	140
E202A	A	1	68	17	5	2	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	97
E202B	A	1	33	7	5	2	1	1	2	2	1	0	0	0	0	0	0	0	0	0	0	0	54
KFOR1A	A	1	77	14	2	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	97
KFOR1B	A	1	87	12	6	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	108
KFOR2A	A	1	39	16	1	3	0	1	4	1	2	0	0	0	0	0	0	0	0	0	0	0	67
KFOR2B	A	1	57	22	9	3	0	0	3	1	1	0	0	0	0	0	0	0	0	0	0	0	96
FCC1A	A	1	32	22	21	10	12	1	2	3	7	0	0	3	0	0	2	1	2	1	0	0	119
FCC1B	A	1	41	7	21	6	13	1	1	16	2	0	0	1	3	0	0	3	0	0	0	0	115

Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Total
FCC2A*	A	1	9.33	8	29.3	2.67	10.7	0	0	8	0	0	0	0	8	0	4	2.67	0	0	0	0	82.7
FCC2B	A	1	6	5	18	4	19	0	1	1	0	0	0	1	4	0	0	0	0	0	0	0	59
K10B1A	A	1	17	4	11	2	153	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	192
K10B1B	A	1	33	5	14	13	18	0	0	1	0	0	0	0	10	0	2	3	0	0	0	0	99
K10B2A	A	1	10	4	12	9	153	0	7	4	0	0	0	0	1	1	2	1	1	0	0	0	205
K10B2B	A	1	1	5	13	6	31	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	61
KCC1A	A	1	6	2	9	0	0	0	3	2	1	0	0	1	0	0	0	0	0	0	0	0	24
KCC1B	A	1	14	4	8	1	1	0	1	1	0	0	1	0	0	0	0	4	0	0	0	0	35
KCC2A	A	1	28	8	11	3	1	0	4	2	0	0	0	1	0	0	4	1	0	0	0	0	63
KCC2B	A	1	6	6	14	3	2	0	2	8	1	0	0	1	0	0	0	0	0	0	0	0	43
MFOR1A	A	2	0	8	6	3	3	0	9	12	4	0	0	2	0	0	0	0	0	0	0	0	47
MFOR1B	A	2	3	13	4	9	0	0	10	1	0	0	0	2	0	0	0	0	0	0	0	0	42
MFOR2A	A	2	0	14	10	2	0	0	17	4	1	0	0	4	1	0	0	0	0	0	0	0	53
MFOR2B	A	2	0	14	11	1	0	0	12	6	2	0	0	3	0	0	0	0	0	0	0	0	49
E201A	A	2	0	17	16	0	3	0	19	2	0	0	1	1	0	0	0	0	0	0	0	0	59
E201B	A	2	0	18	14	1	3	0	39	1	1	0	0	1	1	0	0	0	0	0	0	0	79
E202A	A	2	0	35	7	0	0	0	24	3	3	0	0	0	0	0	0	0	0	0	0	0	72
E202B	A	2	0	35	14	19	0	2	14	2	2	0	0	1	0	0	0	0	0	0	0	0	89
KFOR1A	A	2	0	27	6	0	2	1	9	1	3	0	0	0	0	0	0	0	0	0	0	0	49
KFOR1B	A	2	7	20	11	0	0	1	6	9	6	0	0	1	0	0	0	0	0	0	0	0	61
KFOR2A	A	2	0	23	7	6	1	6	6	0	1	0	0	0	1	0	0	0	0	0	1	0	52
KFOR2B	A	2	2	24	14	0	3	63	13	6	11	0	0	5	0	0	0	0	0	0	0	0	141
FCC1A	A	2	1	4	11	0	31	0	8	3	0	0	0	1	3	0	0	0	0	3	0	0	65
FCC1B	A	2	1	9	14	3	22	1	5	2	0	0	0	2	0	0	0	0	0	0	0	0	59
FCC2A*	A	2	0	4	2.67	0	52	0	5.33	1.33	0	0	0	0	1.33	0	0	0	0	2.67	0	0	69.3
FCC2B	A	2	0	1	14	0	43	0	2	0	1	0	0	1	0	0	0	0	0	2	0	0	64
K10B1A	A	2	9	3	9	0	61	4	3	3	0	0	0	2	0	0	0	1	0	0	0	0	95
K10B1B	A	2	18	2	44	2	32	0	4	5	0	0	0	3	0	0	0	1	0	0	0	0	111
K10B2A	A	2	7	6	12	0	24	0	8	11	0	0	0	3	1	0	0	0	0	1	0	0	73
K10B2B	A	2	0	6	13	0	16	2	7	1	0	0	1	1	0	0	0	0	0	0	0	0	47
KCC1A	A	2	0	7	7	0	3	1	4	0	5	0	0	2	2	0	0	0	1	0	0	0	32
KCC1B	A	2	0	4	5	0	0	1	2	0	0	0	0	1	0	0	0	0	0	1	0	0	14
KCC2A	A	2	1	27	18	16	6	3	2	10	0	0	0	1	0	0	1	0	0	0	0	0	85

Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Total
KCC2B	A	2	1	4	14	1	5	3	6	0	2	0	0	2	0	0	0	1	0	0	0	0	39

[1] For the juvenile experiment (J), sampling session 1 was 12/03/03, and sampling session 2 was 02/16/04. For the adult experiment (A), sampling session 1 was 06/18/04, and sampling session 2 was 08/20/04.

* Sample based on three traps instead of four; consequently, the values were adjusted by multiplying the number captured by 4/3.

APPENDIX 3. Biomass (mg) of invertebrates captured outside each enclosure during the two invertebrate sampling sessions in the juvenile and adult experiments. Invertebrates are presented by Order.

Site/Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Fragment[2]	Total
MFOR1A	J	1	3.56	4.61	7.35	3.09	0	3.17	0	1.24	29.59	0	2.70	0	0	0	0	209.98	0	0	0	0	1.62	266.89
MFOR1B	J	1	2.66	2.52	4.95	0.88	0	0	22.20	0.06	159.00	0	7.50	0	0	3.76	0	0	0	0	0	0	2.58	206.11
MFOR2A	J	1	3.64	9.26	38.75	2.64	0	11.25	0	0.10	41.08	0	0	0	0	0	0	0	0	0	0	0	7.29	114.01
MFOR2B	J	1	3.71	30.48	7.83	0.10	0.16	0	0	1.63	168.62	0	0	0	0	0.11	0.18	85.82	0	0	0	0	7.65	306.30
E201A	J	1	2.87	82.22	14.24	0	0	0.67	0	5.15	9.27	0	0	0	0	0	0	0	0	0	0	0	5.76	120.18
E201B	J	1	5.18	58.79	25.15	0	1.19	0	0	0.92	18.87	0	0	1.17	0	0	0	0	0	0	0	0	4.92	116.19
E202A	J	1	5.13	4.73	21.24	1.24	0	10.27	0	4.86	8.17	0	20.55	0	0	0	0	0	0	0	0	0	9.30	85.47
E202B	J	1	6.11	3.88	15.24	1.20	0	2.25	0	0.10	0	0	0	0	0	0	0	0	0	0	0	0	9.78	38.56
KFOR1A	J	1	3.70	2.74	24.23	1.43	0	2.97	34.60	0.56	0	0	3.01	0	0	0	0	0	0	0	0	0	17.80	91.05
KFOR1B	J	1	11.10	13.72	1.51	0.85	0	2.48	2.30	0.50	0	0	6.23	0	0	0	0	0	0	0	0	0	1.66	40.36
KFOR2A	J	1	6.03	9.62	4.71	1.17	0	2.12	0	0.40	0	0.11	0	0	0	0	0	0	0	0	0	0	2.94	27.09
KFOR2B	J	1	15.52	54.92	19.57	0.70	0	0.06	0	1.00	0	0.19	2.18	0	0	0	0	0	0	0	0	0	1.78	95.92
FCC1A	J	1	7.49	14.19	0	3.27	0.91	0	0	0.21	80.53	0	1.71	0	0	0	0	0	0	0	0	0	7.61	115.91
FCC1B*	J	1	5.69	2.31	0	0.07	0	0	0	0.93	44.27	0	0	0	0	0	0	0	0	0	0	0	7.01	60.27
FCC2A*	J	1	4.61	32.10	1.66	1.29	0	1.99	0	13.94	13.85	0	0	19.84	0	0	0	0	0	0	0	0	10.18	99.45
FCC2B	J	1	7.30	26.60	16.78	1.01	0	0	20.77	5.43	0	0	0	0	0.14	0	0	0	0	0	0	0	10.50	88.51
K10B1A*	J	1	5.71	0	0	1.04	0	2.36	0	3.63	0	0	0	0	0	0	0	0	0	0	0	0	3.64	16.39
K10B1B	J	1	6.53	2.55	0.27	0.09	0	1.70	0	1.59	5.02	0	0	0	0	0.21	0	19.83	0	0	0	0	2.21	40.00
K10B2A	J	1	2.24	56.34	7.14	1.64	0	27.18	29.70	0.46	0	0	0	0	0.06	0	0	0	0	0	0	0	0.78	125.52
K10B2B	J	1	3.26	0.88	0.35	1.71	0	5.38	0	0.62	11.13	0	0.19	0	0	23.74	0	0	0	0	0	0	0.96	48.22
KCC1A	J	1	3.02	1.57	1.93	1.31	0.19	1.67	0	0.17	6.66	0	1.44	0	0.11	0	0	0	0	0	0	0	0.53	18.60
KCC1B	J	1	3.18	49.62	0	0.07	0.54	2.48	0	1.12	0	0	0	0	0	0	0	0	0	0	0	0	1.37	58.37
KCC2A	J	1	2.94	1.84	2.78	0.78	0	3.45	0	0.76	0	0	0	0	0	0	0	0	0	0	0	0	1.21	13.75
KCC2B*	J	1	15.44	3.34	2.72	0.52	0	0	0	1.28	0.68	0	0	0	0	0	0	0	0	0	0	0	2.65	26.63
MFOR1A	J	2	5.45	0.34	0	0.22	0	0.25	11.45	0.33	3.84	0	0	0	0	0	0.07	32.24	0	0	0	0	2.39	56.58
MFOR1B	J	2	2.23	6.45	0	0.56	0	0	0	0.44	4.33	0	0	0	0	0	0.13	48.37	0	0	0	0	2.73	65.24
MFOR2A	J	2	5.03	3.43	4.18	2.56	0	0	0	0	28.81	0	0	0	0	0	0	46.02	0	0	0	0	9.97	99.99
MFOR2B	J	2	8.28	0.48	10.65	1.30	0	0	0	1.38	8.79	0	0	0	0	0	0	115.21	0	0	0	0	2.68	148.78
E201A	J	2	10.09	33.25	0.58	0.16	0	0	19.47	0	12.36	0	0	0	0	0	0	0	0	0	0	0	3.78	79.69

Site/Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Fragment[2]	Total
E201B	J	2	27.49	0.40	2.21	0.04	0	0	0	0.04	19.31	0	0	0	0	0	0.04	0	0	0	0	0	9.10	58.63
E202A	J	2	8.50	0.12	0.76	0	0	0	19.94	0	0	0	0	0	0.06	0	0	0	0	0	0	0	6.77	36.14
E202B	J	2	11.33	0.59	25.42	0	0	0	32.94	0.41	0	0	0	0	0	0	0	0	0	0	0	0	3.63	74.32
KFOR1A	J	2	1.99	8.57	0.58	0.37	0	0	0	0.45	0	0	0	0	0	0	0	0	0	0	0	0	1.93	13.89
KFOR1B	J	2	3.12	0.90	0.15	0	0	0	0	0.15	0.13	0	0	0.24	0	0	0	0	0	0	0	0	1.19	5.89
KFOR2A	J	2	4.25	0.77	5.43	0	0	0	0	0	17.19	0	0	0	0	0	0	0	0	0	0	0	1.26	28.90
KFOR2B	J	2	6.92	2.20	7.52	0.68	0	0	20.94	0.36	16.51	0	0	0	0	0	0	0	0	0	0	0	1.72	56.84
FCC1A	J	2	10.51	0.94	4.02	4.99	0	1.32	0	0.07	0	0	0	0.59	0	0	0	97.54	0	0	0	0.49	7.63	128.09
FCC1B	J	2	8.87	3.27	2.65	0.54	0	0.80	0	2.60	0	0	1.01	0	0	0	0	428.24	0	0	0	0	9.41	457.40
FCC2A*	J	2	15.97	0.77	21.80	0.11	1.45	0	0	0.09	0	0	0	4.712	0	0	0	0	0	0	0	0	14.84	59.75
FCC2B	J	2	25.77	0.72	0	0.15	0	0	0	7.32	5.23	0	0	0	0	0	0	192.49	0	0	0	0	14.48	246.17
K10B1A	J	2	11.34	2.43	2.84	0	0.23	1.48	0	4.24	0	0	0	0	0	0	0	0	0	0	0	0	4.02	26.58
K10B1B	J	2	3.49	9.39	0	0	0	1.42	0	0.59	0	0	0	0	0	0	0	47.06	16.68	0	0	0	3.15	81.76
K10B2A	J	2	3.42	0	5.71	0.89	0	1.12	0	10.86	22.38	0	0	0	0	0	0	0	0	0	0	0	3.41	47.79
K10B2B	J	2	2.96	0.44	11.74	0.23	0	0	0	1.18	0.64	0	0	0	0	0	0	139.92	0	0	0	0	4.53	161.64
KCC1A	J	2	1.73	0	2.08	0.69	0	1.35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.26	7.09
KCC1B*	J	2	4.99	3.17	3.49	0.43	0	0	0	3.63	0.24	0	0	0	0	0	0	0	0	0	0	0	2.97	18.92
KCC2A*	J	2	3.32	0	4.69	0.03	0	1.29	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	1.36	10.93
KCC2B	J	2	3.98	0.55	0.29	0	0	0	0.08	0.11	0	0	0	0	0	0	0	0	2.50	0	0	0	2.28	9.79
MFOR1A	A	1	3.08	498.38	14.94	7.01	6.36	0	10.14	0.05	200.48	0	0	0	0.04	0	0.08	172.08	0	0	0	0	3.44	916.07
MFOR1B	A	1	2.90	419.28	3.75	4.18	7.55	0	30.94	0.24	327.82	0	0	0	0	0	0	0	0	2.28	0	0	3.70	802.64
MFOR2A	A	1	1.65	710.22	8.66	8.40	0	0	0	0.03	700.62	0	0	0	0	0	0	0.07	0	0	0	0	3.90	1433.55
MFOR2B	A	1	0.89	243.95	14.24	4.75	8.80	0.36	4.23	0	206.64	0	0	11.70	0	0.45	0	41.07	0	0	0	0	4.07	541.15
E201A	A	1	0.95	498.69	3.42	0	5.67	0	24.25	0.95	59.00	0	0	0	0	0	0	771.90	0	0	0	0	4.45	1369.27
E201B	A	1	2.37	790.87	0.39	0.39	0.15	0	36.43	0.28	5.50	0	0	0	0	0	0	0	0	0	0	0	3.34	839.72
E202A	A	1	3.01	224.36	1.23	0.08	0.20	0	21.11	0.09	0	0	0	0	0	0	0	0	0	0	0	0	2.60	252.67
E202B	A	1	2.15	109.15	16.81	0.04	0.17	0.01	12.72	1.85	3.11	0	0	0	0	0	0	0	0	0	0	0	5.06	151.07
KFOR1A	A	1	4.58	225.41	2.76	0	0.20	0	3.87	0.04	6.46	0	0	0	0	0	0	0	0	0	0	0	13.20	256.51
KFOR1B	A	1	4.30	405.73	11.52	0	0	0	0	0	13.27	0	0	0	0	0	0	0	0	0	0	0	15.84	450.67
KFOR2A	A	1	3.29	528.81	1.64	2.14	0	0.04	14.22	0.08	11.15	0	0	0	0	0	0	0	0	0	0	0	3.50	564.87
KFOR2B	A	1	3.79	783.70	16.32	0.15	0	0	9.47	0.15	5.13	0	0	0	0	0	0	0	0	0	0	0	4.14	822.85
FCC1A	A	1	1.01	141.25	81.39	0.63	15.01	5.29	0.21	0.18	218.08	0	0	27.39	0	0	0.09	6.06	735.74	0.57	0	0	2.43	1235.32
FCC1B	A	1	0.55	16.69	76.86	0.15	11.82	10.43	0.11	5.66	6.99	0	0	7.00	0.06	0	0	116.31	0	0	0	0	3.59	256.21

Site/Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Fragment[2]	Total
FCC2A*	A	1	0.40	93.70	102.43	0.30	11.25	0	0	0.27	0	0	0	0	0.39	0	0.17	1009.21	0	0	0	0	3.94	1222.05
FCC2B	A	1	0.31	96.06	75.63	0.27	27.68	0	0.08	0.15	0	0	0	3.19	0.26	0	0	0	0	0	0	0	4.73	208.35
K10B1A	A	1	0**	13.42	41.39	0.24	320.28	0	0	0	0	0	0	0	0.23	0	0	0	0	0	0	0	5.47	381.04
K10B1B	A	1	1.07	0.29	41.99	0.50	37.83	0	0	0.04	0	0	0	0	0.51	0	0.11	67.43	0	0	0	0	2.04	151.81
K10B2A	A	1	0.40	2.55	34.87	1.13	257.98	0	25.58	0.45	0	0	0	0	0.07	0.77	0.08	4.68	104.20	0	0	0	3.08	435.81
K10B2B	A	1	0.07	52.53	38.62	1.24	74.33	0	0.10	9.72	0	0	0	0	0	0	0	15.11	43.56	0	0	0	3.51	238.78
KCC1A	A	1	0.54	11.47	26.56	0	0	0	0**	0.10	3.60	0	0	1.04	0	0	0	0	0	0	0	0	2.64	45.96
KCC1B	A	1	0.53	12.69	22.87	0.07	0.34	0	0.16	0.11	0	0	0.46	0	0	0	0	135.71	0	0	0	0	2.03	174.97
KCC2A	A	1	0.65	32.56	23.21	0.16	0.35	0	9.81	0.23	0	0	0	0.96	0	0	0.15	17.21	0	0	0	0	3.31	88.59
KCC2B	A	1	0.30	29.54	36.47	0.30	0.59	0	0.09	0.58	4.55	0	0	6.10	0	0	0	0	0	0	0	0	2.65	81.16
MFOR1A	A	2	0	226.88	25.74	0.61	21.07	0	106.46	17.86	17.97	0	0	44.93	0	0	0	0	0	0	0	0	4.80	466.31
MFOR1B	A	2	0.16	342.70	19.55	0.35	0	0	71.64	1.52	0	0	0	47.32	0	0	0	0	0	0	0	0	3.87	487.13
MFOR2A	A	2	0	246.02	40.86	0.62	0	0	254.75	7.44	16.80	0	0	63.51	0.04	0	0	0	0	0	0	0	2.56	632.61
MFOR2B	A	2	0	159.37	48.79	0.37	0	0	72.58	11.69	42.06	0	0	18.26	0	0	0	0	0	0	0	0	1.62	354.74
E201A	A	2	0	272.69	73.88	0	17.06	0	228.04	2.84	0	0	0.84	12.43	0	0	0	0	0	0	0	0	0.57	608.36
E201B	A	2	0	304.37	68.92	0.32	21.67	0	440.86	0.50	25.32	0	0	28.17	0.06	0	0	0	0	0	0	0	1.83	892.02
E202A	A	2	0	845.28	30.62	0	0	0	290.70	0.10	101.11	0	0	0.00	0	0	0	0	0	0	0	0	2.52	1270.34
E202B	A	2	0	979.40	53.05	0.98	0	0.35	156.47	5.37	40.40	0	0	2.63	0	0	0	0	0	0	0	0	3.94	1242.58
KFOR1A	A	2	0	1052.85	29.03	0	8.25	2.78	97.90	2.77	93.59	0	0	0	0	0	0	0	0	0	0	0	3.25	1290.43
KFOR1B	A	2	0.25	566.59	58.60	0	0	17.06	59.37	11.15	161.85	0	0	19.24	0	0	0	0	0	0	0	0	3.80	897.89
KFOR2A	A	2	0	1001.48	39.22	1.31	0.27	9.21	4.32	0	28.10	0	0	0.00	2.28	0	0	0	0	0	0.06	0	2.45	1088.70
KFOR2B	A	2	0.09	869.42	62.34	0	15.20	303.32	196.24	0.35	252.71	0	0	71.83	0	0	0	0	0	0	0	0	8.41	1779.90
FCC1A	A	2	0.15	47.49	41.33	0	39.22	0	80.61	13.80	0	0	0	14.78	0.32	0	0	0	0	7.13	0	0	2.13	246.96
FCC1B	A	2	0.07	347.95	51.72	0.73	28.86	0.14	14.89	0.10	0	0	0	30.84	0	0	0	0	0	0	0	0	2.31	477.60
FCC2A*	A	2	0	3.67	1.87	0	100.19	0	53.85	0.26	0	0	0	0	0.14	0	0	0	0	10.76	0	0	0.75	171.49
FCC2B	A	2	0	0.06	48.53	0	64.82	0	2.90	0	73.93	0	0	1.62	0	0	0	0	0	4.08	0	0	1.59	197.52
K10B1A	A	2	1.06	11.52	23.19	0	141.87	0.38	6.98	4.13	0	0	0	40.88	0	0	0	10.33	0	0	0	0	1.58	241.92
K10B1B	A	2	1.78	10.81	59.99	0.51	54.96	0	37.47	0.18	0	0	0	37.89	0	0	0	55.57	0	0	0	0	1.56	260.72
K10B2A	A	2	0.44	2.82	41.32	0	40.11	0	145.20	0.40	0	0	0	87.13	0.03	0	0	0	0	2.34	0	0	1.04	320.81
K10B2B	A	2	0	3.33	50.43	0	21.04	0.14	203.74	2.28	0	0	2.39	36.22	0	0	0	0	0	0	0	0	1.79	321.36
KCC1A	A	2	0	102.11	19.81	0	2.62	0.06	2.17	0	219.86	0	0	58.57	0***	0	0	0	259.82	0	0	0	2.63	667.65
KCC1B	A	2	0	50.41	22.22	0	0	1.15	22.87	0	0	0	0	14.83	0	0	0	0	0	1.04	0	0	0.92	113.44
KCC2A	A	2	0.13	184.23	57.58	0.97	7.52	0.18	1.73	3.36	0	0	0	23.12	0	0	0.06	0	0	0	0	0	5.15	284.03

Site/Enclosure	Exp't	Session[1]	Collembola	Coleoptera	Araneae	Acari	Hymenoptera	Lepidoptera	Orthoptera	Diptera	Diplopoda	Dermaptera	Isopoda	Chilopoda	Homoptera	Haplotaxida	Siphonaptera	Pulmonata	Gastropoda	Thysanura	Neuroptera	Mecoptera	Fragment[2]	Total
KCC2B	A	2	0.07	1.74	53.97	0.13	2.52	0.13	59.52	0	175.53	0	0	49.36	0	0	0	5.34	0	0	0	0	2.03	350.36

[1] For the juvenile experiment (J), sampling session 1 was 12/03/03, and sampling session 2 was 02/16/04. For the adult experiment (A), sampling session 1 was 06/18/04, and sampling session 2 was 08/20/04.

[2] "Fragment" includes all invertebrates that were too small to classify to Order, and body parts that were unidentifiable.

* Sample based on three traps instead of four; consequently, the values were adjusted by multiplying the biomass by 4/3.

** Sample was dropped prior to weighing, and biomass estimate was inaccurate. Therefore, zero was entered.

*** Data entry error; no biomass was entered.