

AN ABSTRACT OF THE THESIS OF

Rene N. Horton for the degree of Master of Science in Entomology presented on June 5, 1995. Title: Characteristics of *Typhlodromus americanus* Chant and Yoshida-Shaul (Acari: Phytoseiidae) as a Biological Control Agent of *Oligonychus ununguis* (Jacobi) (Acari: Tetranychidae).

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Abstract approved: _____
Jack DeAngelis

The life history, temperature, humidity, and feeding requirements of the phytoseiid predator mite, *Typhlodromus americanus* Chant and Yoshida-Shaul were tested in the laboratory. Occurance of the mite in the field during different times of the year was investigated as well. Effects of temperature and humidity on egg hatch, the feeding requirements of the larvae, the amount consumed by each life stage, the length of each life stage and suitability of different food sources were investigated in the laboratory. The use of the mite as a biological control agent was evaluated by using the information gained from the laboratory experiments.

T. americanus was originally discovered in plantation grown Douglas-fir in western Oregon. Since that time the mite has been found on a number of other hosts throughout North America. The mite is active year round in the Christmas tree plantations of the Willamette Valley in Oregon. The adult is found in or near the one year old bud scars and the eggs are typically deposited there also.

Life parameters were measured providing a net reproductive rate of 4.23, a mean generation time of 24.45 days, and an intrinsic rate of increase of 0.059. The intrinsic rate of increase was low when compared to other predator mites and numerical response to prey increase would not be possible with such a low rate.

The optimal temperature for the shortest eclosion time (54.4 hr.) and the highest survival (96.4%) was 26° C. The regression of temperature vs. time to hatch gave a 90% R^2 with both the slope and intercept significantly different from zero. Humidities above 70% had survival rates over 96% and eclosion rates in the range of 50-58 hours. The relative humidity at which 50% of the population died was 58.6%.

The mite was found to feed readily on the pest mite *Oligonychus ununguis* (spruce spider mite), as well as *Tetranychus urticae* (two spotted spider mite), and corn, oak, and Douglas-fir pollens. The larval form of the predator mite does not require food to molt to the protonymph, but the protonymph does require food to molt. If water is provided the entire time from egg to death, the protonymph can survive about ten days. Females consumed more *Tet. urticae* than males in both the immature and adult stages. The *T. americanus* that were fed corn pollen and *Tet. urticae* (complete diet) lived for over 115 days. Mites raised on oak and corn pollens did not survive as long (only 70-80 days), and those raised on Douglas-fir pollens did not reach adulthood. Egg production was observed on the complete diet, but not on the diets of pollen. The largest number of eggs were laid around the twelfth day after the molt to adult.

Control and management of field conditions to improve habitat for *T. americanus* will be the best approach for its use as a biological control agent. As it does not respond numerically to prey increase, it will be more effective in a regulatory role to prevent these increases while the prey is at low levels.

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June 5, 1995

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Phytoseiidae) as a Biological Control Agent of *Oligonychus ununguis* (Jacobi)
(Acari: Tetranychidae).

by

Rene' N. Horton

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

MASTER OF SCIENCE

Completed June 5, 1995

Commencement June 1996

Master of Science thesis of Rene' N. Horton presented on June 5, 1995

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Acknowledgments

I would like to thank the Oregon Department of Agriculture for helping fund this research. I am also thankful for the cooperation of Pat and Betty Malone at the Sunrise Tree Farm and the Holiday Tree Farm for allowing me to collect samples from their fields. I am grateful to the members of my committee Drs. Jack DeAngelis, Brian Croft, Joseph Beatty, and Charles Boyer for all of their help and support. I appreciate the love and support of my parents Corine and Gary Horton and hope they realize how much it has helped me.

Lastly, I would like to extend my thanks to all of the members of the Department of Entomology. The office staff, students, and Professors have been generous with their help and guidance and have made my time in Oregon a pleasure.

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Characteristics of *Typhlodromus americanus* Chant and Yoshida-Shaul (Acari: Phytoseiidae) as a Biological Control Agent of *Oligonychus ununguis* (Jacobi) (Acari: Tetranychidae).

Introduction

Christmas tree production is the seventh largest crop in Oregon in terms of gross dollar sales. In 1992, 6,120 acres were harvested and wholesaled at \$9.00 per tree (Miles 1993). Since each acre harvested yields about 1280 trees, 7,840,000 trees were sold giving a total wholesale value of \$70,753,000 (Miles 1993). *Oligonychus ununguis* (Jacobi), the spruce spider mite is considered an important early and late season pest of conifers world-wide. This mite causes yellowing or bronzing of the needles of infested trees and premature needle drop. The damage lowers the value of the trees and may render them unmarketable (Jeppson et. al 1975). The phytoseiid predator *Typhlodromus americanus* (Chant and Yoshida-Shaul) is often found in conjunction with *O. ununguis* (West & DeAngelis 1993) but its potential as a biological control agent is unknown. Along with *T. americanus*, *Amblyseius andersoni* (Chant) has been found in Oregon also in association with *O. ununguis*, but at lower densities (West & DeAngelis 1993).

The purpose of this study was to characterize the phytoseiid predator *T. americanus* in terms of its potential as a biological control agent. Spraying from helicopters for spruce spider mite control is expensive both economically in cost of helicopter rental and pesticide as well as environmentally to water and soil. Pesticides can also cause large losses of predator populations. Information such as life tables providing fecundity, survival rate, developmental time, as well as feeding preferences, active stages, and temperature and humidity requirements for egg development are used to characterize *T. americanus* in terms of its use as a biological control agent.

Literature Review

Oligonychus ununguis

Oligonychus ununguis (spruce spider mite) has a wide host range, including: true fir (*Abies sp.*), false cypress (*Chamaecyparis sp.*), juniper (*Juniperus sp.*), spruce (*Picea sp.*), pine (*Pinus sp.*), Douglas-fir (*Pseudotsuga sp.*), redwood (*Sequoia sp.*), arborvitae (*Thuja sp.*), hemlock (*Tsuga sp.*) (Regan 1988), and has also been recorded on chestnut (*Castanea sp.*) (Saitô 1983). Seven overlapping generations have been recorded in the Pacific Northwest with adult populations being most dense in spring and fall (Regan 1988). Most injury is reported during hot, dry weather because multiple generations are developing at the same time (Schread 1951). Literature reports that the most serious outbreaks occur in spring and early fall, but states hot, dry seasons seem to favor these mites (Schread 1951, Kramer & Hain 1989, Sadof & Gibb 1992).

The spruce spider mite over winters as eggs deposited at the base of needles or other similarly protected areas. When eggs are first laid, they have a stipe and are grayish-brown, but they change to a darker orange-brown in a few days (Jeppson et. al. 1975). Eggs that have overwintered hatch in April, when the eggs are exposed to a temperature of 20°C or more and the mites can complete development in 11-23 days depending on the temperature (Jeppson et. al. 1975). Mites go through five stages: egg, larva, protonymph, deutonymph, and adult. Larva have six legs and are pinkish at first and then turn greenish after feeding. Adults are colored orange to black (Jeppson et.al. 1975).

The temperature threshold for activity is 6-7°C. Young immatures prefer to feed in the lower part of the crown on the new shoots and needles. Adults do not show a feeding preference (Jeppson et. al. 1975). Adult females can lay about 45 eggs in their lifetime, and 60-80% of the eggs will develop into females. The spruce spider mite is slow to spread from localized infestations (Jeppson et. al. 1975)

Oligonychus ununguis does not require high humidity to develop normally (Boyne & Hain 1983, Kramer & Hain 1989, Boudreaux 1958). Hot dry weather favors outbreaks of spruce spider mite and is detrimental to many predator mites (Kramer & Hain 1989). Experiments on humidity requirements for development of spruce spider mites showed that there was little difference between 30-40% and 50-60% Relative Humidity (RH) but that high humidity (88-98%) was detrimental. At high humidity, only 41% of original females in the experiment reached the adult stage. Females held at moderate and low RH also had higher fecundity than those held at high RH (Boyne & Hain 1983).

High RH can interfere with feeding of ovipositing spruce spider mites. Loss of moisture by evaporation through the cuticle is an important way for spruce spider mite to remove water from plant juices allowing concentration of nutrients. If RH in the environment is high, it will prevent evaporation from the cuticle. Cuticular lobes on the body which are only present on active summer females are responsible for increased surface area used for evaporation (Boudreaux 1958). Females that died at high RH's were still "plump" when compared with those that died at lower RH's which shriveled and dried up (Boudreaux 1958). Spruce spider mites ovipositing at these lower RH's laid more eggs at a higher rate than those at higher humidities (Boudreaux 1958).

At temperatures above 29°C *O. ununguis* eggs do not survive (Boyne & Hain 1983). Low survival at temperatures greater than 29°C is not uncommon for other species of *Oligonychus* (Boyne & Hain 1983). Average fecundity also drops as temperature rises, but fecundity rates increase. Maximum intrinsic rate of natural increase (r_m) occurs at 26°C (Boyne & Hain 1983). Mean generation time also decreases as temperature increases. At 26°C a population has the capacity to double every 4.41 days (Boyne & Hain 1983). This short doubling time allows mite populations to quickly increase and cause large amounts of damage; hence the need to control the mite early before outbreaks are possible (Regan 1988).

O. ununguis has been studied on Japanese chestnut (*Castanea crenata*) where it was characterized by its webbing behavior. The spruce spider mite builds web nests. These nest webs are used as cover for feeding, walking and laying eggs. These mites have

been observed using guy ropes to keep their eggs in an upright position for a brief period of time in order to waterproof them. According to Saitô (1983) the web nest type only develops on stable hosts such as evergreens and bamboo's. All of these observations are on chestnut leaves, not needles like those of the Douglas-fir. Field observations of *O. ununguis* on Douglas-fir have detected only small amounts of webbing (Personal Observation). Eggs are laid on the needles of Douglas-fir, usually in the crease of the needle. Web threads are normally used by *O. ununguis* as life lines but can also be used as ballooning threads when population densities become too great and resources deteriorate (Saitô 1983).

Typhlodromus americanus

Typhlodromus americanus, originally described as *Typhlodromus exhilaratus americanus*, Chant & Yoshida-Shaul was first found on plantation-grown Douglas-fir in western Oregon (Chant & Yoshida-Shaul 1986). It has also been found in Maryland, Washington, D.C., New Jersey, and North Carolina on a number of host plants including mock orange, arborvitae, juniper, boxwood, and wisteria (Chant & Yoshida-Shaul 1986). Other than taxonomic studies this mite has not been the subject of research and very little is known about its biology or ecology.

Life tables are a summary of the life of a typical cohort (Price 1975, see Appendix). Life table analysis has been used to characterize phytoseiids in terms of their potential as biological control agents. For example a life table for *Amblyseius barkeri* (Hughes) was used to describe its possible effectiveness as a control of *Thrips tabaci* (Bonde 1989). Among the many observations made were developmental stages, number of thrips eaten, time of first mating, number of eggs laid, and number of dead mites. The life table analysis has been used to determine the duration of the immature stages, consumption rates of prey, cannibalistic traits, as well as showing that mating is necessary for oviposition, and peak oviposition rate (Bonde 1989). Another example would be

Castagnoli and Simoni's (1990) life table on *Amblyseius cucumeris* (Oudemans). A life table was made for *A. cucumeris* and its development on three different kinds of food. The foods included *Quercus* sp. pollen, *Tet. urticae*, and *Thrips tabaci* (Lind.). It was found that developmental times, eggs laid, female longevity, juvenile mortality, and sex ratio were effected by the different foods. This information might easily be used for mass rearing the predators (Castagnoli & Simoni 1990).

Some predatory mites such as *A. cucumeris* are able to utilize diverse food sources, both prey and pollen, with pollen allowing for longer survival and more offspring (Castagnoli & Simoni 1990). Other mites such as *T. pyri* are able to utilize plant juices and mildews as well as prey and pollen. It is even possible that some phytoseiid mites require plant food sources for total nutrition and to achieve their reproductive potential (Chant 1959). Food sources likely associated with *T. americanus* are *O. ununguis* and Douglas-fir pollen (West & DeAngelis 1993), but *Tet. urticae* and *Quercus* sp. pollen are common food sources for other phytoseiids (Castagnoli & Simoni 1990).

Relative humidity is a critical factor in the survival of egg and immature stages of phytoseiids (Croft et. al in press). Phytoseiids differ in their requirements for atmospheric moisture. For example, *Metaseiulus occidentalis* (Nesbitt) and *Neoseiulus fallacis* (Garman) were reared together at different water vapor pressures to determine whether or not coexistence was possible. The two mites responded to water vapor pressure in opposite ways. *M. occidentalis* reproduced more readily at higher water vapor pressures while the *N. fallacis* population grew more rapidly at lower vapor pressure. Considering the variability of humidity in nature it would be possible for these two mites to live together, but they would flourish at different times depending upon prevailing weather (Mangini & Hain 1991).

Croft et. al (1993) showed that *N. fallacis*, *A. andersoni*, and *Typhlodromus pyri* Scheuten all had high mortality rates at relative humidities below 50%, and almost no mortality at a relative humidity of 95%. They also suggested that to some extent ingestion of adequate prey in the larval and protonymph stages can make up for lower humidity, in

that unfed larva and protonymphs tended to have a higher mortality rate than those that were fed (Croft et. al in press).

Life stages of *T. americanus* and the amount of prey consumed in each will give information on the mite's potential as a biological control agent. Life stages of *T. americanus* have not yet been determined, but literature on congeneric species such as *Typhlodromus pomi* Parrott (Hiroshi & Chant 1986) and *Typhlodromus exhilaratus* Ragusa (Ragusa 1981) and phytoseiids in general suggests that *T. americanus* passes through 5 stages; egg, six-legged larva, eight-legged protonymph and deutonymph, and finally an eight-legged, reproductively capable adult.

Croft & Croft (1993) examined the feeding habits of 3 phytoseiid species and suggested that the life stage with the highest consumption rate might characterize the ability of a species to control pest outbreaks. *M. occidentalis* was shown to be a voracious predator in the larval stage and therefore thought to more closely follow outbreaks of prey. If *T. americanus* follows this pattern, it might prove to be an effective predator of *O. ununguis* at high prey density. To prevent outbreaks, on the other hand, *T. americanus* must act at lower prey density, probably not feed as a larvae, capable of feeding on other phytoseiids and could be cannibalistic like *T. pyri* (Croft & Croft 1993).

The way *T. americanus* might be used as a biological control agent in commercial Christmas tree production depends on which life history strategy the phytoseiid uses. If the larvae must feed, and if other stages starve rapidly, need large amounts of prey to develop, and does not readily feed on other phytoseiids like *M. occidentalis*, then it might respond numerically vs. a linear reproductive method, to prey outbreaks. This life strategy, however, might not be effective at lower prey densities and would tend to disperse from these areas (Croft & Croft 1993). If *T. americanus* is more like *T. pyri* and the larvae are less active and other stages need less prey to develop, cannibalize and take other phytoseiids as prey, and are associated with lower prey densities, then the adult might be the more effective predatory stage. This would suggest that it would take more time for the predator's population size to increase in the event of an outbreak of prey and the mite would be more effective at lower prey densities (Croft & Croft 1993).

Characterization of *T. americanus* as a potential biological control agent of *O. ununguis* in plantation-grown Douglas-fir might significantly impact commercial Christmas tree production in Oregon. Life table information will provide developmental data as well as prey and environmental requirements. The overall objective is to develop life history data for *T. americanus* to support its use as a biological control agent for spruce spider mite in Douglas-fir and, perhaps, in other conifers as well.

Objectives and Rationale

At present, control of the spruce spider mite in Christmas tree plantations is achieved through large scale insecticide spraying. This is expensive both economically and environmentally. Helicopters are used to spray entire fields and use of miticides are generally followed by subsequent outbreaks due to the large scale loss of predatory mites (Nettleton et. al. 1977).

Cosmetic damage to the trees can cause a loss in value, the populations of spruce spider mite must be kept at levels low enough to ensure that no noticeable damage will occur. Since the phytoseiid predator *T. americanus* is often found in conjunction with the spruce spider mite, it is a good candidate for a biological control agent. The purpose of this project is to characterize the phytoseiid predator *T. americanus* in terms of its potential as a biological control agent. The long term goal is to use *T. americanus* as a part of a biological control program for the spruce spider mite in Christmas tree plantations.

Information such as a detailed life table providing fecundity, survival rate, and developmental time, as well as feeding preferences, active stages, and temperature and humidity requirements for egg development will be used to characterize *T. americanus*.

Methods and Materials

Rearing *T. americanus*

Typhlodromus americanus, initially collected from a Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) Christmas tree plantation in western Oregon, were reared on arenas modified from McMurtry & Scriven (1971). Lab colony arenas were constructed using plastic pan (22.5 x 22.5 x 5 cm), foam sponge (17.5 x 17.5 x 2.5 cm) and a square black plastic tile (17.5 x 17.5 cm) set on the sponge. Cotton batting or paper towel strips were folded over the edges of the tile into the water filled space between the sponge and the pan's edge. The wet cotton or paper towel served as a moisture barrier to keep the mites on the tile and as a source of water for the colony. Cover slips, with a few strands of cotton wool, were placed on the tile to provide a place for the mites to rest and lay eggs. Mites were held at room temperature and the relative humidity was held above 70%. Colony arenas were held in a chamber (57 x 40 x 15 cm plastic box) with salt solutions to control humidity (Winston & Bates 1960). Air was circulated in the box by an aquarium pump with tubing placed through a small hole in the lid. All predator mite transfers were made with a damp 5/0 spotters paint brush.

Rearing *Tet. urticae*

Predator mites were fed all stages of *Tetranychus urticae* (Koch) and Douglas-fir pollen three times weekly. *Tet. urticae* was reared on lima bean (*Phaseolus limensis* L.). Lima bean seeds were planted in plastic bags (40 x 30 cm) with small wholes punched in the bottom for subirrigation. The sides of the bags were folded over making it half the

original size and stiffening the walls. Bags were filled with horticultural grade vermiculite and seeds planted approximately 1 cm deep. Two bags were placed in plastic trays (38 x 25 x 14 cm). Seeds were allowed to germinate and grow for about 7 days (Scriven & McMurtry 1971). The plants were then infested with *Tet. urticae* by placing infested leaves on new plants. After 7 to 10 days, infested leaves were harvested. The eggs were collected by hand and transferred to the arenas with the 5/0 spotters paint brush.

Collection of *Oligonchus ununguis*

Over twenty - 7 foot Douglas-fir trees were examined for *O. ununguis*. The spruce spider mites were collected by vigorously shaking tree branches over a white piece of paper attached to a clipboard. A magnifying glass was then used to identify the mites and a damp 5/0 paint brush was used to place the mites onto a 50 X 9 mm plastic petri dish (Falcon # 1006, Becton Dickinson & C., Lincoln Park, NJ). The petri dish was coated around the inside edge with Tanglefoot^R (The Tanglefoot Co., Grand Rapids, MI) and a damp piece of cotton was placed in each dish to keep the humidity high. Mites were also provided with a Douglas-fir needle as food, and held at room temperature.

Effects of temperature and humidity on *T. americanus* eggs

Gravid female mites were allowed to deposit eggs over a 12 h period on a clean arena as described above. Eggs were placed in 50 X 9 mm plastic petri dish arenas which were held in a 22.5 X 22.5 X 5 cm plastic pan with a black plastic tile suspended by 90 X 15 mm petri dishes over salt solutions to control relative humidity of the surrounding air (Winston & Bates 1960). The arenas were held in an environmental chamber at constant temperature and 16:8 L:D photo period.

Temperature and relative humidity were varied to determine effects on egg mortality. Temperatures tested were 10, 18, 26, and 34°C. Mortality vs. temperature was examined in terms of a lethal temperature (LT₅₀) at a relative humidity of 70%. Relative humidities tested were 50, 70, 80, and 95%. Mortality vs. relative humidity was examined in terms of a lethal humidity (LH₅₀) at a temperature of 26°C (Croft et. al. 1993). Egg mortality was determined by egg desiccation or collapsing and recorded daily. Three replications of each temperature and relative humidity were made. Optimal temperature and humidity was determined for egg survival.

Life table construction

Life tables were constructed using laboratory cultures of *T. americanus*. Ten to fifteen gravid females were allowed to oviposit on a clean arena for 24 h then removed. This provided approximately 10 eggs for each cohort. The arenas consisted of 50 X 9 mm plastic Petri dishes with lids removed. The inside edge of each dish was coated with Tanglefoot^R which prevented escape of the mites. A cotton dental wick (1 cm diameter) protruding into the arena provided water. The arenas were held in 22.5 X 22.5 X 5 cm plastic pans at 26 ± 1°C and 70 ± 10% relative humidity and constant light. Mite development was monitored initially at 24 h intervals. Data were recorded on pre-printed data sheets. Data recorded were: 1.) number dead and mortality factors if determinable (unhatched eggs were recorded as dead), 2.) number of eggs at start of the experiment, 3.) larvae hatched from the eggs, 4.) number of protonymphs and deutonymphs successfully molted from previous stages, 5.) sex, and 6.) the number of eggs laid in each dish. Ten replications were made. From the data a complete diet life table was constructed following the methods of Carey 1993 (See appendix).

Effects of food type on life table parameters

Food type effects were addressed by studies on field-collected *T. americanus* reared in the laboratory. Ten to fifteen gravid females were placed on a clean arena and allowed to oviposit for 12 h and then removed providing approximately 10 eggs per replicate. The arenas were the same Petri dish design described above and were kept at $26^{\circ}\text{C} \pm 1^{\circ}\text{C}$ and $70\% \pm 10\%$ relative humidity. The food types used consisted of *T. urticae* and corn pollen as the basis of comparison, and individual pollens including corn, Douglas-fir, and oak. Mites were fed every other day and checked for mortality every day. Five replications of Douglas-fir, three of corn, and three of oak pollens were made. Data were collected as above and differences in development were compared by the intrinsic rate of natural increase (r_m) (Southwood 1992). Fecundity, adult survival, and generation time all effect the rate at which populations increase. All of these factors are combined in r_m as a indicator of food quality. Optimal food will provide maximum fecundity which will be evident in a high value for r_m .

Feeding requirements of larvae

Gravid females were transferred to clean arenas and then removed after 12 h yielding approximately 10 eggs. The eggs were observed through development to characterize larval feeding requirements. The larvae were unfed and kept with or without water. Five replications of each with and without water were conducted. These observations were used to determine larval developmental requirements. Data were then used to determine in which life stage, the larva or the protonymph food consumption began.

Egg consumption of different sexes and stages

Adult females of *T. americanus* were allowed to oviposit on a clean petri dish over a 12 h period. The eggs were placed singly into petri dishes that had been divided into four sections by Tanglefoot^R. The mites were fed *T. urticae* eggs only. Eggs were replenished every 12 h and consumed eggs were counted and removed. The mites were kept at constant temperature of $26^{\circ}\text{C} \pm 1^{\circ}\text{C}$ and a relative humidity of $70\% \pm 10\%$ throughout the trial. The mites were allowed to develop through adulthood, each isolated from contact with others. Females in the original trial were considered unmated due to the imposed isolation. Egg consumption for females and males and oviposition for females were recorded. Twenty-four individuals were raised in the experiment. An additional experiment using mated, egg laying females was made to determine prey egg consumption.

Adult unmated female egg laying behavior

Various stages of *T. americanus* up to deutonymph were isolated from the lab colonies in petri dishes divided into four sections by Tanglefoot^R. The eight female mites raised were given an abundance of food (*T. urticae* all stages) and allowed to develop to adulthood. Adult females were kept and males were discarded. Isolation ensured that the adult females were unmated. Females were given excess food and kept in a constant environment of $26^{\circ}\text{C} \pm 1^{\circ}\text{C}$ temperature and $70\% \pm 10\%$ relative humidity. Oviposition was recorded for the unmated females.

Observations of *T. americanus* feeding on *O. ununguis*

Randomly selected *T. americanus* from the lab colonies were taken and put in 50 X 9 mm plastic petri dishes that had the inside edges coated with Tanglefoot^R. A small piece of wet cotton was placed in the dish to provide water. Field collected spruce spider mites were removed from the paper using a 5/0 spotters paint brush. The mites were placed in a similar petri dish as described previously with the inclusion of a Douglas fir needle for transport and storing in the lab at room temperature. The spruce spider mites were transferred to the dishes with the *T. americanus* and interactions were observed. The number of eggs laid by *T. americanus* was recorded as well as the hatch of those eggs. Observations of the feeding behavior of *T. americanus* were also recorded.

Year long collection of *T. americanus*

Monthly samples of Douglas-fir branches were collected from a Christmas tree plantation in western Oregon (Sunrise Tree Farm, Kings Valley, Or). Fifteen to twenty branches were removed from the trees and returned to the laboratory. Samples were cooled in a refrigerator for at least 24 h to slow activity of the mites for easier collection. The samples were examined under a microscope for predator mites including dissection of one and two year old branch junctions. Permanent slide mounts were made of the collected mites. Specimens were mounted in Hoyer's (Krantz 1978), and labeled with location of collection, date, and identification. The number and species of each predator mite and its date of collection were recorded on a data sheet.

Results

Collection of *Oligonychus ununguis*

The spruce spider mite (*O. ununguis*) proved very difficult to rear experimentally because they live on conifers. Therefore, when spruce spider mites were needed for prey, they were collected from the field. The first sample of spruce spider mites collected were held in petri dishes without food or water. They all died within 24 h. The second and subsequent samples were provided with Douglas-fir needles and a piece of cotton wicking soaked in water. The mites survived for three to four days under these conditions. The mites were not observed to feed or drink. Generally, eggs were laid on the Douglas-fir needles provided, and only rarely on the petri dish surface. The eggs were firmly attached to the substrate and all attempts to remove them resulted in severe damage. All eggs failed to hatch.

Effects of temperature and humidity on egg hatch

I measured the effects of ambient temperature and humidity on egg hatch. I tested temperatures between 10 to 34°C and relative humidities between 50 and 95%. These extremes represent the conditions I encountered under summer field conditions in western Oregon.

For temperatures less than or equal to 26°C percent hatch was above 93% (Table 1). At 34°C however, percent hatch dropped significantly to about 28% (Table 1). Although the shortest development time was at 34°C it was not significantly different from the development time at 26°C. Note that the highest standard errors were at the extreme temperatures perhaps indicating a certain degree of developmental plasticity.

This mite is capable adjusting its development to the surrounding conditions with in limits set by the temperature extremes of less than 10° and less than 34°C. Overall the mite has a high survival rate at moderate to low temperatures as compared to temperature that would be considered extreme in the field. The linear regression of temperature versus time to eclosion was best fit by the multiplicative form of the regression model ($\ln Y = \ln a + \ln(x)$, Figure 1). R^2 was above 90% and both the slope and intercept were significantly different than zero ($P < 0.0001$).

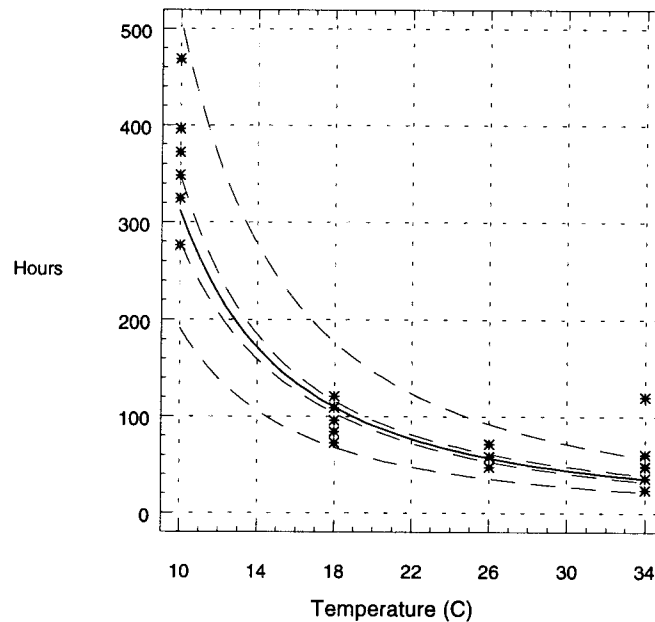
Table 1. Mean hours to eclosion of larvae and percent hatch of *T. americanus* eggs at different temperatures. RH= 70%, 16 : 8 light : dark phases.

°C	n*	Hatch(%)	Hours	SE
34	28	28.6	51.2a ¹	10.8
26	28	96.4	54.4a	1.5
18	20	100.0	102.0b	3.1
10	16	93.8	340.4c	12.8

* no. of eggs at each temperature

¹ Means followed by the same letter within a column are not significantly different ($P > 0.05$; LSD test).

Figure 1. Regression of temperature vs. time to eclosion for *T. americanus*. Regression using surviving eggs only. $\ln Y = \ln 9.84 - 1.78(\ln X)$. Slope and intercept significant at <0.0001 , $R^2 = 0.904$. Dotted lines represent the 95% confidence and prediction limits respectively.



I also measured the time to eclosion for eggs held at relative humidities between 50 and 95%. The eggs held at humidities above 70% nearly all hatched, but those at lower humidities were not as successful (Table 2). The shortest eclosion time was for eggs held at 50% RH but this was also the lowest hatch at only 4.2%. Mites held at 95% relative humidity had 100% survival, but their development rate was 15 hr longer. Overall the percent hatch decreased as the relative humidity decreased.

Lethal humidities (LH) calculated for the population were all within 15% of each other (Table 3). The lethal humidity for half of the population (LH_{50}) was 58.6%. The slope for the regression line was steep (-24.2), suggesting a rapid response to changes in humidity, especially at the lower humidities in the experiment.

Table 2. Mean hours to eclosion of larvae and percent hatch of *T. americanus* eggs at different relative humidities. Temperature 26°C, 16 : 8 light : dark phases.

%RH	n*	Hatch(%)	Hours	SE
95	18	100.0	50.5a ¹	2.0
80	20	100.0	57.7bc	1.2
70	28	96.4	54.9ab	1.4
60	21	52.4	62.2c	3.9
50	24	4.2	35.5	0.0

* no. of eggs at each treatment.

¹ Means followed by the same letter within a column are not significantly different (P<0.05; LSD test).

Table 3. Lethal humidities for *T. americanus* eggs held at 26° C, 16 : 8 light : dark phases.

Lethal Humidity	Humidity (%)	Limits
LH ₁₀	66.1	63.3 - 71.1
LH ₅₀	58.6	56.1 - 60.9
LH ₉₀	51.9	47.6 - 54.5

Slope = -24.2 ± 4.3 , n = 111. Slope and limits from Polo-PC (1987).

Life table parameters

Life table analysis was used to determine the average life span, time in each stage, and requirements of the larval stage. Diet was varied to determine what foods were necessary for development and reproduction. Life table parameters are given in Table 4. The r_m of *T. americanus* as compared to other phytoseiid mites is given in Table 5.

Table 4. Life table parameters of *T. americanus* held at 26°C and 70% RH fed *Tet. urticae* and corn pollen.

Net Reproduction rate R_o (per generation)	4.225
Mean generation time T (days)	24.453
Intrinsic rate of increase r_m (per female per day)	0.059
Finite rate of increase (λ) (per day)	1.061
Doubling time (days)	11.762

Typhlodromus americanus passes through five stages; egg, larva, protonymph, deutonymph, and adult. Larvae do not require food to molt to protonymphs. Eggs placed in a petri dish without food or water developed into larvae and then protonymphs with a survival rate of 70%. The entire survival time for egg stage to death of the protonymph was about six days (Figure 2). The protonymphs died after a short time. Those mites provided with water lived about 4 days longer than those not given water (Figure 2). Therefore mites with access to water have approximately 4 days longer to find the food necessary to continue development at least under these conditions.

Table 5. Intrinsic rate of increase (r_m) for selected Phytoseiid mites.

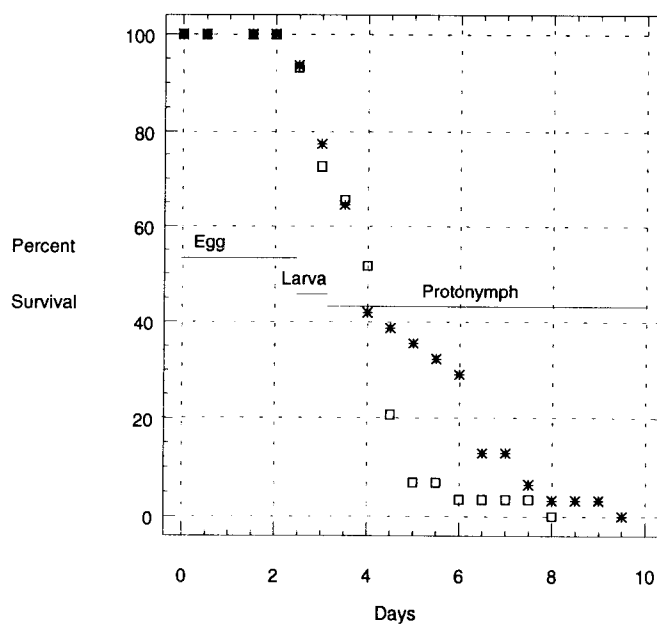
Species	r_m
<i>Typhlodromus americanus</i>	0.059 ^a
<i>T. pyri</i>	0.076
<i>Amblyseius potentillae</i>	0.188
<i>T. occidentalis</i>	0.190
<i>A. barkeri</i>	0.22 ^b
<i>Phytoseiulus persimilis</i>	0.374

* All values from Helle & Sabelis 1985 unless marked.

^a Value from life table.

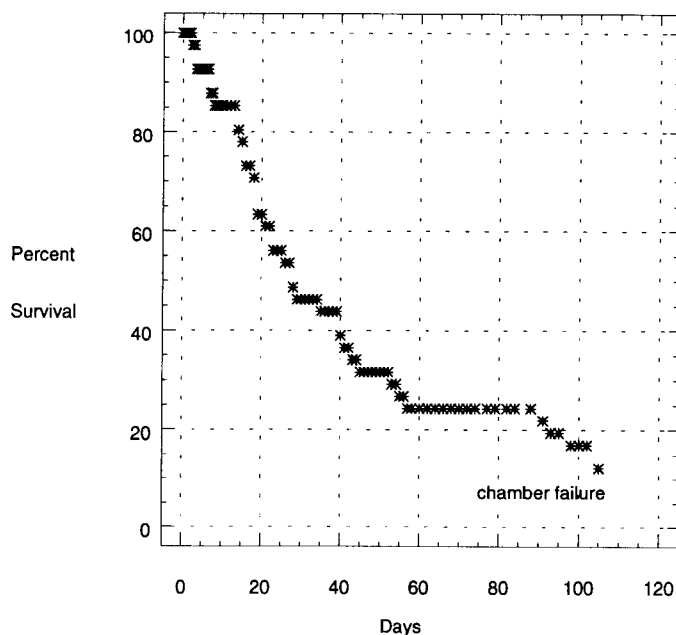
^b Bonde 1989.

Figure 2. Survival of unfed immature *T. americanus* at 26° C / 70%RH. = without water, * = with water.



Typhlodromus americanus was extremely long lived when provided with a complete diet of *Tet. urticae* and corn pollen (Figure 3). The predator mites lived over 100 days and the experiment was ended only due to the failure of the environmental chamber. Extreme high temperatures caused by the failure of the cooling system killed some of the mites, but even at temperatures of over 40°C some of the mites survived a short time. By the slope of the line, I estimate that maximum survival could have been as long as 120 days under normal conditions (Figure 3).

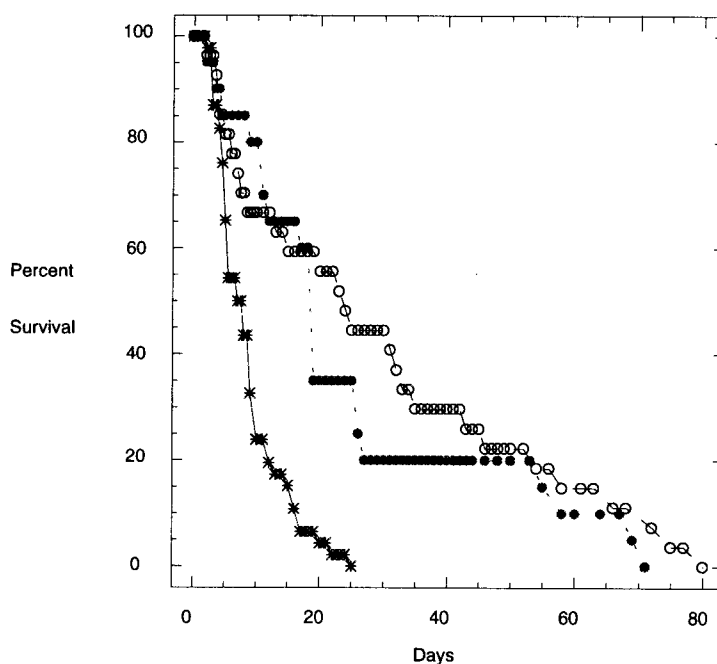
Figure 3. Survival of *T. americanus* fed corn pollen and *Tet. urticae* (complete diet). Environmental chamber failure occurred at approximately day 115.



Predator mites that were given an incomplete diet (pollen only) did not survive as long as those given a complete diet of pollen plus all stages of prey spider mites (Figure 3 & 4). Those mites given only corn pollen survived the longest, about 80 days. Survival on oak pollen was the next longest with the oldest mite reaching 70 days. Douglas-fir pollen

produced the shortest survival time, with mites living only about 25 days and not reaching adulthood (Figure 4). This would seem unusual as these mites are living in Douglas-fir plantations and this would be the most available pollen.

Figure 4. Survival of *T. americanus* fed corn pollen, oak pollen, and Douglas-fir pollens. ° = corn pollen, ● = oak pollen, and * = Douglas-fir pollen.



T. americanus given corn pollen plus *Tet. urticae* (the complete diet) took an average of 9.08 days to develop from the egg to adult. Stage duration (Carey 1993) for each stage is given in Table 6. The larval stage was the shortest stage as only about half a day. All other stages required two to three days. Duration for the immature stages was assumed to be the same for males and females because I could not distinguish them as immatures. From the 41 eggs laid, 26 females and 6 males survived to adults for a sex ratio of 4.3 females to males.

Table 6. Stage duration¹ for immature stages of *T. americanus* fed two different diets at 26°C, 70% RH and 16 : 8 light : dark phases.

Stage	Corn pollen + TSSM			Corn pollen only		
	N	Days	Var.	N	Days	Var.
Egg	41	2.56	0.29	27	2.38	0.60
Larva	40	0.68	0.07	27	0.62	0.06
Protonymph	38	3.05	0.08	27	2.15	0.12
Deutonymph	38	2.79	0.58	25	2.54	0.10
Total Immature	---	9.08	1.02	--	7.69	0.82

¹ Carey 1993.

Mites given the incomplete diet (corn pollen only) required one and a half days less time to develop (7.69 versus 9.08 days, Table 4). Duration for the immature stages was also assumed to be the same for females and males, the same as for those given the complete diet. From the 27 eggs laid in this experiment, of those surviving to adulthood 14 were female and 6 were male. This is only 2.3 females for every male, suggesting that the ratio of females to males is biased toward the females overall. The egg and larval stages were roughly the same as those from the complete diet. The significant difference was in the protonymph stage. Those mites given corn pollen only took almost an entire day less to develop to deutonymphs. The time required for prey manipulation could be a factor in lengthening the time required by those mites given the complete diet. The energy used for searching and manipulation, as well the time for manipulation would increase the time needed for development.

Reproduction coincided with a steady decline in survival, but when egg laying ceased the survival curve flattened out (Figure 5). *T. americanus* fed the complete diet began laying eggs after about ten days and continued until almost the 60th day. Egg production peaked at about the 20th day. The egg production then decreased steadily along with the decrease in percent survival. By the 60th day the mites had stopped laying eggs. The decrease in percent survival also stopped for over 20 days after the mites stopped laying eggs. The egg production period for these mites was almost 50 days. Over these 50 days, egg production was fairly constant (Figure 6). However, those females without access to males did not oviposit at all.

Figure 5. Number of eggs laid and survival of *T. Americanus* vs. days.

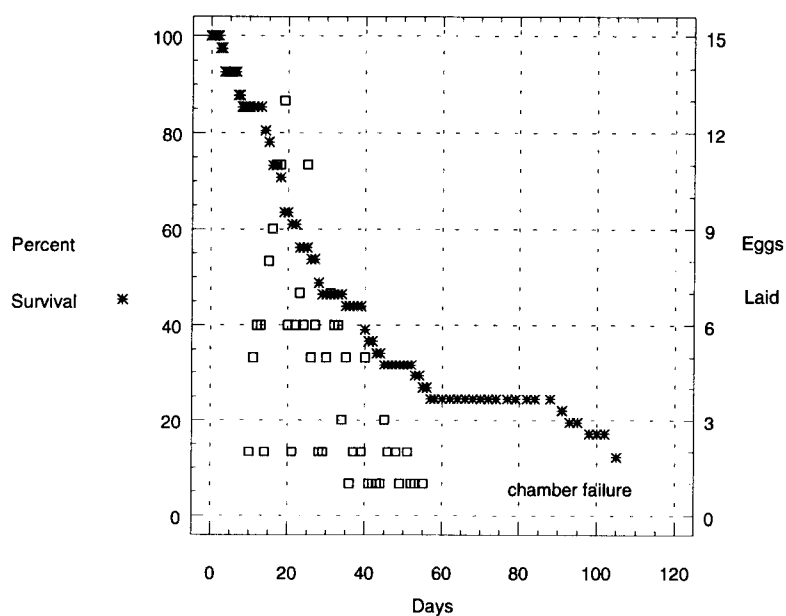
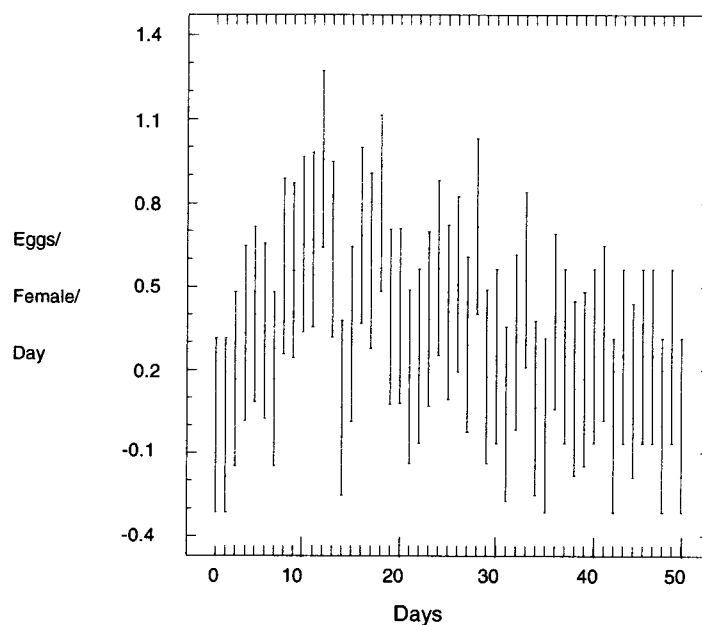


Figure 6. Mean egg production \pm s.e. for *T. americanus* at 26° C / 70% RH.



By comparison the *T. americanus* fed the incomplete diets of oak, corn and Douglas fir pollens did not produce eggs. However, predator mites held on *Tet. urticae* alone did successfully oviposit. Altogether, the complete diet of *Tet. urticae* and the incomplete diets of corn and oak pollen provided for long survival, while those mites raised on Douglas-fir pollen were shorter lived and did not reach adulthood. The complete diet and *Tet. urticae* alone allowed for reproduction. Therefore nutritional stresses are likely to hinder the reproductive process for these mites.

Egg consumption by different sexes and stages of *T. americanus*

Tet. urticae eggs alone are sufficient for normal development of *T. americanus* from egg to adult (Table 7). The number of *Tet. urticae* eggs consumed for each stage of

each sex as well as for mated and unmated females was determined. Larvae did not feed before molting. Male and female protonymphs and deutonymphs when taken individually, consumed roughly the same number of eggs. However, the total number of eggs consumed for all immature stages was significantly different between the two sexes with males consuming 68.7 ± 7.6 eggs and females almost double this number (100.3 ± 6.2 , $P < 0.009$). Adult females also consumed significantly more eggs per day (29.4 ± 1.8) than did adult males (17.3 ± 1.9 , $P < 0.0005$). Finally, unmated females ($N = 7$) consumed fewer *Tet. urticae* eggs (29.4 ± 1.8) than did mated females ($N = 6$, 43.6 ± 4.9). These were also significantly different at $P < 0.01$ (LSD test).

Table 7. Egg consumption by life stage for *T. americanus* fed *Tet. urticae* eggs. 26° C / 70% RH.

Stage	Eggs Consumed						
	Male	SE	N	Female**	SE	N	P*
Larva	0.0	0.0	11	0.0	0.0	7	N/A
Protonymph	29.9	4.5	11	45.1	9.2	7	0.12
Deutonymph	38.5	6.4	11	55.1	3.9	7	0.07
Total Immatures	68.7	7.6	11	100.3	6.2	7	0.009
Adults (daily)	17.3	1.9	11	29.4	1.8	7	0.0005

* LSD; ** unmated females, no eggs laid.

Observations of *T. americanus* feeding on *O. ununguis*

I observed *T. americanus* feeding on *O. ununguis* to determine if the predator was actually feeding on this particular spider mite species and how the prey mites were captured and manipulated. I placed five predatory mites in a petri dish with spruce spider mites collected from the field. *T. americanus* voraciously attacked the motile stages of *O. ununguis*. However, I did not observe the predator attacking any prey eggs and I did not find any eggs that looked as though they had been attacked. The predator mite would actively search for prey, but would seldom pursue those prey mites that were not originally contacted from the front. Most of the observed attacks on adult prey were frontal. Predators used their front legs to grab the prey mites by a front leg. After puncturing the front leg of the prey, the predator used it as a straw to suck out the hemolymph. This is not the method used normally by mites well adapted to the prey species being fed on (Croft personal communication). Food could be observed moving into the digestive track and coloring the mites green. After several days, the mites would regain their normal coloration (a tannish color) with only a few dark spots in the digestive track.

During the observation period of 6-8 days, four of the female predator mites laid a total of six eggs. Only two of these eggs subsequently hatched. Of the remaining four, three did not hatch and mold was observed on their surfaces, and the final larva did not fully eclose. Of the two successful eclosions, one larva died in the Tangle trap surrounding the dish and the other was lost from observation.

Monthly collection of *T. americanus*

I collected branch samples during the dry periods of selected months of the year to determine at what times of the year the predator is present in field-grown Douglas-fir. The field was located about 12 miles from Corvallis, in Kings Valley, Oregon. Spruce

spider mite is considered to be an early and late season pest of Douglas-fir grown for Christmas trees, so I sampled the branches to determine if the predator mite was present at these times of the year. Only one sample (June, 1994) yielded no *T. americanus* (Table 8). The predatory mite was even found in adult form during the winter months and was active when brought into the lab. This mite is present all year and over winters in at least the active adult stage.

Table 8. Monthly samples of Douglas fir branches for *T. americanus*.

Year/Month	no. of branches	no. of <i>T. americanus</i>
93/August	20	3
94/January	18	2
94/March	18	1
94/April	19	2
94/June	17	0
94/July	19	9
94/August	20	10

Discussion

Typhlodromus americanus (Chant & Yoshida-Shaul) appears to be a good candidate for a biological control agent of spider mites in Douglas-fir tree plantations. This predator exhibits a wide host range including pollens and Tydied sp. in addition to the spruce spider mite (West & DeAngelis 1993). It appears to continue to develop and be active during every season, even during the winter months and, it can survive for long periods of time in the absence of prey mites. However, it reproduces slowly and therefore is unable to respond numerically during outbreaks of prey mites.

Life table parameters

The r_m (intrinsic rate of increase) of *T. americanus* (0.059) was extremely low as compared to other phytoseiid mites. Other mites in the *Typhlodromus* genus such as *T. pyri* also have relatively low r_m . The intrinsic rate of increase is a determinant of a mites ability to multiply in a closed stable population where age specific fertility and mortality has converged (Carey 1993). This rate can be influenced by food type. The rate is determined in the absence of competitors and with an abundance of food, which should be the ideal conditions for maximal r_m . *T. americanus* lambda (daily finite rate of increase) was 1.061 which is lower than the rate estimated for a predator that would numerically respond to outbreak populations of prey (Helle and Sabelis 1985).

Typhlodromus species that have been studied require multiple matings for maximal egg production (Castagnoli & Liguori 1991, Helle & Sabelis 1985). Unsuitable foods can also lower fecundity. Females that do not get proper nutrients may either fail to reproduce or have a very low fecundity (Amano & Chant 1986, Castagnoli & Liguori 1991, Helle & Sabelis 1985). Small numbers of males compared to females and lack of males in some trials might account for low egg production. Females might have been denied access to males simply because males could not mate with all females available.

Males that do not get proper nutrients may have problems producing full compliments of sperm, lowering the number of fertilized eggs that can be produced by females (Helle and Sabelis 1985). Artificial substrate may have also caused some problems for mites. Cover slips provided for egg laying may have been unsuitable. Smooth surface area of the plastic dish and lack of natural cover may also have induce increased activity and searching behaviors (Croft & Zhang 1994).

Low rate of egg production and extremely long survival found in the laboratory experiments might indicate that the experimental diet was not adequate for maximum fecundity (Croft personal communication). Scriven and McMurtry (1964) and Amano and Chant (1986) used a combination of eriophyid and tetranychid mites as prey for *Amblyseius hibisci* and found a significantly increased rate of oviposition over use of tetranychids as sole prey. Energy normally used for egg production probably provided mites with the ability to live for longer periods of time than would normally be found with a proper diet. A variety of food sources in combination might be required to give the maximum intrinsic rate of increase (Castagnoli and Simoni 1990).

Food requirements

The influence of different diets on the development of immature stages of phytoseiids mites has been the focus of many studies. Food quantity and quality have major effects on developmental times and fecundity (Amano & Chant 1986, Castagnoli & Simoni 1990, Croft & Croft 1993, Freise & Gilstrap 1985, Helle & Sabelis 1985, McMurtry & Scriven 1964, Ramsy et. al. 1982, Ragusa 1981). Food requirements for individual phytoseiid mites vary. In their natural habitat, a wide variety of foods are available such as live prey, pollen, honeydew, and plant juices. (Castagnoli and Simoni 1990). *Typhlodromus americanus* is associated in the field with various conifer pollens, spruce spider mites (*Oligonychus ununguis*), eriophyid, and tydeid mites (West & DeAngelis 1993). Many phytoseiids in the genera *Typhlodromus* and *Amblyseius* have

been classified as generalist predators. Possible alternative preys have been identified as eriophyid, tydeid, and tarsonemid mites (Lindquist 1983). *T. americanus* was observed feeding on an unknown tydeid mite as well as on the spruce spider mite in Christmas tree plantations (West and DeAngelis 1993). Preferences for specific species of prey have been documented amongst other phytoseiids (Helle and Sabelis 1985). A study of prey preferences for *T. americanus* would be valuable for its potential to discover alternative food sources. Gut content analysis of mites collected from the field is suggested as the most reliable way to determine what foods predators are utilizing (Helle and Sabelis 1985). Since tydeid mites are not pests and are believed to feed on pollens, addition of pollen to fields could increase their numbers (Calvert and Huffaker 1974), and increase the food base for predators when the spruce spider mite is not present in large numbers.

Pollen is an ideal food source in that it is easily obtained and does not require the handling time that live prey requires. *T. exhilaratus* developed to adult and was able to reproduce using *Carpobrotus* sp. (sea fig) pollen as its sole food source (Castagnoli & Liguori 1991). *T. americanus* also developed to adulthood on all pollens tested except Douglas-fir, but was unable to reproduce in these experiments. However, a small colony given Douglas-fir pollen was observed to reach adult and produce a small number of eggs. This is not uncommon; other phytoseiids such as *Amblyseius californicus* sp. (Friese & Gilstrap 1985), *Phytoseiulus* sp., and *Typhlodromus* species (McMurtry & Scriven 1965) do not reproduce on pollen after the first generation. *A. californicus* has a lower survival rate for immatures developing on *Malephora crocea* (Coppery mesemb) pollen as well. This however would seem to be variable within a genus as McMurtry and Scriven (1965) raised six different *Amblyseius* species on *Mesembryanthemum* sp. (ice plant) pollen and reported good results for every one. Pollen source is very important as nutrient values of each species of pollen is different. Eleven of 23 pollens fed to *Amblyseius hibisci* were accepted and allowed survival and reproduction (Kennett et al. 1979). Besides variable nutrients in each pollen the size and resistant wall layer (exine) can play a role in pollen suitability (Helle & Sabelis 1985).

Prey consumption of phytoseiid mites varies between life stages and sexes. Each stage and sex has different requirements depending on its length and life history function. Larvae are non-feeding and inactive. Egg and larval stages do not require any food to molt to the next stage. *T. americanus* larvae are inactive, nonfeeding as opposed to other larvae described as active feeding and the rare active non-feeding type (Bonde 1989).

The protonymph and deutonymph stages of *T. americanus* feed voraciously. Females consumed significantly more (over 30%) than males. This can be attributed to size differences, with females eating more to develop larger body mass required for egg production (Helle and Sabelis 1985). Low food levels can retard or stop development of immature stages and cannibalism is common in some mites when phytoseiid prey densities are low (Helle and Sabelis 1985). *T. americanus*, however, did not show any obvious cannibalistic tendencies.

Egg laying females require a larger amount of prey as compared to non-egg laying females and males because egg production requires high amounts of nutrients (Bonde 1989, Helle and Sabelis 1985). Reproducing *T. americanus* females consumed one third more prey than non-reproducing females. *T. americanus* males are only two thirds the size of females, and when compared to non-reproducing females, they consumed only two thirds the amount of prey.

The influence of prey and pollen on development of *Typhlodromus exilaratus* been studied (Ragusa 1981). In these studies, *T. exilaratus* developed faster on a number of pollens than on prey (Castagnoli & Liguori 1991 & 1986, Ragusa 1981). Similarly in my studies, *T. americanus* took one and a half days less time to develop from egg to adult when given pollen alone. *T. americanus* and *T. exilaratus* both have non-feeding larvae, and only protonymphs and deutonymphs fed on prey. Time difference in development between those predator mites raised on pollen and those raised on prey may be accounted for by some a factor such as more time required for capture, handling and consumption of the prey. Ragusa (1981) suggested that webbing produced by prey mites such as *T. urticae* could impede movement and searching activities of immature mites as it does

adults. Prey mites that do not produce webbing could lessen the difficulty immatures have in procuring food and therefore reduce developmental times.

Some phytoseiids have a higher survival rate for immatures raised on pollens than for those raised on live prey. *Amblyseius cucumeris* exhibited ten percent higher survival on pollen than on tetranychid prey (McMurtry & Scriven 1965). *T. americanus* raised on the combined diet of pollen and tetranychid prey had only a single fatality more than those raised on pollen alone. This difference in combination with the fact that *T. americanus* does not readily reproduce on pollens suggests that tetranychid prey is a better food source and is required for production of subsequent generations.

Unsuitable foods such as those lacking beta-carotene were shown to cause a lack of diapause response in *Amblyseius potentillae* (Helle and Sabelis 1985). Unsuitable foods can also induce diapause and cause females to stop egg production while still allowing them to survive for long periods of time, thus affecting fecundity (Amano and Chant 1986, Schuster and Murphy 1991). Laboratory conditions do not offer the wide variety of food available in the field and therefore these situations are not able to tap the full potential of mites.

Environmental requirements

Besides the affect of food availability, juvenile mortality of *T. americanus* can be largely attributed to temperature and humidity. Temperature and humidity are physical factors which have immense effect on survival of phytoseiid mites (Helle & Sabelis 1985). Ranges of survivable temperatures and humidities are often consistent with those found in the habitat of the mite. The egg stage is highly susceptible to high temperatures and low humidities. Eggs can be severely desiccated by high temperatures and low humidities and will not hatch. Larvae and nymphs are less susceptible to low humidities and high temperatures in that they can move to new sites and can get water by drinking or prey consumption. In addition, the ability to cannibalize other predator mites when prey

are not abundant gives those species who do not use alternative foods such as pollens, a chance to complete development. Adults are the least susceptible stage as they can also move to new locations for water and prey and are capable of living for longer periods of time with out food (Helle & Sabelis 1985).

The LH_{50} (58.6%) for *T. americanus* is reasonable considering humidities encountered in Christmas tree plantations where it is found. The climate of western Oregon where these mites were collected is moderate, without long periods of extreme temperatures (high or low) or lack of moisture (personal observation). This would also conform with the moderate RH of 50-60% in which the spruce spider mite has the highest fecundity and longest survival (Boyne & Hain 1983). Phytoseiid eggs fail to hatch if immersed in water or if exposed to high humidity of approximately 100% RH (Helle and Sabelis 1985). High humidities did not have adverse affects on *T. americanus* eggs. I observed that *T. americanus* laid eggs under cover slips in the laboratory and at the base of the previous years growth in the field on Douglas-fir branches. This choice of egg deposition sites is protected and generally is less susceptible to desiccation.

Mites are poikilothermic, so temperature determines the rate at which they develop. Development of most phytoseiids is linear within a range of 15° to 30°C (Helle and Sabelis 1985). The lowest temperature at which each species of mite will develop is different as is the total development time at each temperature. *Typhlodromus doreenae* has a lower threshold of 8.4°C which allows it to develop during winter in Australia. *T. americanus* took 14 days to develop at 10°C. *T. americanus* would be able to develop during the winter in Christmas tree plantations where temperatures are often above 10°C. Adults of *T. americanus* are also active at this temperature. Egg development can be impeded by high temperatures as well, as with *T. doreenae* at 37.5°C. Only 28% of *T. americanus* eggs survived to hatch at 34°C. High temperatures reduce survival and do not significantly shorten developmental time between 26° and 34° C. Adults can survive at these higher temperatures for short periods of time. Failure of the environmental chamber in one experiment caused a group of mites to be exposed to temperatures in excess of

40°C for a period of at least 12 hours. These mites were still alive and active when discovered.

Conclusions

Typhlodromus americanus is like *T. pyri*, a generalist predator, not relying on any one species of prey and is capable of using pollen and plant resources during times of prey shortage (Croft and Zhang in press). *T. americanus* seems well suited to surviving when spruce spider mite populations are low. This predator would be a good biological control agent to keep spruce spider mite at low levels. It would not however be a good control agent after outbreaks. It does not respond numerically to prey population increases (low fecundity). Its use of other food sources also suggests that it does not have a high specificity for the spruce spider mite.

Since this mite has such low fecundity and a complex diet it would not be a good candidate for mass rearing. The best way to increase the populations of this mite is to manage plantations for natural populations. Spot spraying trees with high numbers of spruce spider mite instead of whole field sprays would allow predator populations to survive within fields and recolonize the sprayed trees. Allowing fields to have species complexes similar to natural tree stands, such as ground cover and other predatory species, will also encourage *T. americanus* abundance. Further research should be done on this mite's habitat and food sources to discover its main function in this complex system.

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APPENDIX

Data Analysis

Information such as the date, chamber number, food type, temperature, RH, and species of mite was recorded at the top of the sheet. (Figure 1A.) Data recorded for the construction of the life table were:

1. time (h) since start of observation
2. number dead at observation
3. number of eggs remaining
4. number of larvae present
5. number of protonymphs present
6. number of deutonymphs present
7. number of adults present and sex of adults
8. number of eggs laid since the last observation
9. and cause of death if known

Standard formulas from Carey (1993) were used to calculate the life table parameters. The calculations for each life table parameter are given below along with an explanation of the formula.

Net Reproductive Rate

$$R_0 = \sum L_x m_x$$

Where $L_x = l_x - 1/2d_x$. l_x is the proportion surviving from birth to the age x (# of individual at start of experiment minus the number dead at the given time x . d_x is the fraction dying between the interval x and $x+1$ (# dead at end of interval x divided by the # of individuals at start of experiment). m_x = the age specific number of female offspring per female (the total # of daughters produced by the original individuals divided by the total number of females at the midpoint of the time period between x and $x+1$). More than

50% of the offspring were female in the experiments, so I used the experimental percentage of 69% females in this calculation. This is the average number of females that will be born to the original cohort females.

Mean Generation Time

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x}$$

Where l_x and m_x are as described above and x is the exact age of the mite at that interval. This is the amount of time it will take to increase the population by a factor equal to the net reproductive rate.

Intrinsic Rate of Increase

$$r_m = \ln R_0 / T$$

Where R_0 and T are calculated from above formulas. This is the rate of natural increase in a closed stable population with a constant age specific schedule of births and deaths.

Finite Rate of Increase

$$\lambda = e^{r_m}$$

Where e is a constant and r_m is as described from above. This is the daily growth rate of the population.

Doubling Time

$$DT = \ln 2/r_m$$

Where the $\ln 2$ is constant and r_m is as described from above. This is an expression for geometric increase that gives the time required for the population to double in size.

Figure A1. Data sheet example.

[illegible]