Life history, survivorship and parasitoid complex of the jumping gall wasp, *Neuroterus saltatorius* (Edwards), on Garry oak, *Quercus garryana* Douglas.

by

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We accept this thesis as conforming
to the required standard

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ABSTRACT

Garry oak, *Quercus garryana* Douglas, ecosystems on Vancouver Island currently occupy <1% of their original distribution and are threatened mainly by urban encroachment and industrial development. The recent population increase of an oak gall wasp, *Neuroterus saltatorius* (Edwards) (Hymenoptera: Cynipidae) has caused extensive leaf necrosis and foliar scorching and has added to the concern for the long-term health of this native species. Cynipid communities tend to be regulated by parasitoids (Hymenoptera: Chalcidoidea) and as a result, are normally found at non-damaging levels. The high gall wasp infestation levels and rapid spread throughout *Q. garryana* stands on Vancouver Island might have arisen because of the accidental introduction of this species (c.1986) without the associated parasitoid community. The objectives of this study were to examine the life history and describe the mortality factors of *N. saltatorius.*

Eight sites on southern Vancouver Island, reflecting a range in infestation ages, were surveyed in 1992-94. Gamic females were larger, emerged over a shorter period of time and had a greater number of smaller eggs than agamic females. Agamic galls began to drop during June and the peak drop occurred from the end of June to the middle of July; pupae and adults were found in galls in the soil by the middle of September.

Three chalcidoid species were recovered from the gamic generation and ten emerged from the agamic generation; *Mesopolobus* sp. nr. *longicaudae* Donganlar was the most common in the gamic generation and *Aprostocetus pattersonae* (Fullaway) and *Amphidocius schickae* (Heydon and Boucek) were the most common in the agamic generation. *Amphidocius schickae* and *Aprostocetus verrucarii* (Balduf) were also identified as hyperparasitoids. The parasitoid complex of *N. saltatorius* was found to have a high degree of overlap with other oak gall wasps found in B.C. prior to this infestation but peak parasitoid emergence occurred after most of the agamic galls had fallen to the ground.

Gamic generation survivorship was very high; mortality factors principally affected survivorship in the agamic generation. Contrary to most studies, it was found that chalcidoid parasitoid attack was not a large contributor to host mortality possibly due to poor synchrony of parasitoid activity with *N. saltatorius* development. The greatest sources of mortality for agamic generation galls on the foliage were failed development, fungal infections and desiccation. Survivorship in the agamic generation was found to be lowest in populations of *N. saltatorius* at older infestation areas. The low number of viable galls collected at older sites might indicate that mortality from several sources will cause a decline in local jumping gall wasp populations.

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DEDICATION

This thesis is dedicated in the memory of my Grandma, Ena Maidens.

INTRODUCTION

Garry oak and associated insects

The distribution of Garry oak, *Quercus garryana* Dougl., extends from the Santa Cruz mountains in California northward to coastal areas of Washington and British Columbia (Glendenning 1944; Stein 1990). It is the only native *Quercus* found in B.C. and Washington and is the principal species in Oregon; its geographic range spans more than 15° latitude and occupies 106,000 km^2 (Washburn and Cornell 1979). Garry oak is a slow growing tree (Elias 1987) with an irregular form that occupies dry, south or west facing slopes in British Columbia. In B. C., Garry oak occupies dry, south or west facing slopes and is found growing along the southeastern portion of Vancouver Island, from Victoria north to Merville, and on the adjacent islands in the Gulf of Georgia ; isolated groves are located at Port Alberni (probably planted), Sumas Mt. and Yale (Krajina *et al.* 1982). Locally known as Garry oak, *Q. garryana* is also referred to as white oak, post oak, Oregon white oak, Brewer oak or shin oak in other parts of its range (Stein 1990).

Historically, Garry oak appears to have evolved as a component of arid pine -oak forests that have repeatedly advanced northward and retreated as North American climates have warmed and cooled. Oak regeneration continues but many oak stands are being invaded and superseded by maples (e.g. *Acer macrophyllum* Pursh) or conifers (primarily *Pseudotsuga menziesii* (Mirb.) Franco) and threatened by urban encroachment and industrial development (Nuszdorfer *et al.*, 1991). Hebda (1993) and Stein (1990) both state that unless steps are taken to reverse the pressures on this species, its position as a prominent component of the western flora will continue to diminish.

Quercus garryana is an architecturally complex plant that supports a large number of arthropod species. On Vancouver Island, Evans (1985) recorded greater than 800 species of insects and mites associated with *Q. garryana*; 140 feed directly on this host and several of these are gall formers (Duncan pers. comm.). Galls are formed on more than 60 plant genera by species of at least eight arthropod orders but midges (Diptera: Cecidomyiidae) and wasps (Hymenoptera: Cynipidae) are the two major groups (Shorthouse 1973). Galls are formed on every part of the plant, including the roots, stems, leaves, flowers and acorns and the majority are found on *Quercus* and *Rosa* spp.

Insect damage to *Q. garryana* is usually not severe or long-lasting and mortality is uncommon (Evans 1972). However, high insect population levels often attract our attention, especially if the host tree is of conservation importance. Winter moth, *Operophtera brumata* (Linn.), (Lepidoptera: Geometridae) western oak looper, *Lambdina fiscellaria somniaria* (Hulst) (Lepidoptera: Geometridae), an oak leaf phylloxeran, *Phylloxera* sp. nr. *glabra* (Heydon) (Homoptera: Phylloxeridae) and a leaf roller, *Pandemis cerasana* (Hubner) are widely distributed phytophagous feeders, with a preference for *Q. garryana* (Evans 1985; Stein 1990). In British Columbia, severe outbreaks of the winter moth occurred in the late 1970's and early 1980's and threatened to cause severe, long-lasting effects on the health of *Q. garryana* (Roland 1986). The release of a parasitic tachinid fly, *Cyzenis albicans* (Fall.) and an ichneumon wasp, *Agrypon flaveolatum* Grav. , have functioned to reduce populations to non-damaging levels (Embree and Otvos 1984; Roland 1994), although inter-year fluctuations occasionally draw attention to this species as a serious threat to the health of the oaks.

Biology of cynipids and *Neuroterus saltatorius*

Gall forming by the Hymenoptera is remarkable for its complexity of structure and ecological relations (Mani 1964). Throughout North America, the genus *Quercus* is host to over 600 cynipid gall formers (Borror *et al.* 1989) of which 112 species are known to occur along the Pacific Coast (Weld 1957).

Cynipids (Hymenoptera: Cynipoidea) have a worldwide distribution (Weld 1957). There are about 1000 species described for the Cynipinae worldwide and this subfamily is the sole representative in north temperate areas (Gauld and Bolton 1988); the classification and description of North American Cynipinae has been done by Kinsey (1923) and Weld (1957). All members of this subfamily are either gall makers or inquilines that is, a gall inhabitant that does not directly attack the gall maker but feeds on the gall tissue (Shorthouse 1973). The size and shape of the gall is indicative of each species since each species produces a unique gall type (Rosenthal and Koehler, 1971a). Secretions from ovipositor accessory glands are injected during oviposition and stimulate gall development (Mani 1964; Cornell 1983). Galls provide nutrition as well as protection from the physical environment and natural enemies (Weis *et al.* 1988).

In 1986, the foliage of several Garry oaks near Mill Hill (west of Victoria) were severely scorched by a cynipid gall former, *Neuroterus saltatorius* (Edwards) (Duncan pers. comm.). High numbers of galls on the underside of the leaves were causing extensive leaf necrosis and by mid- July, these trees were suffering from severe foliar scorching (Fig. 1). This was the first record of this species in British Columbia; a checklist of insects associated with Garry oak (Evans 1985) and Pacific Forestry Canada insectary records have no record of this species.

Neuroterus saltatorius is native to western United States and was probably accidentally introduced from the Pacific Northwest. Range identifications have come from collections in Washington, Oregon, California and Texas and hosts are *Quercus alba* Linn., *Q. arizonica* Sarg., *Q. douglasii* Hook & Arn., *Q. dumosa* Nutt., *Q. garryana*, *Q. lobata* Neé, *Q. stellata* Wangenh.and *Q. virginiana* Mill. (Krombein et al. 1979).

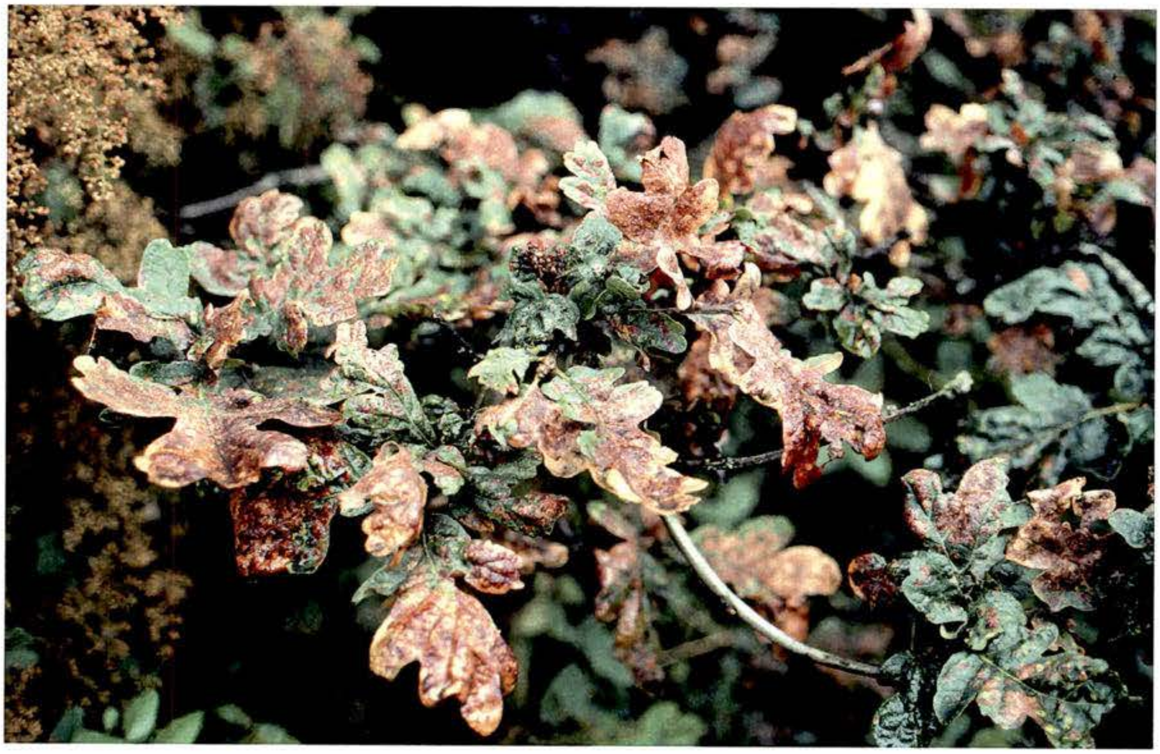

Figure 1. Foliar scorching of *Q. garryana*, primarily due to an infestation of *N.saltatorius* (Sidney, B.C., July 20, 1993).

To date, *Neuroterus saltatorius* has infested oak stands in Victoria, Sooke and north to Duncan and less damaging populations have found in Nanaimo (Bennett 1993) and on Saltspring Island (Duncan, pers. comm.). Surveys have failed to detect *N. saltatorius* on the following Gulf Islands: Cabbage, Galiano, James, Portland, Saturna, Sidney and South Pender; another *Neuroterus* species, *N. washingtonensis* Beutenmueller, has been found on Vancouver Island (pers. obs.).

Neuroterus is a relatively large genus with six subgenera, all strictly confined to white oaks: *Diplobius* (containing *N. saltatorius*), *Neuroterus, Dolichostrophus* (containing *N. washingtonensis*), *Pseudoneuroterus, Neospathegaster* and *Spathegaster*, (Kinsey 1923). Kinsey (1923) and Fullaway (1911) published descriptions of the agamic generation of *N. saltatorius* and Rosenthal and Koehler (1971a) described the gamic generation and reported the daily flight patterns and emergence times of both generations from *Q. lobata* Neé sites in Sacramento County, California. Rosenthal and Koehler (1971a) did not investigate the gall occupants or establish a list of associated parasitoids and inquilines.

In a generalised life cycle of *Neuroterus* , an adult agamic female emerges in the spring from a gall in the soil and oviposits into the *Quercus* foliage through the bud scales. The secretions of the larvae stimulate the continued development of the gall after oviposition (Mani 1964). The first generation develops quickly and gamic adults (male and female) emerge four to six weeks after oviposition. Males usually emerge first and mating takes place immediately once females emerge. Females lay fertilised eggs into the underside of the expanded foliage. The second generation develops over the remaining summer months resulting in several stages of development present on the leaves at any given time. Maturation of the agamic generation may be completed on the foliage or, in the case of species with detachable galls, adults will overwinter in a gall in the duff layer of the soil (Taper *et al.* 1986).

Cynipids are characterised by alternating generations, or heterogeny. A generation consisting of both males and females (gamic) alternates with a female only (agamic) generation (Askew 1985) where the two females differ in appearance, mode of reproduction and the type of galls formed by the offspring. Heterogenic insects will often engage in arrhenotokous parthenogenetic reproduction strategies to produce the generation of males and females. Commonly referred to as haplo-diploidy, males arise from eggs that undergo a reduction division to become haploid (meiosis) and females arise from eggs that remain diploid (mitosis) (Askew 1985). In cynipids, agamic females may be named for the sex of offspring they produce that is, androphores (entirely male) or gynephores (female).

Parasitoid communities

Askew and Shaw (1986) define a community as a "group of species having a high degree of spatial and temporal concordance and ... member species mutually interact ". Consequently, biologically analogous species can be regarded as constituting a community, such as the numerous cynipid species present on a *Quercus* host. The association between several cynipid species would be strengthened if they exploited a common part of the host plant (e.g. detachable, leaf-forming galls).

In general, a large number of insects are attacked by only one or two species although some may be host to 20 or more parasitoids (Askew and Shaw 1986). Oak gall formers are among the many insect groups attacked by parasitoids. The term "parasitoid complex" is useful when referring to a group of parasitoids attacking a particular host. It can be difficult to clearly define host-parasitoid relationships since parasitoid species may be solitary or gregarious, endo- or ectoparasitic, confined to a single host (host-specific), a group of allied hosts, (oligophagous) or to a wide range of hosts (polyphagous).

For several reasons, parasitoid species attack a limited range of gall formers and inquilines and as a result, host-parasitoid relationships can be variable or poorly defined.

(Askew 1961; Hails and Crawley 1991). First, oligophagous and polyphagous species usually attack a particular host stage rather than a particular taxa (Washburn and Cornell 1979). As well, the position or shape of the gall may be important for some polyphagous species (Askew 1961; Shorthouse 1973). Secondly, the timing of the host on the tree will determine which species will attack it since many parasitoids have primary and alternate hosts; at the species level, it is rare to find strict host specificity, perhaps only a strong host preference (Askew 1971). Lastly, parasitoids may be less host specific as the season progresses, attacking a wider range of hosts (Washburn and Cornell 1979).

Generally, there has been high species richness in the number of parasitoids attacking galling insects (Price 1988). The greatest contributors to cynipid mortality have been ectoparasitic members in the families Eulophidae, Pteromalidae, Encyrtidae and Aphelinidae (Hymenoptera: Chalcidoidea) and some eulophids and pteromalids are also obligate hyperparasitoids (Heydon and Boucek 1992). Hyperparasitism is common among chalcidoids (Gauld and Bolton 1988) that is, parasitoids developing on other parasitoids, eventually consuming the host.

Rearing are used to determine taxa associated with a particular gall former and as long as they are free of plant or insect contaminants, they will reveal the species parasitising the cynipid host. There are many difficulties rearing cynipids and optimal conditions are usually achieved with the use of outdoor rearing chambers (Shorthouse 1979). In areas where cynipid populations suffer high levels of parasitism, it can be difficult to collect sufficient host material because of high host mortality (Evans 1967).

Natural mortality factors

The most prominent control agent in the oak-gall community are the parasitic Hymenoptera (e.g. Askew 1961, 1975; Evans 1967; Force 1974; Hails and Crawley 1991; Price 1971; Washburn and Cornell 1979, 1981). Attributing to the success of these parasitoids are their searching abilities and a shorter generation time than their host (Waage and Greathead 1986). Askew and Shaw (1986) concluded that hosts that are completely confined within plant tissue generally have higher levels of parasitism than those that are exposed.

Many chalcidoid species gain access to eggs and larvae by piercing the gall with their ovipositor and laying eggs on or in the cynipid host (Askew 1985). Consequently, the thickness of the wall and the diameter of the gall will limit oviposition success (Askew 1961). These factors will restrict parasitoid attack to a particular stage of host development (e.g. early instar larvae) or range of taxa (e.g. certain size galls) that do not limit oviposition (Cornell 1983).

When a host is protected by a plant gall, ectoparasites are not uncommon (Askew 1971, 1980) and these parasitoids have evolved strategies to circumvent problems associated with attacking an active host (Waage and Greathead 1986). For example, female ectoparasitoids inject venom during oviposition to partially or totally paralyse the host. Piek and Owen (1982) found *Bracon hebetor* Say (Hymenoptera: Braconidae) venom was able to prevent moulting or metamorphosis yet keep the host alive, sometimes for several weeks. The venom, produced from modified accessory glands in females (Gauld and Bolton 1988), maintained the host at an optimal stage for parasitoid development. Equally important, the venom immobilised the host and eliminated the danger that the parasitoid larva might face from dislodgement or injury (Askew 1971; Gauld and Bolton 1988).

In a study of natural populations, it is often desirable to quantify the mortality factors associated with each developmental stage (Morris 1959). Life tables are one of the most useful ways to represent the population dynamics of a species over its life span (Deevey 1947; Harcourt 1969; Southwood 1966). Frequent sampling over successive generations are required for the complete construction of a life table (Harcourt 1969; Askew 1971;

Evans 1972) and in populations of gall formers, partial life tables have been used to document the mortality due to parasitism in alternating generations (Collins *et al.* 1983).

Objectives

The objectives of this projects were to describe the life history, natural mortality factors and parasitoid complex of *Neuroterus saltatorius* in British Columbia.

METHODS AND MATERIALS

Description of study sites

All field work was conducted on southern Vancouver Island in *Q. garryana* rocky outcrop habitat from March 1992 - March 1994 (Fig. 2) . Eight sites were chosen based on their protection from disturbance, accessibility, level and age of infestation (Table 1). Estimates of infestation levels were provided by Bennett and Duncan (1991) and the date of infestation determined by examining infestation maps produced by Pacific Forestry Centre, Canadian Forestry Service and by talking to property owners.

All trees within the stand were mapped and numbered and five trees were randomly selected for weekly surveys from a random number table (Zar 1984). On each of the five trees, five numbered, aluminum identification tags were attached to randomly selected buds so that the same population was examined each week. Trees were excluded from surveys and gall collections if they suffered from high levels of defoliation or if lower branches could not be reached from the ground. Gall collections and observations were only made from the lower branches because Askew (1962) reported no spatial zonation of spangle

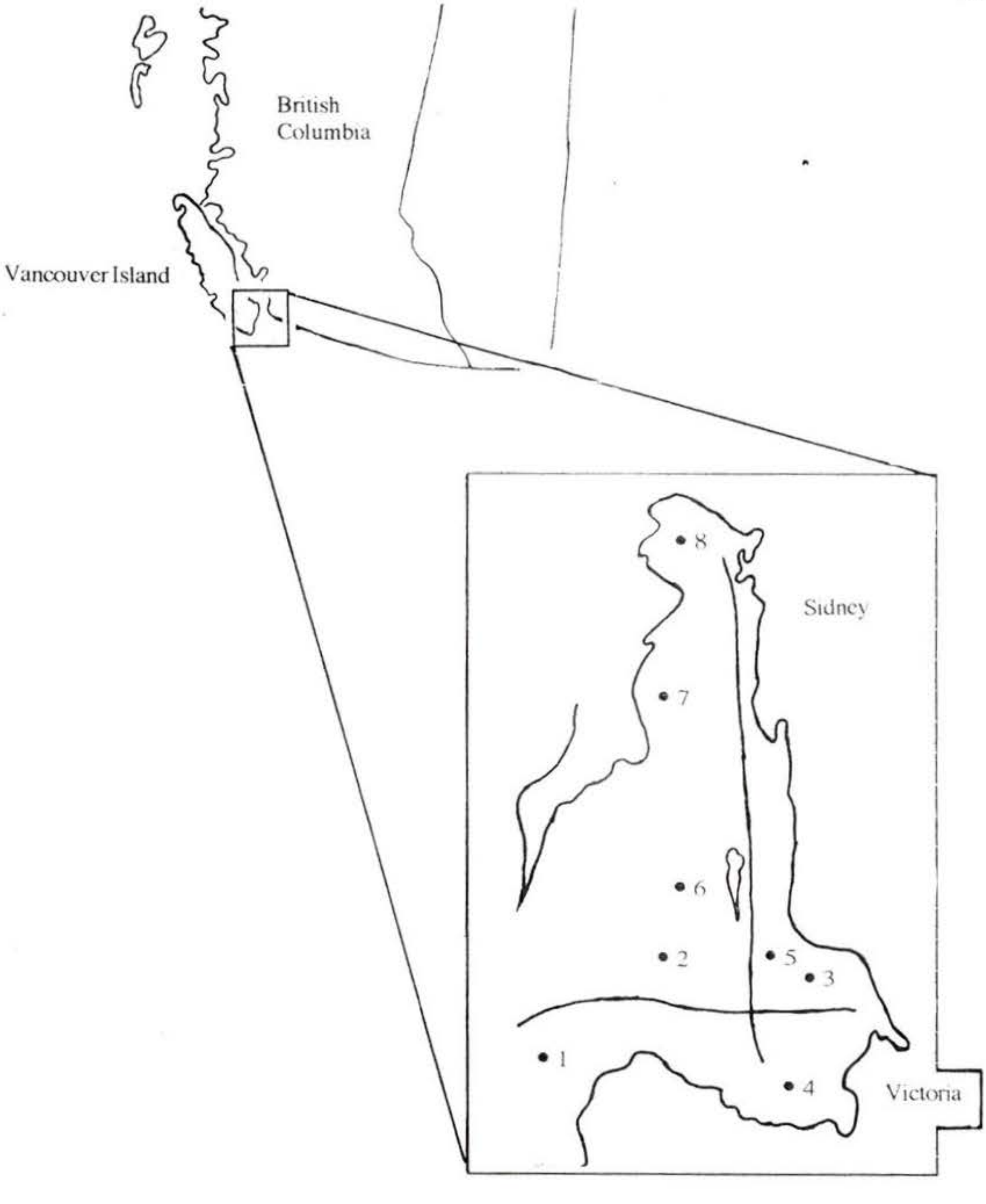

Figure 2. Location of study sites on Vancouver Island, British Columbia: 1 Mill Hill; 2 Santa Anita; 3 Mt. Douglas; 4 Oak Bay; 5 Blenkinsop; 6 Beaver Lake; 7 Mt. Newton and 8 Tatlow.

Table 1. Site descriptions for *N. saltatorius* surveys and gall collections. Year of infestation was determined from infestation maps provided by Canadian Forest Service and information from property owners in 1991. Level of attack assignments were based surveys conducted by Bennett and Duncan (1991).

Site No.	Location	Date of first infestation	Level of attack	No. of trees	Average DBH (m)
1	Mill Hill	1986	Moderate	33	.10
2	Santa Anita	1989	Moderate	31	.32
3	Mt. Douglas	1990	Heavy	21	.23
4	Oak Bay	1991	Light	32	.21
5	Blenkinsop	1990	Moderate	34	.18
6	Beaver Lake	1989	Heavy	27	.26
7	Mt. Newton	1990	Moderate	26	.18
8	Tatlow	1994	Absent	33	.32

galls, *Neuroterus* spp., on mature trees and Rosenthal and Koehler (1971a; b) determined that galls of both generations of *N. saltatorius* were more numerous close to the ground.

Plants were not thoroughly inventoried within sites however, most contained a mix of native and introduced plants common to *Quercus garryana* habitats in the Victoria area. Santa Anita was unique because English ivy, *Hedera helix* Linn. excluded most plant species throughout the entire site. Horses were present at Beaver Lake and Tatlow sites and they would occasionally eat oak foliage and disturb the numbered tag system.

Sites were sampled biweekly on Monday's (Blenkinsop, Mt. Douglas and Oak Bay) and Tuesday's (Tatlow, Mt. Newton, Beaver Lake, Santa Anita and Mill Hill). Gall collections during the rain were not ideal so sampling was restricted to those days without rain but surveys were not weather dependent.

Statistical analysis were conducted on Statview 512+ and Cricket Graph III 1.5.

Life history measurements

Developmental stages

Documenting the stages of development over time is one method of describing the life history of a species (Wangberg 1975; Braune 1979) so at weekly intervals, gamic galls (*n*=400/site) were collected from Oak Bay (April 19 - June 7, 1993) and Mill Hill (May 10-June 7). Beginning on June 23, seven biweekly collections of agamic galls (*n*=400/site) were made from the same sites. Agamic galls were collected from the soil between September 22 and December 1 from Mill Hill (*n*=3) and Oak Bay (*n*=4). These gall collections served two primary purposes: 1) to document the life stages over time and 2) to determine mortality factors and levels of survivorship.

To document development in each generation, leaves with galls (*n*=20) were collected from four trees at Oak Bay and Mill Hill sites and stored in plastic bags in a cold room (4°C) until they were examined, usually within 2-3 days of collection. Five galls were selected (without looking) from each leaf using a 1cm^2 grid. Galls were dissected, the contents examined and observations made regarding the condition of the leaf or gall were recorded. The contents of the galls were presented as a developmental progression over time, identifying only those individuals that survived. Both generations of *N. saltatorius* were plotted separately using percent abundance over the sampling intervals and in the agamic generation, the foliage and soil collected individuals were plotted separately.

Adult emergence trends

Yellow sticky traps were used to monitor adult emergence of both generations. The emergence of agamic females in the spring was investigated in 1992 (*n*=6 sites) and 1993 (*n*=8 sites) by setting out two double-sided "yellow sticky tape" strips (Westgro Industries, Victoria) 40cm above the ground at two locations in each site. Each strip was 5 cm wide and averaged 16.7 cm long (range 13.4 -19.7 cm). Traps were placed out in the field during the week of March 16, 1992 (after the start of agamic flight) and March 8, 1993 (before the start of agamic flight). In 1993, sticky traps were moved during the week of April 19 and suspended on *Q. garryana* branches to capture gamic males and females (Fig. 3). For both generations, sticky traps were replaced at weekly intervals and stored between sheets of waxed paper in a cold room (4°C) until examination. The number of adults on each side of the trap were counted and one density measurement was calculated. A tabulation of the mean density of adults per site was made for each weekly interval and the number of individuals that emerged in each generation was illustrated, on a plotted scale, for all sites pooled together.

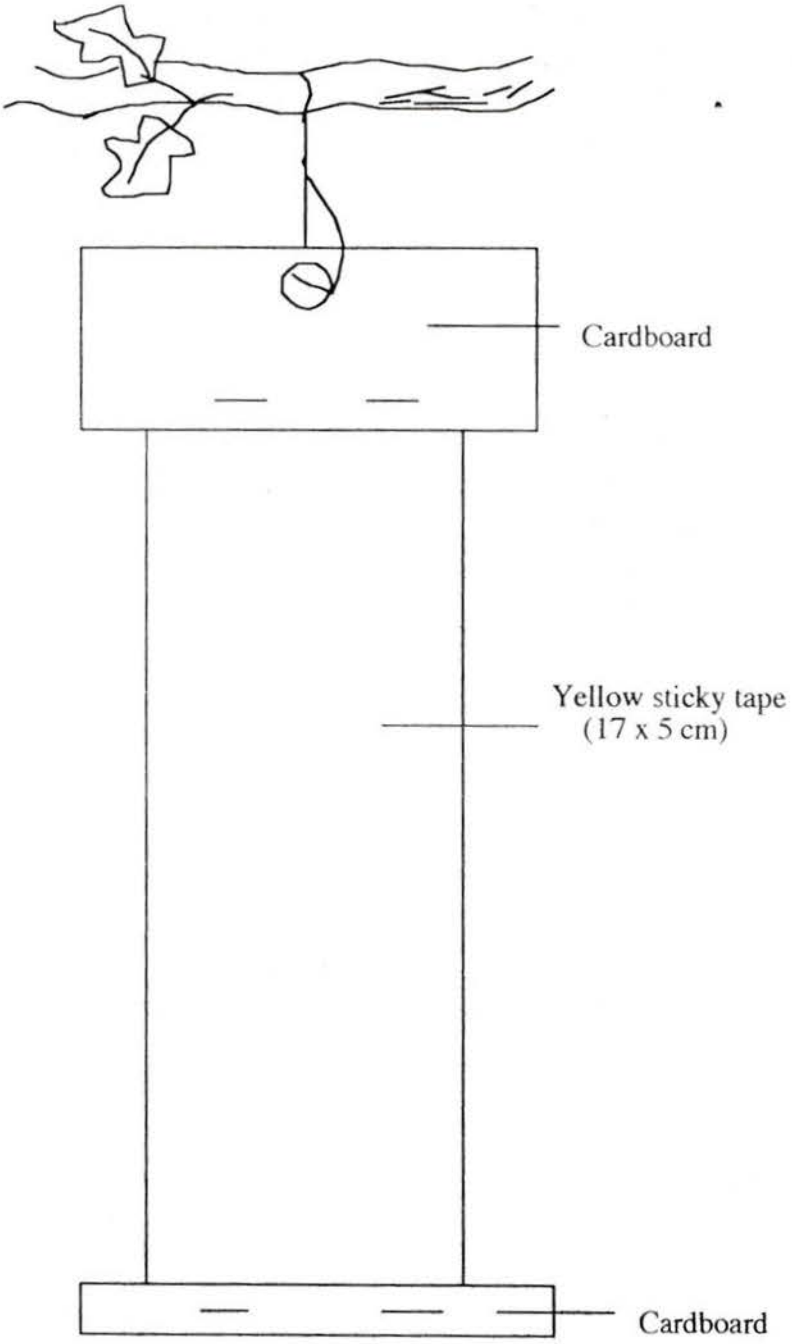

Figure 3. Sketch of the "yellow sticky trap" that was suspended under *Q. garryana* foliage to capture emerging adults of *N. saltatorius* .

Gamic adult sex ratio

The sex ratio of adults in the gamic generation was determined by examining the successful emergence of adults from galls collected April 27 and 28, 1992 at Oak Bay and Mill Hill. Galls were placed in plastic bags in a rearing room (16L:8D and 20° C) and adults were removed daily. This result was compared to the ratio of females and males found while a) dissecting gamic galls for survivorship studies and b) examining yellow sticky traps for the peak emergence of adults. Dissections were conducted April 27-May 19, 1993 from collections at Mill Hill (n=2000) and Oak Bay (n= 3195) and adults and pupae were scored only if they were alive and could be identified to sex. Adults on yellow sticky traps were examined April 27 - May 18, 1993 at Mill Hill (n= 4190) and Oak Bay (n=5275) and all adult *N. saltatorius* counted.

Gamic gall densities

The frequency of gamic and agamic galls on shoots was examined during the week of June 1, 1993. From each site, 12-20 shoots were collected from five, randomly chosen trees. At this time, galls from the first generation were still visible and agamic galls were beginning to form. The number of leaves per shoot and the frequency of leaves with gamic or agamic galls was counted.

The analysis focused on gamic generation galls since it was predicted, from field observations, that all leaves would have agamic galls. Three frequency analyses (mean ± 95% confidence limits) were done: 1) the frequency of leaves with gamic galls, 2) the frequency of leaves with gamic galls taken from shoots that have gamic galls on at least one leaf and 3) the frequency of shoots with gamic galls on one leaf. Preliminary Chi-square analysis found a significant amount of "within tree" and "within site" variation ($p <$ 0.01), therefore, each site was treated separately.

Agamic gall production

Garry oak seedlings were used to examine the production of agamic galls and the effect that flush date (phenology) might have on the production of galls. On May 5, 1992, greenhouse grown seedlings were classified into three flush classes: early (>1 cm of tissue visible), mid (bud broken and visible tissue < 1cm) or late (bud not broken or just starting to break). Four seedlings were selected from each class and placed in a mesh cage. Gamic galls were collected from Mill Hill during the week of May 5 and adults were removed from the galls by dissection. Between 13 and 16 male/female pairs were placed on a petri dish in each of the mesh cages. The seedlings were removed from the cages when all adults were dead and placed in an outdoor compound for the remainder of the summer. The number of galls on the foliage (living or dead) and the number that had been on the foliage (i.e. dropped) were counted every week for 16 weeks (112 days), starting May 12. The cumulative number of galls produced each week was plotted for all seedlings combined. As well, the cumulative number of galls produced by the seedlings in each flush class were plotted over the 112 days.

Agamic gall drop

The rate of agamic gall dehiscence was measure by placing one funnel trap (Fig. 4) under each of three separate trees at Mill Hill, Oak Bay and Blenkinsop. Each trap consisted of a weighted, plastic base, two funnels and a 33 cm^2 catchment area (Sopow 1993). Traps were placed in the field during the week of June 26, 1993 and the trap locations did not change throughout the summer; disturbed traps (e.g. knocked over, chewed by dogs) were replaced. At weekly intervals until October 25, the traps were emptied and the galls counted. The persistent disturbance of one trap at Oak Bay meant that only two of the three traps could be reliably used for analysis.

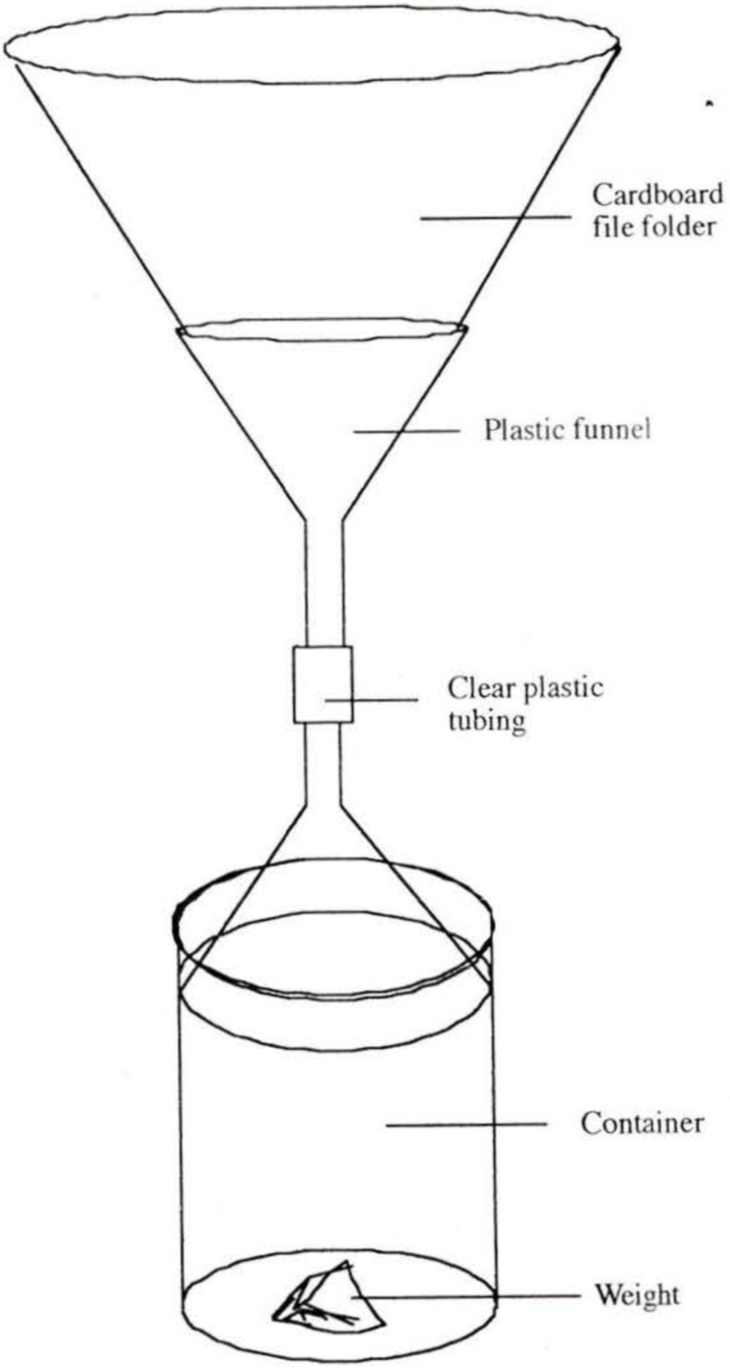

Figure 4. Schematic diagram of the funnel trap used to catch dehisced agamic generation galls of *N. saltatorius* in 1993 (Design by Sopow 1993).

The mean gall drop per week was calculated and plotted for each site. Pairwise comparisons between sites were made with a Wilcoxon paired-sample test ($\alpha = 0.05$) (Sokal and Rohlf 1969) to test for any differences in the number of galls that fell each week among the three sites. Cumulative gall drop was plotted for overall trends in the dropping rate at each of the three sites.

Fecundity

Stemming from Blackburn's work (1991) on fecundity, the size of gamic and agamic females were examined in relation to their fecundity. Fecundity in this study was defined as the number of ova present in a female instead of the actual number of offspring. Gamic galls were collected from Mill Hill on May 5, 1992 (n=35), from Oak Bay on May 3 and 10, 1993 (n=35) and from Oak Bay on May 6, 1994 (n=35). In 1993, agamic females were collected from Mt. Newton on January 28 (n=8) and February 28 (n=8), Mill Hill on October 26 (n=7), Oak Bay on October 27 (n=20) and November 29, 1993 (n=15). Mature females were dissected from galls, preserved in 70 % ethanol and measured between February 10 and June 22, 1994.

On March 24, 1994, gamic females, collected from Blenkinsop, were used to examine the effect of age on the number of eggs present. Females emerged from galls and were kept in outdoor rearing containers for 1, 2 or 3 days (n=10, 8 and 4 respectively) after which they were preserved in ethanol and measured on May 17, 1994.

For each female, the number of eggs, size of eggs (n=10), overall length and abdominal length were measured using an ocular micrometer and a Zeiss Stereoscope at 50X (abdomens were removed from the thorax before measuring). A one-way analysis of variance was used in a step-wise fashion to quantify differences within a sample at one site, then between samples at different sites, then between years, then between gamic and agamic generations; samples were pooled if p>.05. Where significant differences were found, Scheffé's multiple contrasts test (H_O: $\mu_A - \mu_B = 0$) (Sokal and Rohlf 1969) was used to identify the source of variation.

Correlation's were used to examine the relationship between fecundity, overall length and abdominal length.

Parasitoid complex

Identification , abundance and distribution of taxa

The parasitic Hymenoptera associated with both generations of *N. saltatorius* were collected from mass rearings. Gamic galls were collected on May 18, 30 and June 11, 1993 from all but Beaver Lake and Tatlow sites. Galls were reared indoors in a rearing room (16L:8D; 20°C) in plastic bags with a damp, 2 cm blotting disc until June 25, 1993. Adult parasitoids were removed weekly and preserved in 70% ethanol.

Mass rearing of agamic generation material was conducted in 1992 and 1993. In 1992, 400 galls were collected from the foliage every two weeks from June 8 to September 28. In 1993, biweekly collections were replaced with mass collections (> 5000 galls) at Mill Hill, Oak Bay and Blenkinsop (3, 7 and 2 collections, respectively). The mass collections were used to rear parasitoid or inquiline species missed in 1992.

Agamic galls were collected for rearings by randomly collecting oak foliage throughout a site. The galls were removed from the sampled foliage by rubbing the underside of the leaf and then dividing the galls among several 200 cc containers; a Kimwipe served as a lid. Parasitoids were reared outdoors in an effort to retain normal emergence patterns. To prevent the emergence of species not associated with *N. saltatorius*, care was taken to ensure that only agamic gall material was being reared. Rearings were usually checked weekly for parasitoids and the adults removed to prevent re-parasitism.

Hyperparasitic species were collected during dissections. When hyperparasitoids were found in a gall, they were removed with the host tissue, and placed in 00 gelatin capsules. The capsules were stored at room temperature and examined weekly; the successful adult emergents were identified and preserved.

To identify the parasitoid species that might successfully overwinter in the agamic galls, soil samples were collected March 24, 1994 from Blenkinsop. Galls were reared in the lab (20°C) until September 12. The rearings were examined every two weeks and any emergent adults removed.

All parasitoids were preserved throughout the study in 70% ethanol. Identifications were provided by John Huber and Gary Gibson, Biosystematics Research Division (CLBRR), Ottawa; Steve Heydon, Department of Entomology, UC Davis; and John LaSalle, International Institute of Entomology, UK. Voucher specimens have been deposited at the Pacific Forestry Centre, Victoria.

A special permit was obtained to collect agamic galls in Oregon. Twenty locations were sampled along the Interstate 5 during the week of June 29, 1993; agamic galls were found on *Q. garryana* at nine sites. Galls, without foliar material, were brought back into Canada and reared in the quarantine facilities at the Pacific Forestry Centre in Victoria, until September 14.

The list of taxa reared from galls of *N. saltatorius* collected on Vancouver Island and in Oregon was compared to a list of taxa associated with *N. saltatorius* in California and with other cynipids on Vancouver Island. Steve Heydon, UC Davis, CA provided the details for the taxa in California and Sopow (1993) identified and prepared a list of the parasitoids reared by David Evans between 1960-70 at the Pacific Forestry Centre, B.C.

In addition to the list of taxa, agamic rearings provided information regarding the abundance and emergence patterns of parasitoid fauna (1992-93) in the following analyses:

a) the relative abundance of major parasitoids on Vancouver Island and in Oregon (1993);

b) the relative abundance of major parasitoids at Mill Hill, Oak Bay and Blenkinsop;

c) the proportion of major parasitoid species from each biweekly collection date;

d) the proportion of major parasitoid species at two week intervals (irregardless of collection date).

Mortality factors and survivorship

Parasitism from mass rearings

Rearing material used to determine the parasitoid complex also served to provide an approximate indicator of percent parasitism in 1992. Parasitism was calculated for each collection date, at each site, by dividing the total number of galls collected by the number of emerged adult parasitoids. Overall parasitism was calculated by pooling the number of galls collected and the number of emerged parasitoids from each collection date over all sites. To compare parasitism levels throughout the summer, a mean value of parasitism (± SD) was calculated for each collection date, for each site.

Parasitoid-exclusion experiment

Three sites were chosen to evaluate parasitism and emergence on a sequential basis throughout the summer of 1993. When the gamic generation flight had finished (Oak Bay, May 19; Mill Hill and Blenkinsop, May 25), 15 x 30 cm "mosquito netting" sleeves were attached to selected shoots to prevent parasitoids from reaching agamic galls. The sleeves were essentially net bags sewn on three sides, with the opening secured tightly around a branch with string (Fig. 5). At each site, five leaf clusters on eight, randomly chosen trees received a numbered aluminum tag and were covered with a sleeve (*n*=40/site); the number of leaves or galls contained in one sleeve was not constant. Each cluster was checked for

Figure 5. Parasitoid - exclusion sleeves used during the agamic generation of *N.saltatorius*.at Mill Hill, Oak Bay and Blenkinsop, 1993.

phytophagous insects and larvae or adults removed. Every two weeks, four numbers were chosen; three were exposed to parasitoids and the fourth acted as a control (testing the effectiveness of the net to exclude parasitoids). Beginning June 7-8, the first three sleeves were removed for a two-week exposure period. To catch galls as they dropped from leaves, a wire-rimmed, net funnel was placed under the exposed leaves and the 15 x 30 cm sleeve was suspended over the exposed leaves to prevent galls from entering the funnel from above. At the end of the two weeks, the exposed leaves (with galls) were collected, the control was collected, and four more numbers chosen. This procedure continued for 10 sampling dates.

Sampled galls were removed from the foliage and reared outdoors until December 30, 1992. Adults were usually removed every week, identified and preserved in ethanol. The relative abundance of parasitoids was plotted and an estimate of percent parasitism was calculated for each week. When estimating parasitism, the large number of galls in each sample presented a counting problem so I looked to other options. Initially, an electronic seed counter was tried but I was unable to obtain repeatable results. So, a disposable pipette (0.4 x 20 cm) calibrated with a known number of galls was used. All samples with >50 galls were counted using this volumetric method; those samples that were <50 were counted by hand. Parasitism was averaged for the exposed sleeves and compared to the rate of parasitism found in the control.

Parasitism from dropped galls collected in funnels

Agamic galls collected in funnel traps were examined for parasitism levels. Galls were reared outdoors until October 30, 1993 then brought inside. In May 1994, a sub-sample of galls from each week (n=20/trap) was dissected to see how many *N. saltatorius* had successfully developed into adults and as a peripheral investigation, percent parasitism was estimated. Parasitoid-related mortality was defined as the presence of a parasitoid larva or an adult emergence hole in the gall; desiccated larva were excluded because the source of mortality was unknown. Parasitism from dissections was compared to the rate of parasitism in rearings.

Survivorship and sources of mortality

Estimating parasitism from rearings relies on the successful emergence of an adult parasitoid but this may not be an adequate estimate of the total mortality in the population since many adults don't survive to emerge (Van Driesche 1983, 1991). Consequently, survivorship data was collected from gamic and agamic gall dissections. In 1992, mortality estimates from rearings did not reflect the actual mortality in the samples (pers. obs).

Additional analyses were done on agamic galls >1mm on the foliage, galls collected from the soil and galls collected in funnel traps. Mature, agamic galls > 1mm in diameter were randomly selected from the foliage during agamic generation dissections. This was examined specifically to determine the fate of galls that had reached full size. I hypothesized that mature galls remaining on the foliage after peak gall drop would have a higher proportion of parasitoids than galls that fell to the soil, since I had only observed foliage-searching parasitoids. Agamic galls > 1mm were collected from exposed rock outcrops at Mill Hill and Oak Bay on September 19, October 3, 31 and November 28, 1992. Soil samples (>1 kg; n=2/site) were air-dried and stored at 4° C until they were examined, usually within one week. Two hundred galls/sample were manually removed from the soil from each site and dissected. The greatest sampling difficulty was distinguishing current year from previous year galls since galls discolour quickly in the soil. The soil sample collected on October 6 from Mill Hill could not be used because the moisture in the sample had caused the galls to deteriorate.

The contents of a gall were recorded as follows: host surviving, failed development, host dead from unknown causes, mature gall empty, fungal infection, parasitoid present or emerged, predation, unidentified desiccated larva and dropped galls (agamic only). Four broad categories were used to plot the results: surviving *N. saltatorius* , parasitised larvae, failed development and unknown sources of mortality (i.e. all of the remaining observations).

Survivorship results were kept separate for Mill Hill and Oak Bay. The frequency of collection was not the same for each method therefore the results were plotted weekly for the gamic generation and agamic galls collected in the funnels, and every two weeks for the other results.

Cumulative survivorship

Dissections of *N. saltatorius* for developmental stages (see above) were used to calculate the cumulative survival of galls on the foliage from May 3 to September 8, 1993. It was decided that only those galls that dropped before August 15 would be considered as surviving based upon *N. saltatorius* found in funnel traps. Assuming complete oviposition success, the number of eggs at the time of first sampling (w_o) was assumed to be 400 (sample size for each site). The number of individuals surviving (zx) was determined for each collection date by examining the dissection data and the number dying in each interval (dx) calculated from $w_n - w_{n-1}$. The mortality rate (qx) was calculated from dx/zx. Finally, cumulative survivorship was calculated for each site according to the equation $[1-(1-qx)^n]$ (Barclay, pers. comm.).

RESULTS

Life history observations

Agamic emergence and gamic development

Agamic females (Fig. 6) were first observed ovipositing on closed *Q. garryana* buds on March 8, 1992 and March 15, 1993. Females inserted their ovipositor through the bud scales and deposited eggs into the developing leaf tissue. Females were not observed to fly from one bud to the next and apparently a female would not lay all her eggs on one bud. Dead females were frequently found with their ovipositors inserted into buds and several females were often found ovipositing on the same bud. In 1992, the peak agamic flight probably occurred during the week of March 9-16 and the flight period lasted at least three weeks at most sites (Table 2). In 1993, the peak emergence of agamic females occurred March 15-29 and the emergence period lasted four weeks (Table 3). The greatest number of adults found on the sticky traps during a one week period was 486, during the week of March 21 (Fig. 7).

Gamic generation galls were visible three weeks after oviposition. Mature gamic galls appear as conic swellings on the upper and lower surfaces of the leaf (Fig. 8). The galls were found in clusters containing > 10 galls. The frequency of leaves with galls in the gamic generation was highly variable. The percentage of leaves with gamic galls ranged from 1-38 % among sites (Fig. 9). The percentage of leaves with gamic galls taken from shoots that had gamic galls on at least one leaf was higher, 12-58% (Fig. 10); the percentage of shoots with gamic galls on at least one leaf ranged between 1.5 and 58% (Fig. 11). Gamic galls were noticeable by April 2, 1992 and were obvious by mid-April 1993. Pupae and adults were found in galls four and six weeks, respectively, after oviposition (Fig. 12). The entire bisexual generation lasted approximately 10 weeks (Fig. 13).

Figure 6. Agamic female of *N. saltatorius* (Hymenoptera: Cynipidae) (R. Duncan 1993).

Table 2. Emergence of agamic generation adults determined from yellow sticky traps at six sites on Vancouver Island, 1992.

Week of	Mean density per site (adults/cm^2)					
	Mill Hill	Santa Anita	Mt. Douglas	Oak Bay	Beaver Lake	Mt. Newton
Mar 16		.77				.38
Mar 23	<.01	.07	.02	.01	<.01	.01
Mar 30	-	-	<.01	<.01	-	-
Apr 06	<.01	-	<.01	<.01	.01	-
Apr 13	-	-	-	-	-	-

Table 3. Emergence of gamic and agamic adults of *N. saltatorius* determined from yellow sticky traps located at eight sites on Vancouver Island, 1993.

		Mean density per site (adults/cm^2)							
	Week of	Mill Hill	Santa Anita	Mt. Douglas	Oak Bay	Blenkinsop Lake	Beaver Newton	Mt.	Tatlow
agamic									
	Mar 08								
	Mar 15	-	<.01	-	-	-	-	-	-
	Mar 23	<.01	.48	.16	.28	.43	<.01	.04	-
	Mar 29	.10	.26	.04	.18	.61	.08	<.01	<.01
	Apr 04	.02	.04	<.01	.03	.14	.04	.01	-
	Apr 12	.02	<.01	-	-	.01	.01	-	-
	Apr 19	-	-	-	-	-	-	-	-
gamic									
	Apr 27	-	-	-	.02	-	-	-	-
	May 03	<.01	1.25	-	2.99	<.01	-	-	-
	May 10	8.68	12.51	12.85	13.12	12.22	5.23	4.36	.44
	May 18	3.12	.76	.03	.09	.25	.13	.09	<.01
	May 25	-	-	-	-	-	-	-	-

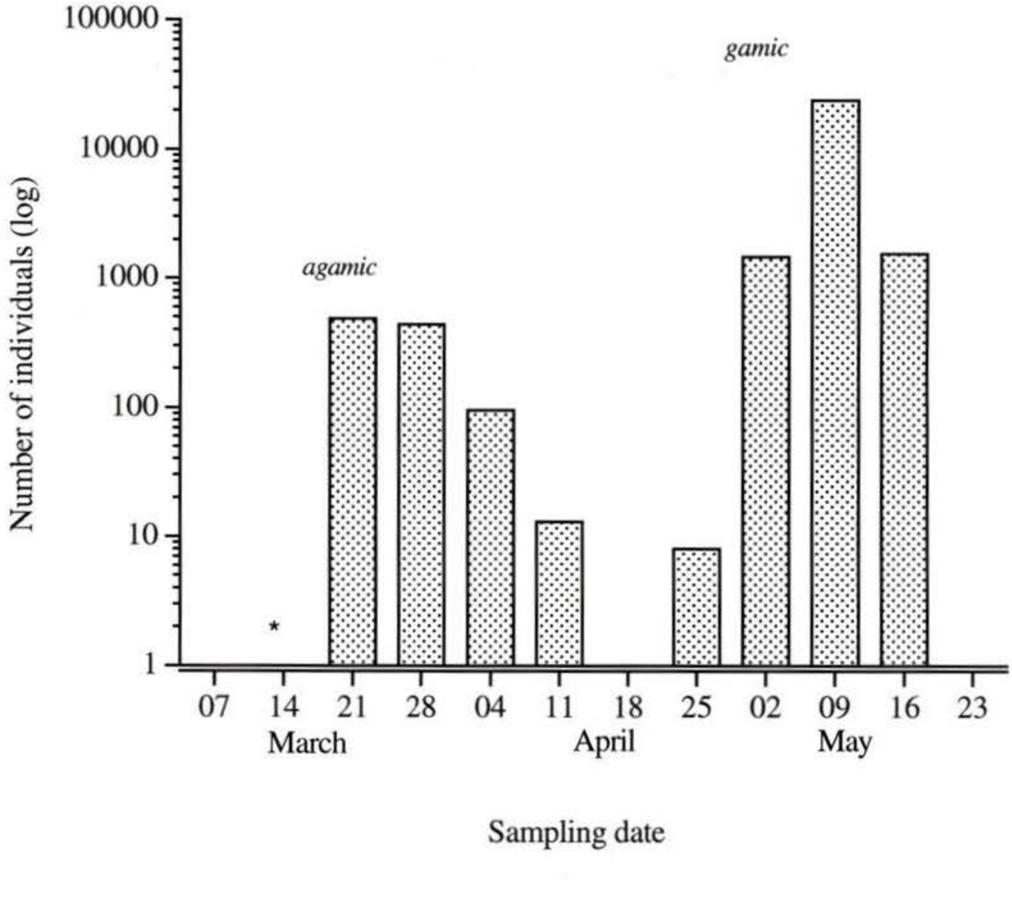

Figure 7. Adult emergence trends for agamic and gamic generations of *N. saltatorius* from yellow sticky traps placed at eight sites around Victoria, B.C. 1993 (* is one individual).

Figure 8. Gamic generation galls of *N. saltatorius* on *Q. garryana* (Victoria, B.C., 1992).

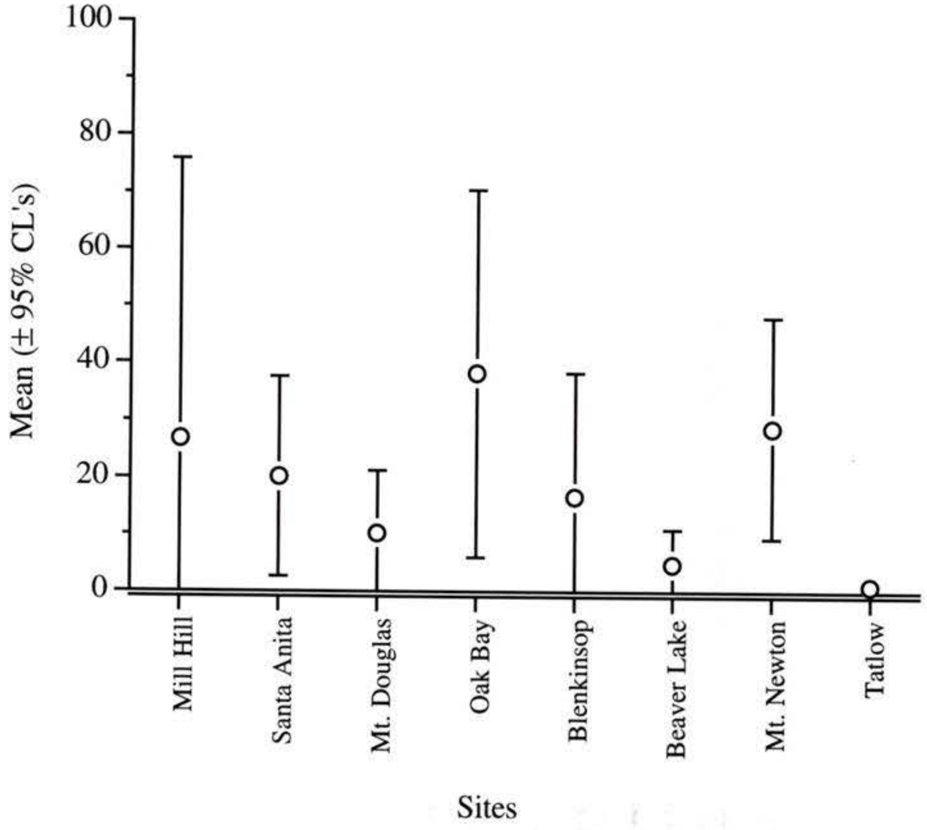

Figure 9. The percentage of leaves with gamic galls, 1993.

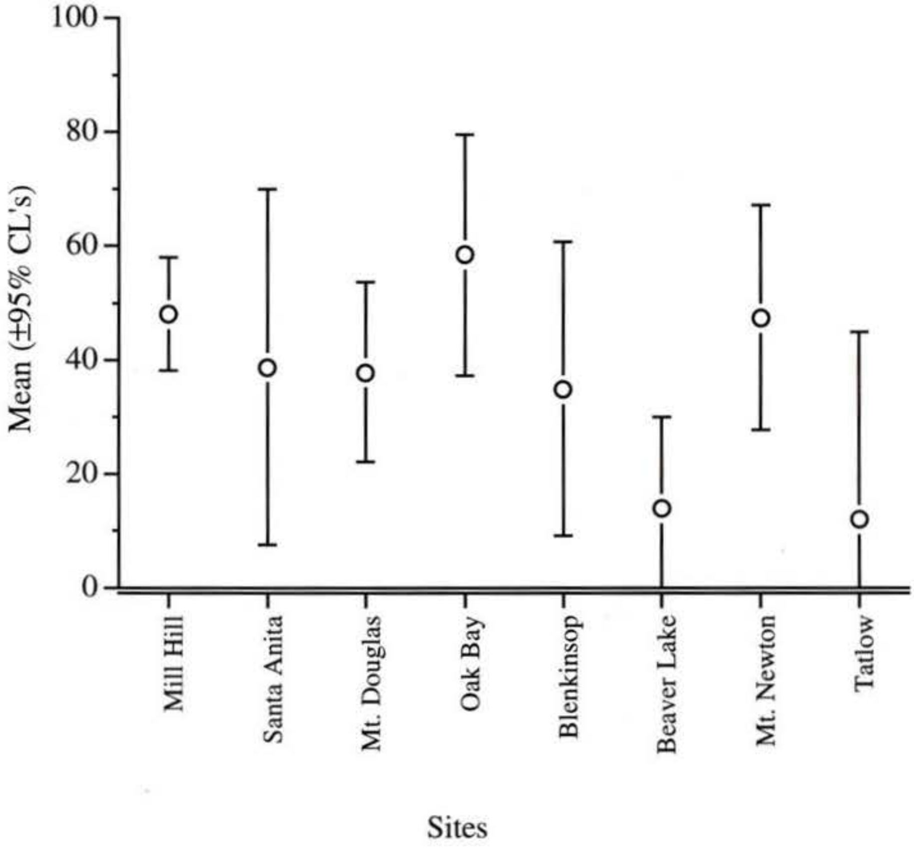

Figure 10. The frequency of leaves with gamic galls on shoots that have gamic galls on at least one leaf, 1993.

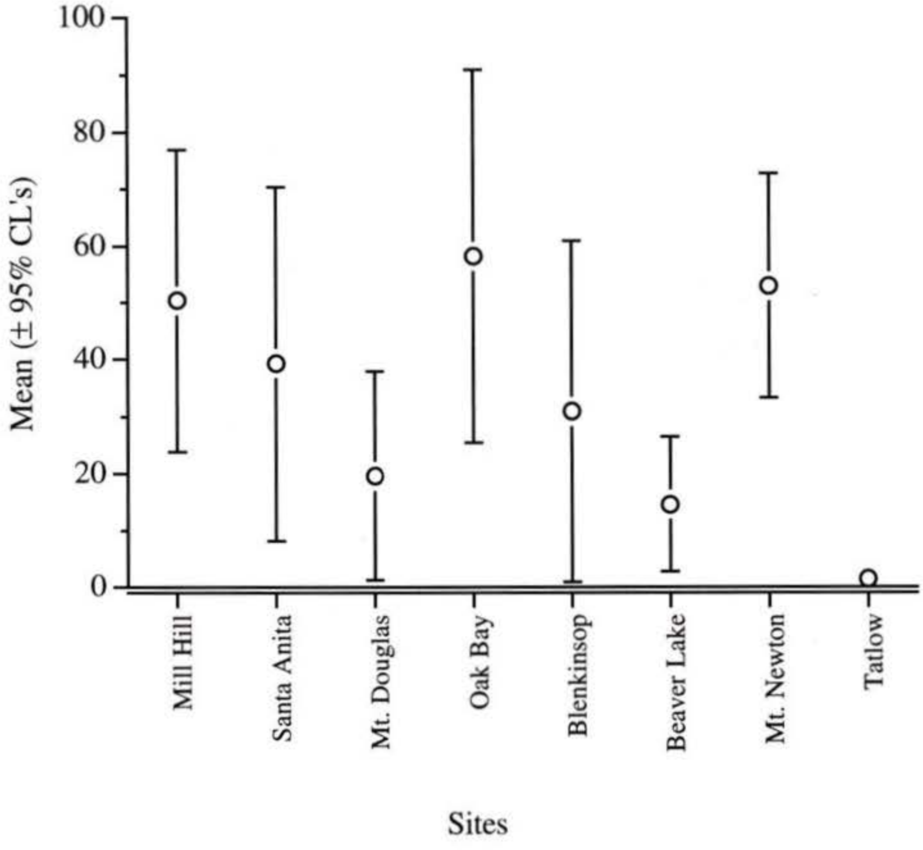

Figure 11. The frequency of shoots with gamic galls on at least one leaf, 1993.

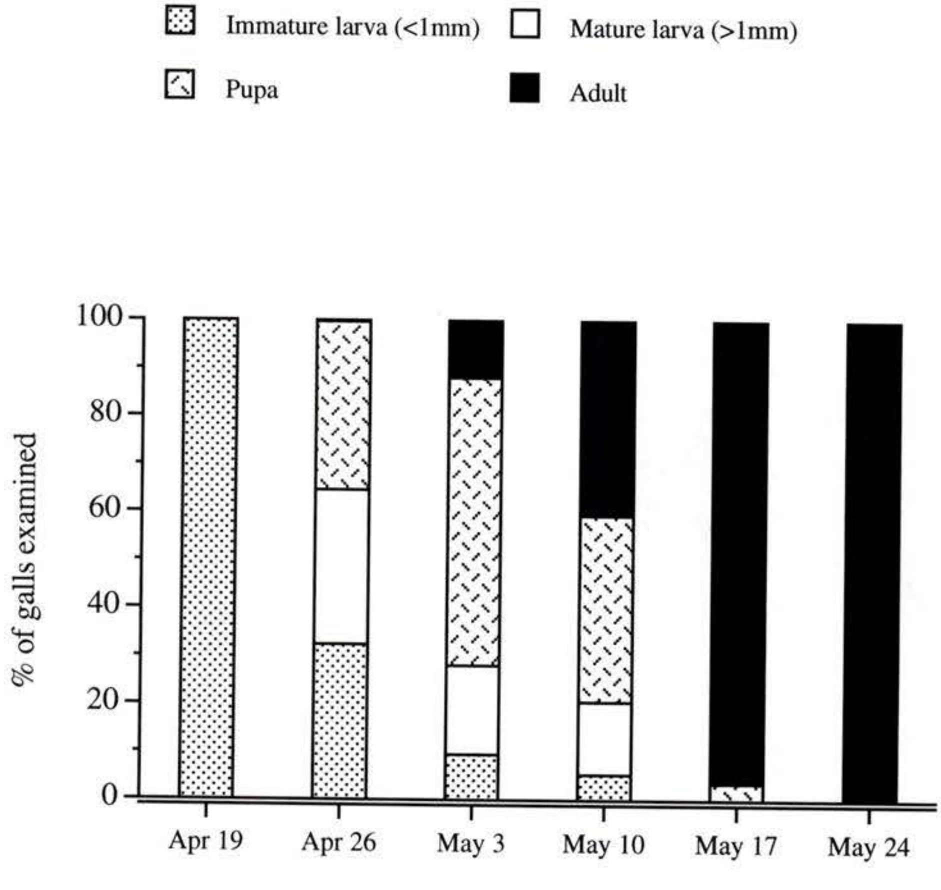

Figure 12. Developmental progression of the gamic generation of *N. saltatorius* on the foliage of *Q. garryana* ; Mill Hill and Oak Bay sites, 1993.

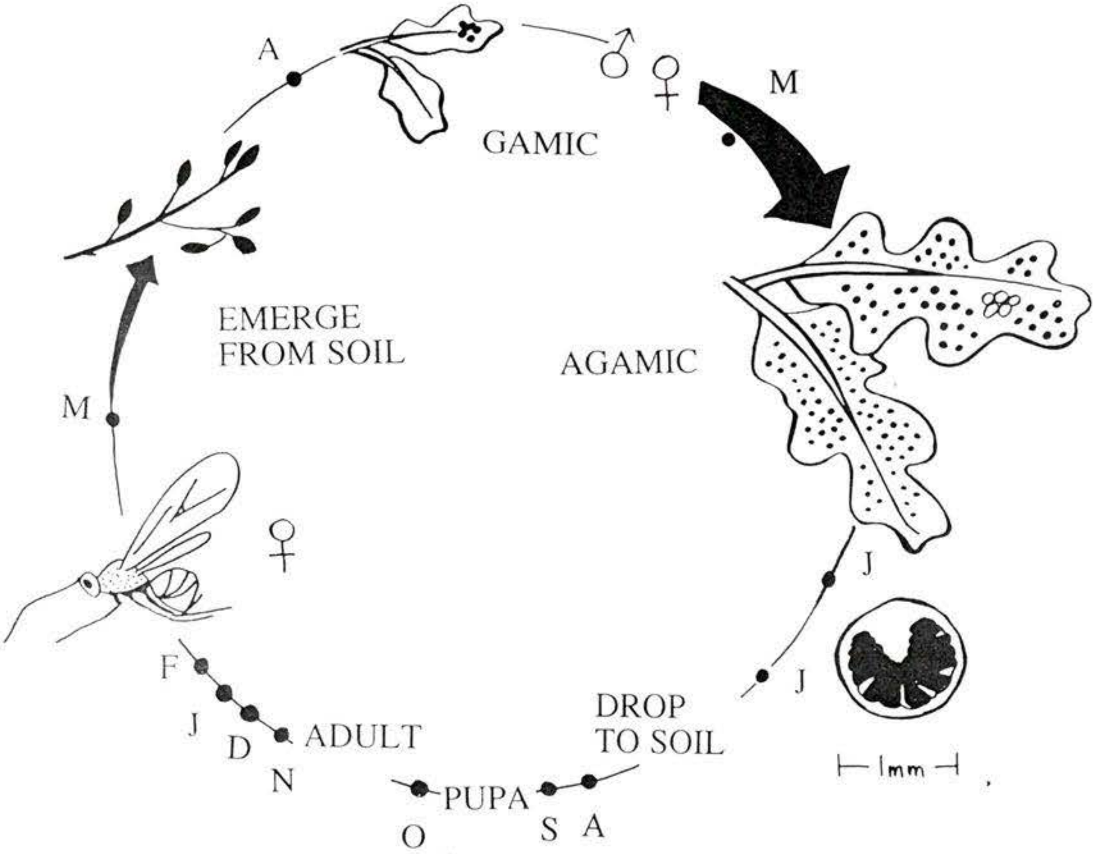

Figure 13. Generalised life cycle of *N. saltatorius* (Hymenoptera: Cynipidae) on *Q. garryana*, Vancouver Island, B.C.

Gamic galls were found segregated into "same sex" clusters on a leaf. Male or female clusters would be found adjacent to each other during dissections but a mixture of both was not found.

Gamic emergence and agamic development

Adult emergence during the gamic generation was more pronounced than the agamic generation and gamic adults (Fig. 14) were often found on the sticky surfaces of vegetation (e.g. *Rhododendron* spp.) as you passed through an infested area. Gamic adults emerge from either the abaxial or surface of the leaf.

Gamic females were collected first on sticky traps during the week of April 27, 1993 (Table 3). Gamic flight lasted two - four weeks in 1993 with a peak emergence May 3 -10; this generation exhibited a more truncated pattern of emergence (Fig. 7). The adults appeared to emerge all at once with very little activity before or after the peak, e.g. site 3 (Mt. Douglas) and site 5 (Blenkinsop). The greatest number of adults found on all sticky traps during a one week period was 23, 798 (Fig. 7), > 50 times more than in the agamic generation. More males (*n*=17,274) than females (*n*=9,547) were found on the traps.

The ratio of gamic females to males varied between the different assessment methods (Table 4). Adults emerged from galls during rearing trials in approximately a 1:1 female : male ratio. However, adults captured on sticky traps were found in a >1:2 ratio, at both sites. In dissected galls, a sex ratio favouring females emerged (2.7:1 and 1.6:1).

Agamic galls on seedlings were found three to four weeks after oviposition (Fig. 15) and development followed a slight exponential pattern. Maturation was slower in seedlings that flushed earlier however, all three classes of seedlings followed the same general pattern (Fig. 16). Field observations indicated that late flushing trees were more heavily infested with agamic galls than earlier flushing trees (which had more gamic galls).

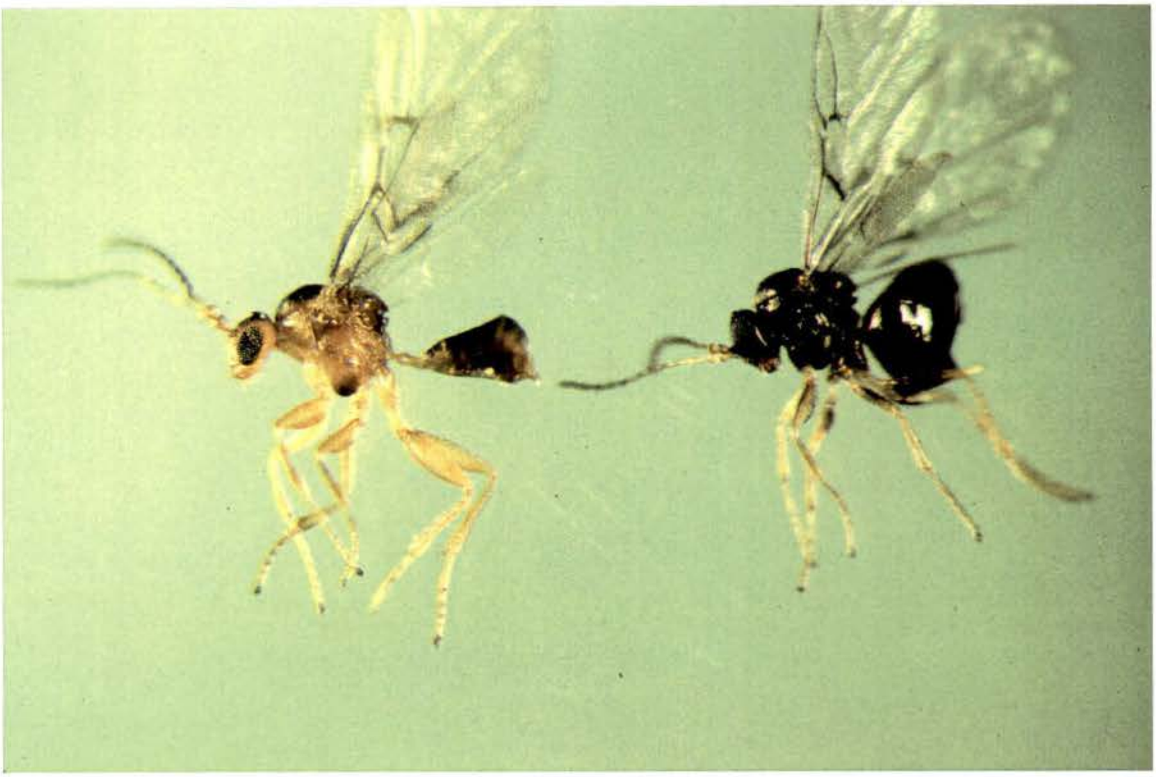

Figure 14. Gamic generation male (left) and female (right) adults of *N. saltatorius* (R. Duncan 1993).

Table 4. Sex ratio's of gamic*N. saltatorius* adults determined from mass rearings, dissections and yellow sticky traps.

Rearing method	Mill Hill			Oak Bay		
	Female (%)	Male (%)	RATIO	Female (%)	Male (%)	RATIO
Mass rearings 1992	54	46	1:1	46	54	1:1
Sticky traps 1993	32	68	1 : 2.1	31	69	1 : 2.2
Dissections 1993	73	27	2.7 : 1	62	38	1.6 : 1

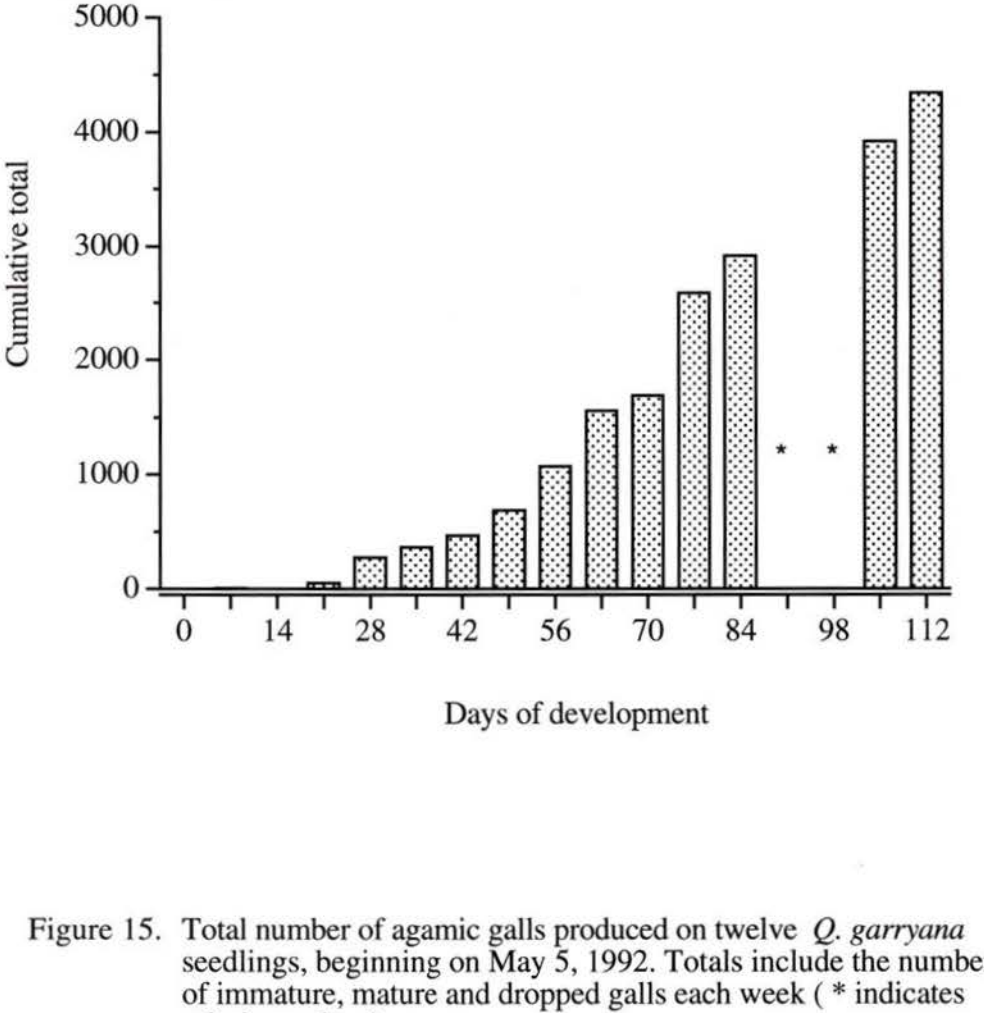

Figure 15. Total number of agamic galls produced on twelve *Q. garryana* seedlings, beginning on May 5, 1992. Totals include the number of immature, mature and dropped galls each week (* indicates missing values).

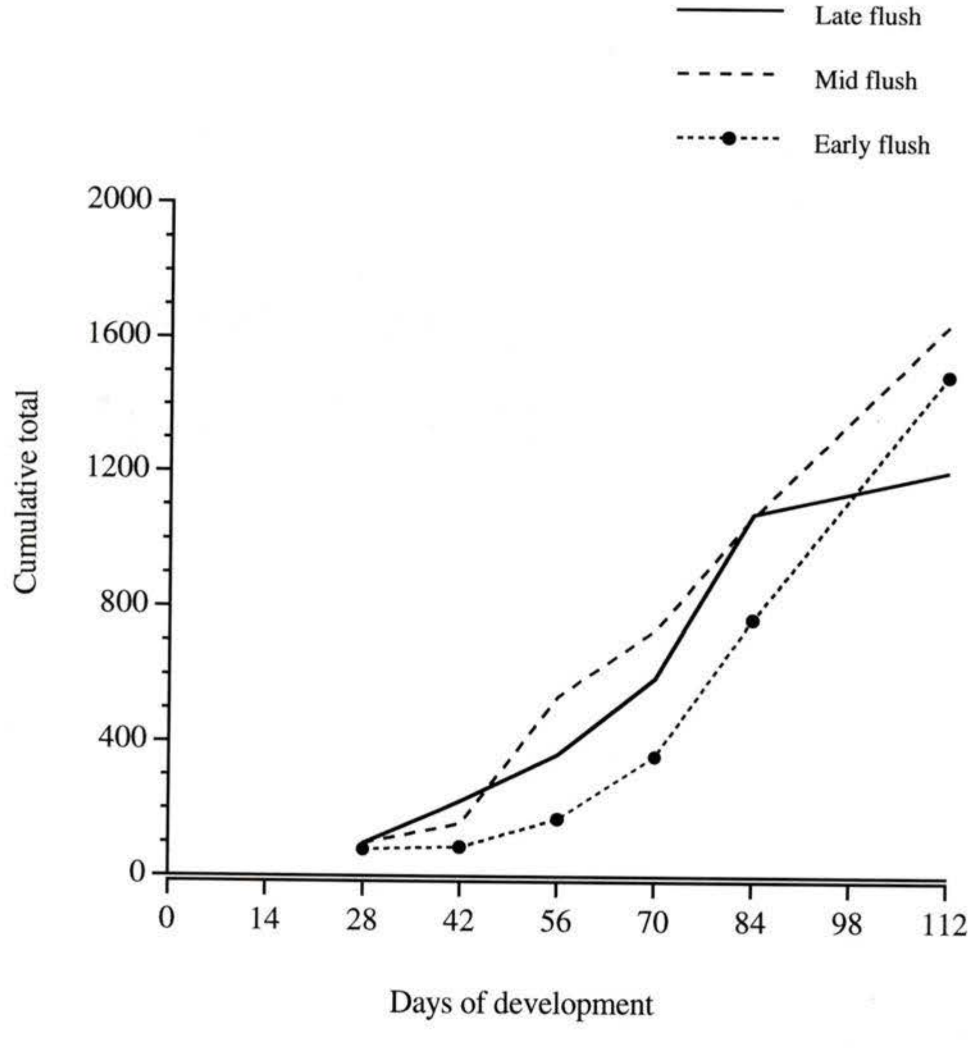

Figure 16. Developmental pattern of agamic galls of *N. saltatorius* on three classes of *Q. garryana* seedlings, beginning May 5, 1992. Total counts include immature, mature and dropped galls.

Development in the agamic generation occurs over a longer period than in the gamic generation and at any given time, galls at various stages of development can be found on the foliage (Fig. 17). Larvae were found on the foliage from June 23 - September 8, 1993 (the last sampling date). Pupae or adults were not found in galls on the foliage (Fig. 18). At the time of the first sampling of galls in the soil (September 22), larvae, pupae and adults were found (Fig. 19). Pupae were found on two sampling dates (October 6 and 27) however, larvae and adults were present in galls until the final sample date (December 1) .

The common name for *N. saltatorius*, "jumping gall wasp" is a reflection of the activity of the larvae in the galls. Once mature, larvae flex rapidly, sometimes touching anterior and posterior ends. The movement of larvae in the galls produces a sound similar to a light rain. Eventually, the flexing movement causes the connection to the leaf to sever and the galls fall. Once on the ground, larvae continue flexing and galls jump around; galls were able to attain a jump height of 2.5 cm during a short experiment in the lab. Jumping behaviour can last for weeks, sometimes months, and is most pronounced if the gall is disturbed. The longevity of the energetic of jumping was discovered serendipitously in 1993. Several galls were brought inside and opened in June 1993 after being outside since July 1992. Surprisingly, live *N. saltatorius* larvae were found and several flexed if they were touched, 11 months after they were removed from a leaf!

In 1993, galls began to fall just prior to the week of June 23. In general, the peak gall drop occurred during the first two weeks of July (Fig. 20) and galls fell between June 23 and October 5. The mean weekly gall drop per site was found to be significantly different ($.02 < P(T_{+} \leq 10;11) < .05$) for pairwise comparisons between Mill Hill and Oak Bay and Mill Hill and Blenkinsop, respectively. The greatest mean number of galls per week fell at Oak Bay. Traps placed at Mill Hill collected fewer galls ($\Sigma=1019$) than the other sites and the week of peak gall drop was not as easily identifiable.

Figure 17. Various stages of development can be found on the foliage during the agamic generation of *N. saltatorius* .

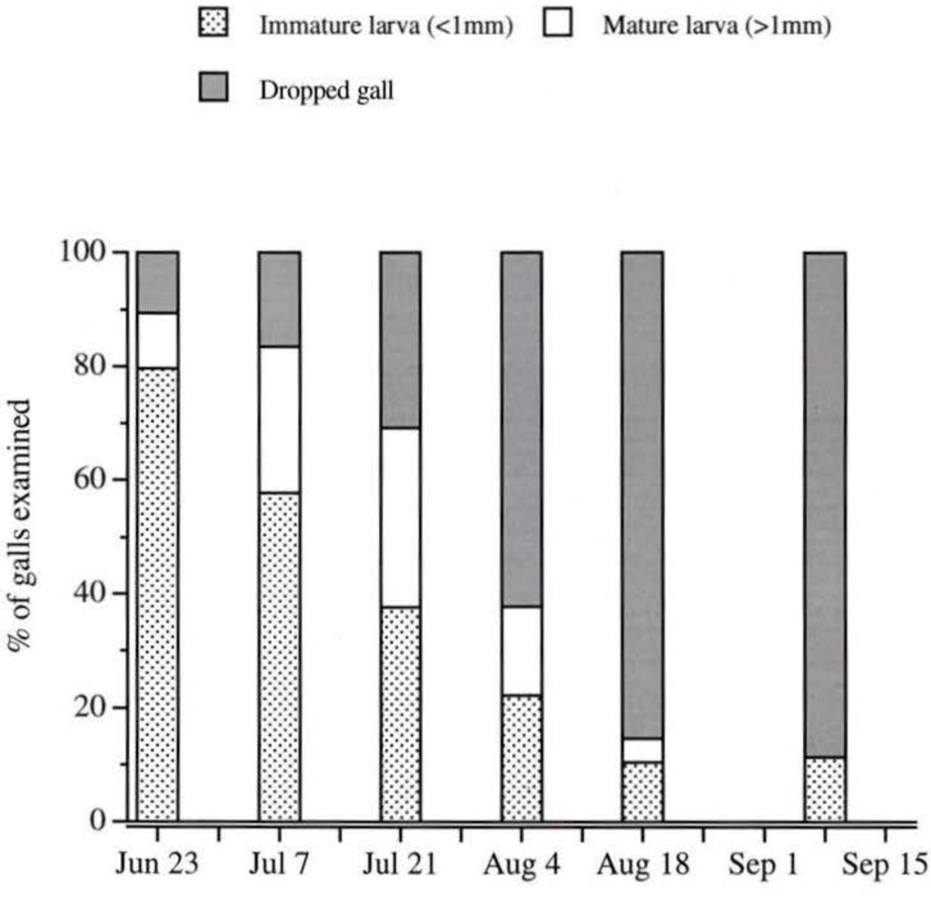

Figure 18. Developmental progression of the agamic generation of *N. saltatorius* on the foliage of *Q. garryana*, 1993.

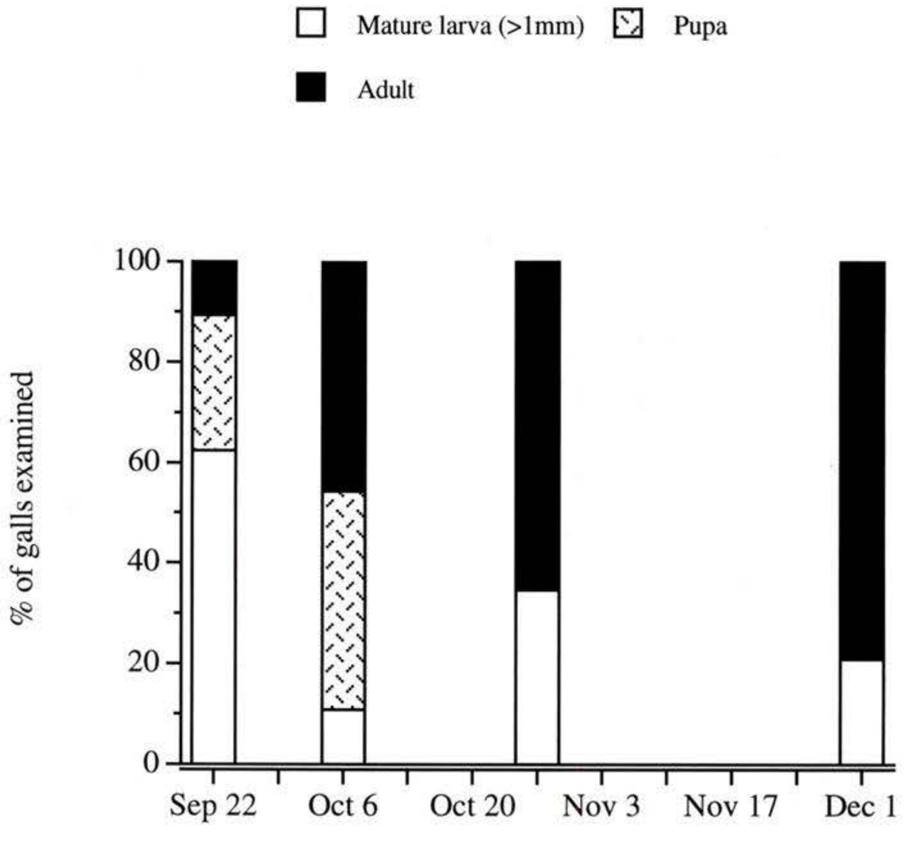

Figure 19. Developmental progression of the agamic generation of *N. saltatorius* once the galls have dropped to the ground, 1993.

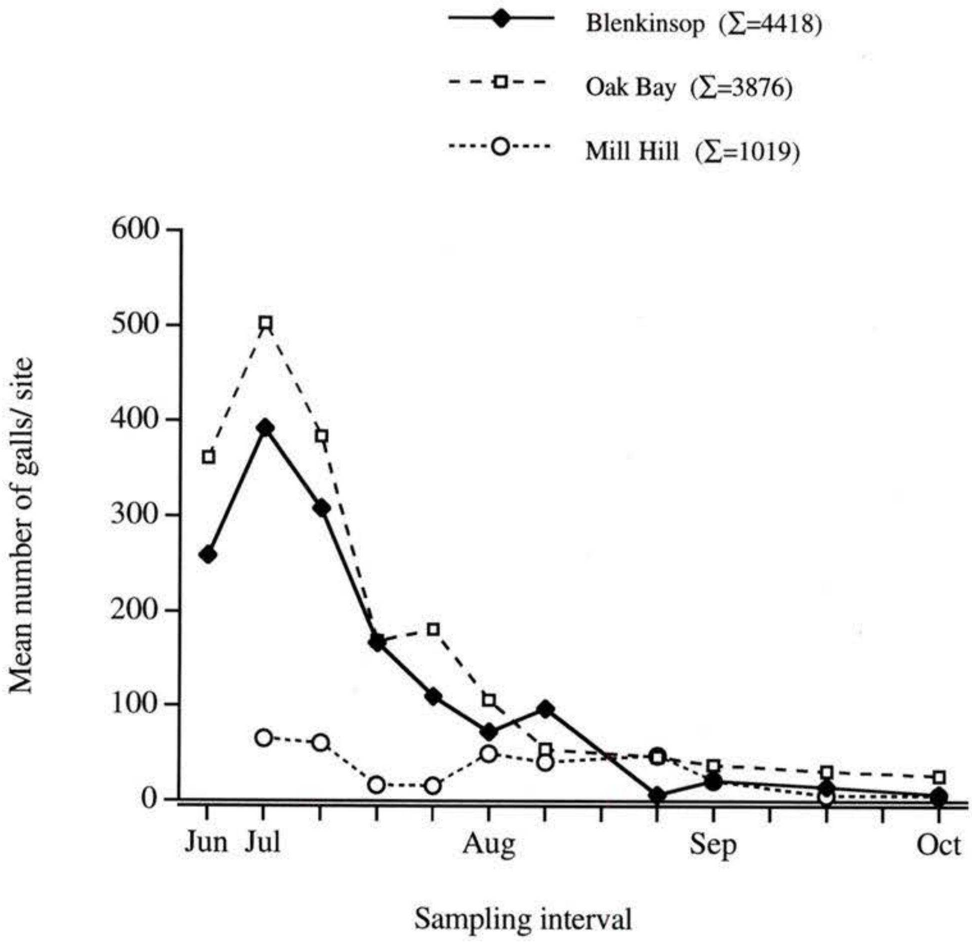

Figure 20. Mean weekly agamic gall drop of *N. saltatorius* from 3 sites, 1993. Traps were positioned at the sites after the galls started to fall.

An examination of the cumulative agamic gall drop indicates that approximately 75% of the galls fell into the traps by the middle of July (Fig. 21) at Oak Bay and Blenkinsop whereas 75% of the galls at Mill Hill had not fallen until near the end of August .

Fecundity

Gamic females collected from Mill Hill in 1992 had more eggs than females collected from Blenkinsop in 1993-94 ($.01<P(F\leq189)<.02$) (Table 5). Agamic females collected between 1993-94 showed no significant differences for the measured variables. The number of eggs from gamic females ranged 43 - 156 (mean 98± 3; n=105) and in agamic females 11-70 (mean 35 ± 1; n=105). In general, gamic females were larger with a greater number of eggs that were smaller than those of agamic females. The number of eggs, found in gamic females, were not related to age ($P(F\leq.56)>.05$).

A linear relationship was found between overall body length and egg numbers in gamic females collected May 1992 and May 1993-4 , and agamic females collected 1992-94 (r= .389, .517, .606, respectively; $p<.01$). Similarly, a strong linear relationship was found between the length of the abdomen and the number of eggs in the same sample (r=.545, .3, .421 respectively; all $p<.01$). There was no correlation between length and the size of the egg, in either gamic or agamic females ($r<.01$; $p>.05$).

Parasitoid complex

Characteristics of parasitoid taxa

Three species of parasitoids were reared from the bisexual generation and ten species were reared from the agamic generation (Table 6). Two parasitoids of the agamic generation were identified as occasional hyperparasitoids, *Amphidocius schickae* (Heydon and Boucek) and *Aprostocetus verrucarii* (Balduf). The parasitoid complex of *Neuroterus*

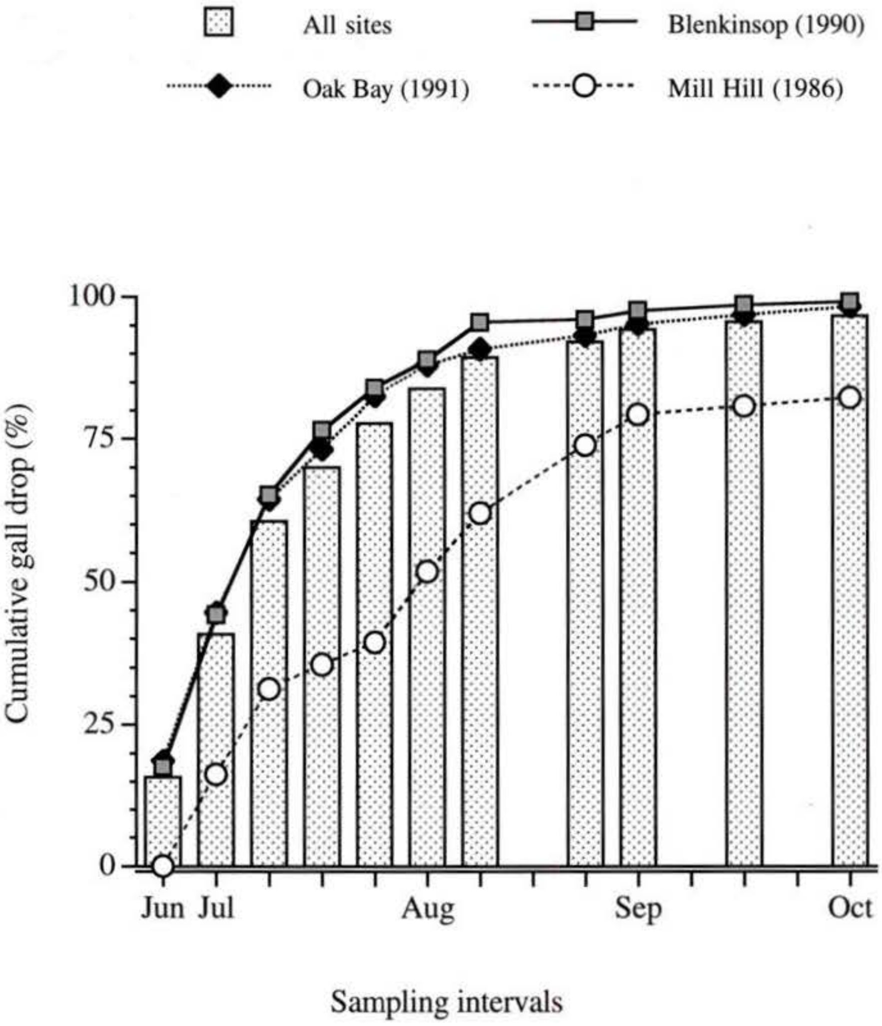

Figure 21. Cumulative agamic gall drop of *N. saltatorius* from three sites in Victoria with infestation dates in parentheis; traps were not counted on weeks where no values are reported.

Table 5. Fecundity and associated measurements of *N. saltatorius* females (mean ± SE). Comparisons were tested with ANOVA and Scheffé multiple contrasts and significant differences are indicated by different letters (*p*<.001).

Site	Date	n	No. eggs	Egg size (mm)	Length (mm)	Abdomen (mm)
Gamic						
Mill Hill	May 1992	35	114 ± 3 ^{a}	.102 ± .001 ^{c}	1.49 ± .016 ^{d}	.803 ± .006 ^{e}
Blenkinsop	May 1993	35	10 ± 5 ^{b}	.105 ± .001 ^{c}	1.51 ± .025 ^{d}	.731 ± .015 ^{f}
Blenkinsop	May 1994	35	93 ± 3 ^{b}	.104 ± .001 ^{c}	1.51 ± .017 ^{d}	.735 ± .011 ^{f}
Pooled	93-94	70	98 ± 3 ^{b}	.104 ± .001 ^{c}	11.51 ± .01 ^{d}	.733 ± .009 ^{f}
Overall		105	-	104 ± <.001	1.51 ± .011	-
Agamic						
Mt. Newton	Jan/Feb 1993	16	33 ± 3 ^{g}	.191 ± .003 ^{h}	1.12 ± .027 ^{i}	.657 ± .016 ^{j}
Mill / Oak	Oct/Nov 1993	42	34 ± 2 ^{g}	.184 ± .002 ^{h}	1.19 ± .017 ^{i}	.656 ± .013 ^{j}
Blenkinsop	Mar 1994	47	37 ± 2 ^{g}	.191 ± .016 ^{h}	1.22 ± .017 ^{i}	.663 ± .014 ^{j}
Overall		105	35 ± 1 ^{g}	.190 ± .001 ^{h}	1.19 ± .011 ^{i}	.661 ± .009 ^{j}

Table 6. List of taxa (Hymenoptera: Chalcidoidea) reared from gamic and agamic galls of *N.saltatorius* on Vancouver Island, 1992-94. Galls were collected from *Q.garryana* and reared outdoors.

Generation	Family	Species
Gamic		
	Pteromalidae	*Mesopolobus* sp. nr. *longicaudae* Doganlar *Amphidocius* n. sp.
	Eulophidae	*Aprostocetus verrucarii* (Balduf)
Agamic		
	Ormyridae	*Ormyrus distinctus* Fullaway
	Pteromalidae	*Amphidocius schickae* (Heydon and Boucek) *Amphidocius* n. sp. *Dibrachys cavus* Walker *Mesopolobus* sp. nr. *longicaudae* Doganlar
	Eulophidae	*Aprostocetus pattersonae* (Fullaway) *Aprostocetus verrucarii* (Balduf) *Aprostocetus* n. sp.
	Eupelmidae	*Brasema* spp. (2)

saltatorius in Oregon on *Q. garryana* consisted of eight species (Table 7), none of which were identified as hyperparasitoids.

Most parasitoid species emerged from mass rearings although the parasitoid-exclusion experiment resulted in two additional species in 1993 - *Dibrachys cavus* Walker and *Gastrancistrus* sp. (Table 8). The most numerous species to emerge from the bisexual generation was *Mesopolobus* sp. nr. *longicaudae* Doganlar (86%) and the species to emerge from the agamic generation were *Aprostocetus pattersonae* (Fullaway) (42.4%), *Amphidocius schickae* (39.9%), *Aprostocetus verrucarii* (14.2%) *Aprostocetus* sp. (2.8%), *Brasema* sp., *Ormyrus distinctus* (Fullaway), *Amphidocius* n. sp., *Mesopolobus* sp. nr. *longicaudae* and *Dibrachys cavus* (all < 1%).

The parasitoid complex of *N. saltatorius* was found to remain reasonably constant throughout its range (Table 9) save for two species. One member of the parasitoid complex in California, *Goullina* sp. and one inquiline, *Synergus* sp., have not been reared from this project. The absence of *Goullina* sp. and the inquiline were not the result of a shortage of rearing material, that is, tens of thousands of galls were reared between 1992-93.
On Vancouver Island, *Aprostocetus pattersonae* and *Amphidocius schickae* were almost equal in abundance when all sites were combined but *Aprostocetus pattersonae* dominated the parasitoid complex in Oregon (Fig. 22). When the primary sites in B.C. were analysed individually, a different trend emerged. The parasitoid complex at older infestation sites (e.g. Mill Hill) was dominated by *Aprostocetus pattersonae* yet newer areas (e.g. Oak Bay and Blenkinsop) were dominated by *Amphidocius schickae* or a combination of *Amphidocius schickae* and *Aprostocetus pattersonae* depending upon the year (Fig. 23).

A departure from the trends outlined above was found when the parasitoid sleeve cages were analysed for species abundances. At all three sites, *Amphidocius schickae* dominated the rearings, almost to the exclusion of all other parasitoid species (Fig. 24).

Table 7. List of taxa (Hymenoptera: Chalcidoidea) reared from the agamic generation of *N. saltatorius*, Oregon, 1993 (reared in quarantine facilities 16L:8D).

Family	Species
Ormyridae	*Ormyrus distinctus* Fullaway
Pteromalidae	*Amphidocius schickae* (Heydon and Boucèk)
	Mesopolobus sp. nr. *longicaudae* Doganlar
Eulophidae	*Aprostocetus pattersonae* (Fullaway)
	Aprostocetus verrucarii (Balduf)
	Aprostocetus n. sp.
	Aprostocetus sp.
Eupelmidae	*Brasema* sp.

Table 8. The origin of parasitoid taxa (Hymenoptera: Cynipidae) reared from gamic and agamic generation galls of *N. saltatorius* collected in B.C. and Oregon, 1992-94. Rearing methods: A mass collection, B funnel trap and C: sleeve cage.

Parasitoid taxa	Location	Collection date	Rear date	No. found	Rearing method
ORMYRIDAE					
Ormyrus distinctus	Mt. Doug	26.VII.93	26.VIII.93	2	A
	Corvalis OR	30.VI.93	06.VIII.93	2	A
	Corvalis OR	30.VI.93	14.IX.93	1	A
PTERMOLIDAE					
Amphidocius schickae	Can/USA	1992-94	1992-94	<1000	A-C
Amphidocius sp.	Can/USA	1992-94	1992-94	< 100	A
Mesopolobus sp.	Can/USA	1992-94	1992-94	< 250	A
Dibrachys cavus	Blenkinsop	02.VIII.93	28.X.93	1	C
Gastrancistrus sp.	Blenkinsop	16.VIII.93	17.XI.93	3	C
	Blenkinsop	16.VIII.93	15.XII.93	2	C
	Blenkinsop	16.VIII.93	24.III.94	2	C
EULOPHIDAE					
Aprostocetus pattersonae	Can/USA	1992-94	1992-94	> 1000	A-C
Aprostocetus verrucarii	Can/USA	1992-94	1992-94	< 500	A-C
Aprostocetus n. sp	Can/USA	1992-94	1992-94	< 250	A-C
Aprostocetus sp.	s. OR	01.VII.93	06.VIII.93	1	A
EUPELMIDAE					
Brasema sp.	Can/USA	1992-94	1992-94	< 25	A
Brasema sp.	Beaver Lake	23.VI.92	14.VIII.92	3	A
Brasema sp	Blenkinsop	19.VII.93		1	B
	Beaver Lake	07. VII.92	20.VIII.92	3	A
	Beaver Lake	22.VII.92	21.VIII.92	3	A
Brasema sp.	Beaver Lake	07.VII.92	20.VIII.92	8	A
	Beaver Lake	07.VII.92	03.IX.92	1	A
	Beaver Lake	07.VII.92	09.IX.92	2	A
	Beaver Lake	22.VII.92	21.VIII.92	5	A
	Beaver Lake	22.VII.92	03.IX.92	1	A
	Beaver Lake	28.VII.92	28.VIII.92	2	A
	Oak Bay	12.VII.93		1	B
	Oak Bay	16.VIII.93		1	B
	Oak Bay	27.X.93		1	B

Table 9. A comparison of the parasitoid species (Hymenoptera: Chalcidoidea) reared from the agamic generation of *N. saltatorius* , on *Q.garryana*, with species that have emerged from other cynipid hosts in B.C.

Parasitoid species	*Neuroterus saltatorius*			Cynipid host in B.C. * 1960-70
	B.C. 1992-93	Oregon 1993	California† 1992-93	
Amphidocius schickae	√	√	√	none identified
Aprostocetus pattersonae	√	√	√	*Neuroterus washingtonensis* Beutenmueller *Bassettia ligni* Kinsey *Liodora pattersonae* (Fullaway) *Sphaeroteras trimaculosa* (McCracken & Egbert) *Besbicus mirabilis* (Kinsey)
Aprostocetus verrucarii	√	√	√	*Andricus opertus* (Weld) *Bassettia ligni* *Besbicus mirabilis* *Liodora pattersonae* *Neuroterus washingtonensis*
Aprostocetus n. sp.	√	√	-	*Bassettia ligni* *Neuroterus washingtonensis*
Brasema spp.	√	√	√	*Andricus opertus* *Bassettia ligni* *Besbicus mirabilis* *Liodora pattersonae* *Sphaeroteras* sp. *Xanthoteras* sp.
Mesopolobus sp.	√	√	-	*Andricus opertus* *Callirhytis* sp.
Goullina sp.	-	-	√	none identified
Ormyrus distinctus	√	√	-	none identified
Synergus sp. (inquiline)	-	-	√	none identified

† Dr. S. Heydon, UC Davis California 1992-93. Host: *Q. lobata*

* D. Evans, Canadian Forest Service 1960-70.

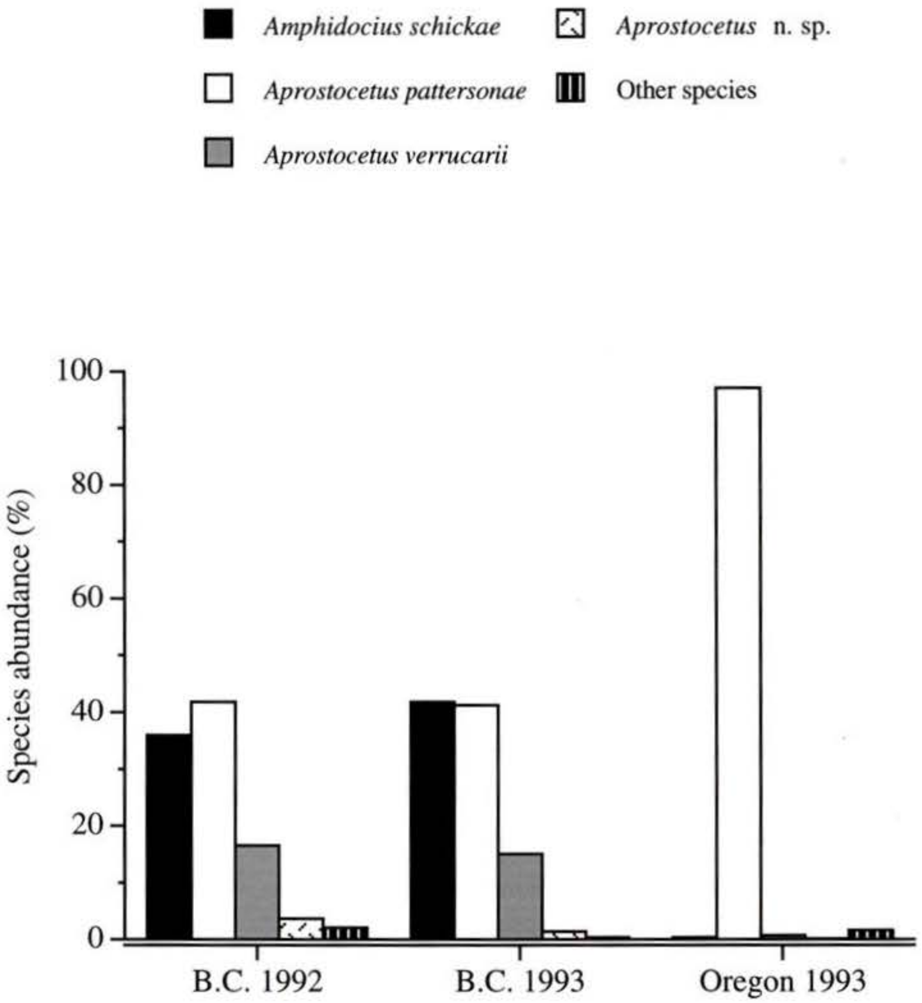

Figure 22 . Comparison of the parasitoids species (Chalcidoidea) reared agamic *N. saltatorius* galls mass collected June - August, 1992-93 from eight sites in Victoria, B.C. with galls collected in Oregon June-July, 1993.

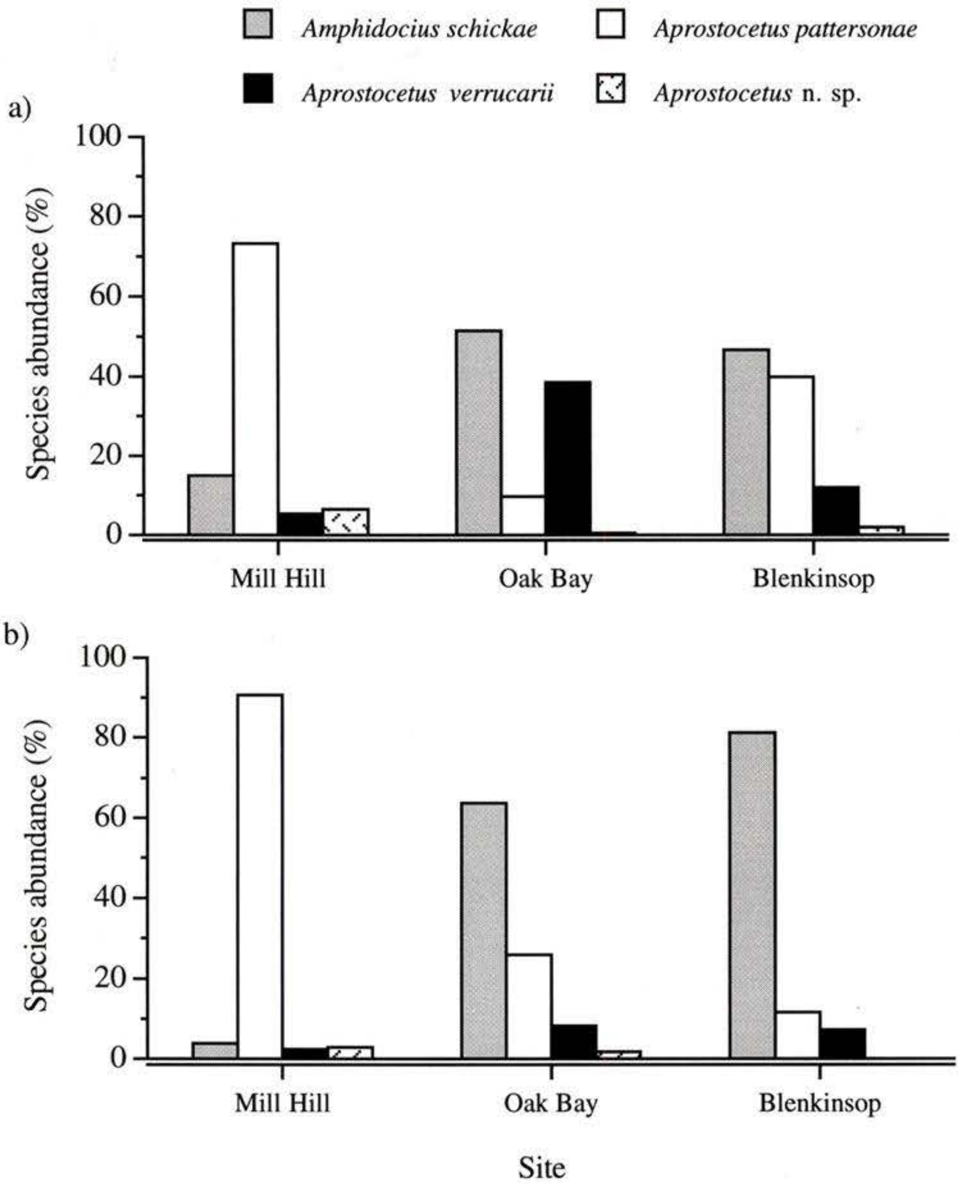

Figure 23. The distribution of dominant species that make up the parasitoid complex of the agamic generation of *N. saltatorius* at three sites in Victoria, B.C.: a) 1992 (*n*=1401) and b) 1993 (*n*=1018).

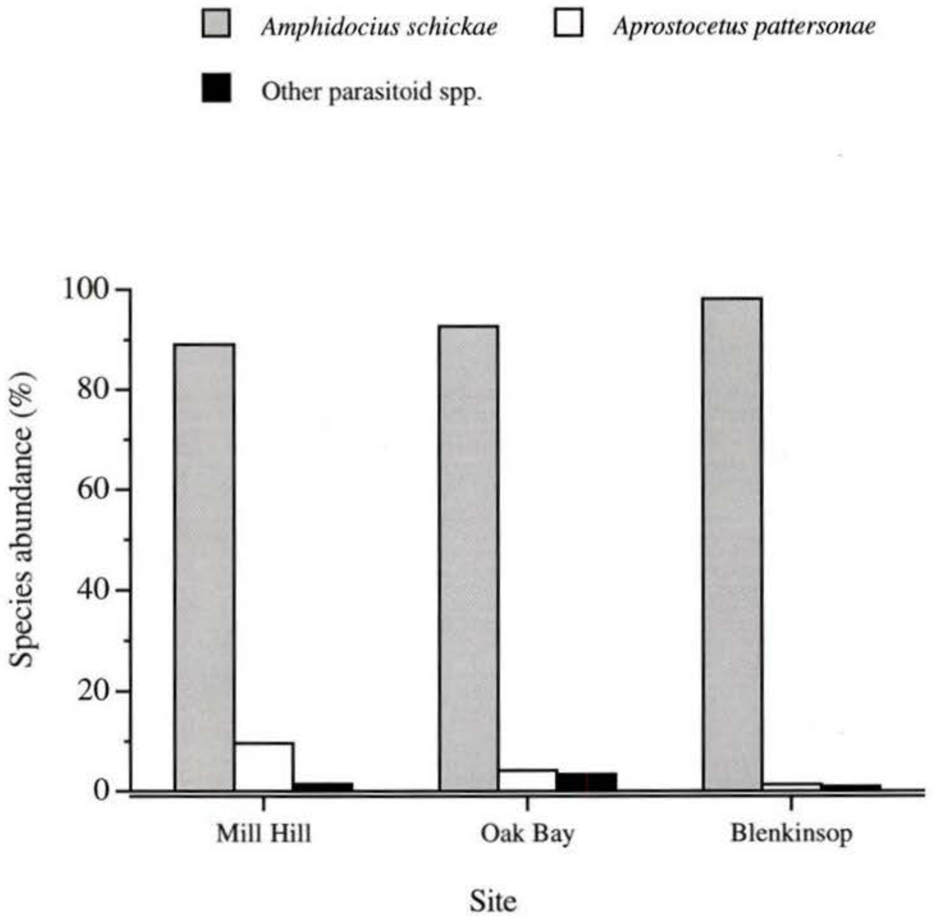

Figure 24. The distribution of parasitoid species reared from agamic galls exposed at two week intervals during a parasitoid-exclusion experiment June 6 - October 27, 1993.

Parasitoid emergence patterns were found to be a function of collection date. Galls collected July 20, 1992 and July 26, 1993 produced the greatest number of adult parasitoids in rearings (Fig. 25). This trend was strongest in 1993; > 50% of all adults emerged from a single collection date. If the collection date is not considered, the greatest number of adults emerged August 15-30, 1992 -93 and October 1-15, 1993 (Fig. 26) again, the trend is more pronounced in 1993. Usually, *Aprostocetus pattersonae* appeared first in rearings and *Aprostocetus verrucarii* was the last, particularly in 1993.

Mortality factors and survivorship

Parasitism from agamic rearings

In 1992, parasitism levels were highly variable and peaked during the weeks of July 6 -August 3 (Fig. 27). Weekly mean parasitism levels ranged from 0% to 20% throughout the summer and most samples showed <10% parasitism (Table 10). Galls collected from Mill Hill, Beaver Lake and Tatlow experienced the highest levels of parasitism during the week of July 6: 19.9, 18.5 and 20.0% respectively. Parasitism of galls were taken from foliage after August 17 decreased at all sites except Oak Bay. At Mt. Douglas and Beaver Lake sites, parasitism was greatest earlier in the summer (June 8-July 20), at Santa Anita, Oak Bay, Blenkinsop and Mt. Newton sites, parasitism was greatest towards the end of the summer (July 6 - August 17) and at Mill Hill and Tatlow sites parasitism was consistently greater than 5% during June and July.

Parasitism in parasitoid exclusion sleeves

Parasitoids were found in both exposed and unexposed galls and the number of galls found on each sleeved shoot was highly variable (Table 11). Parasitism levels ranged from 0 - 50.6% in exposed sleeves and from 0 - 38.5% in control sleeves; mean parasitism levels were usually greater from exposed galls than from controls. Several collections

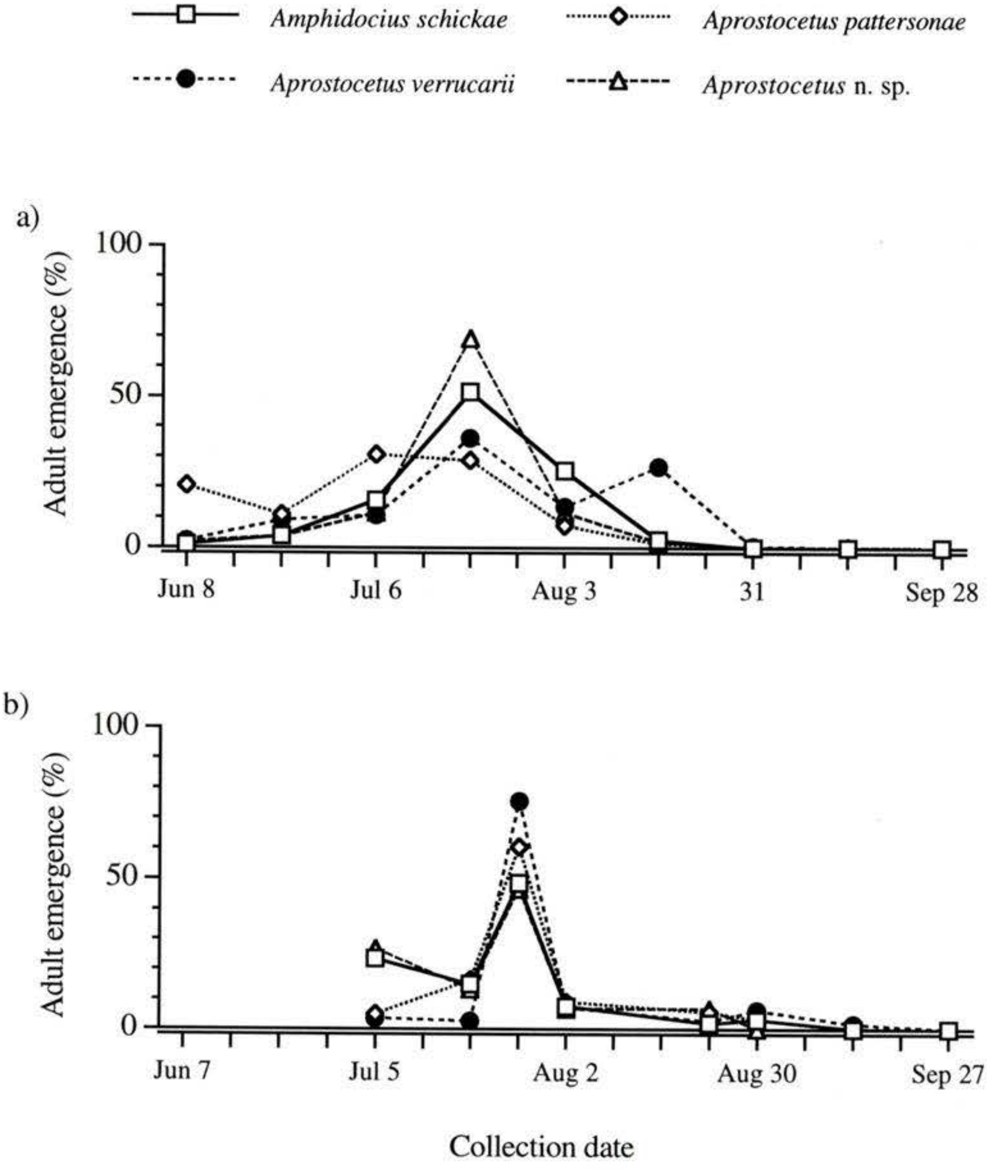

Figure 25. The distribution of parasitoids reared from galls collected at two week intervals in the agamic generation in a) 1992 (*n* = 1401) and b) 1993 (*n*=1018).

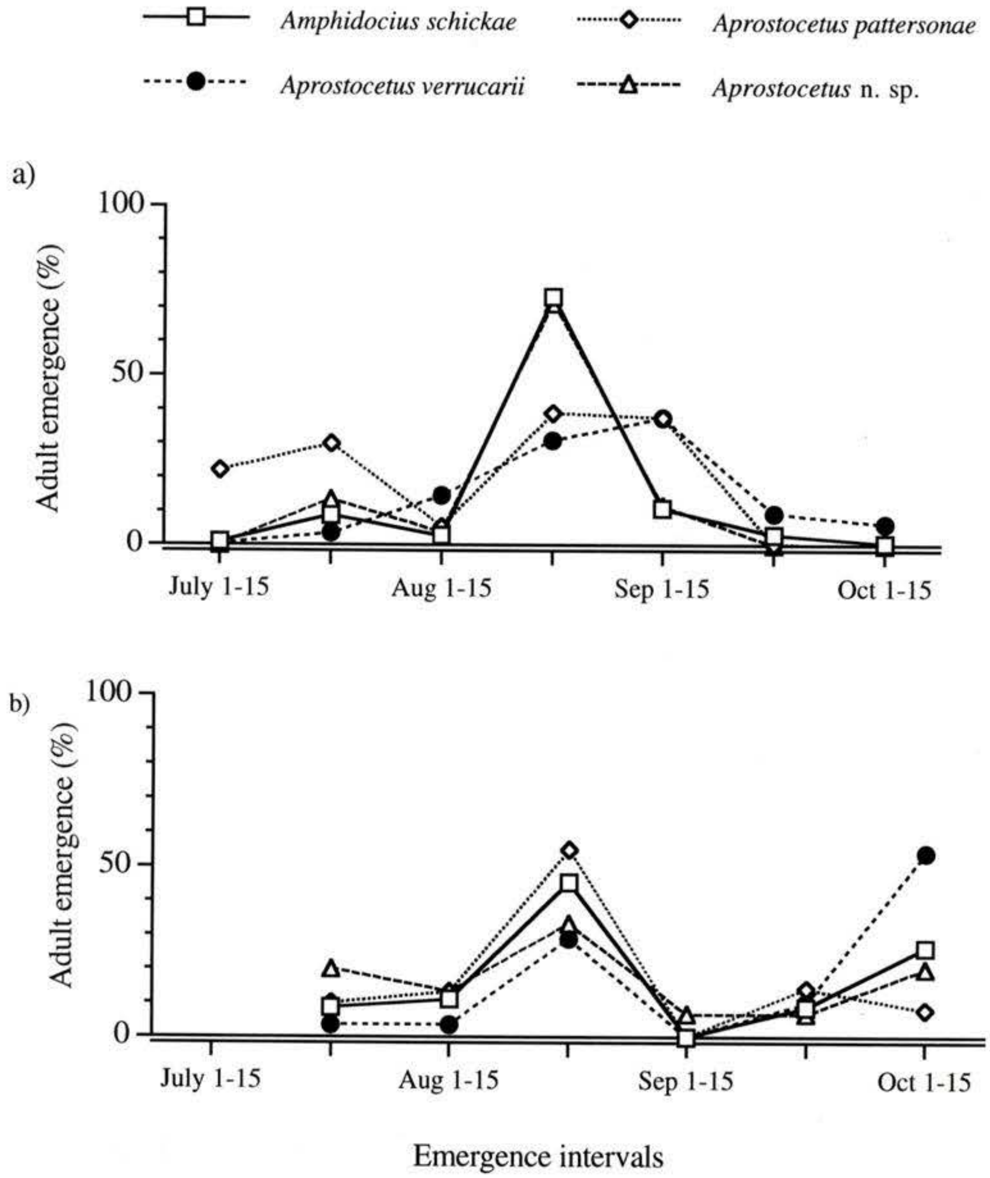

Figure 26. The seasonal emergence pattern of the major parasitoid species reared from agamic galls of *N. saltatorius* collected June - August in a) 1992 (*n*=1401) and b) 1993 (*n*=1018).

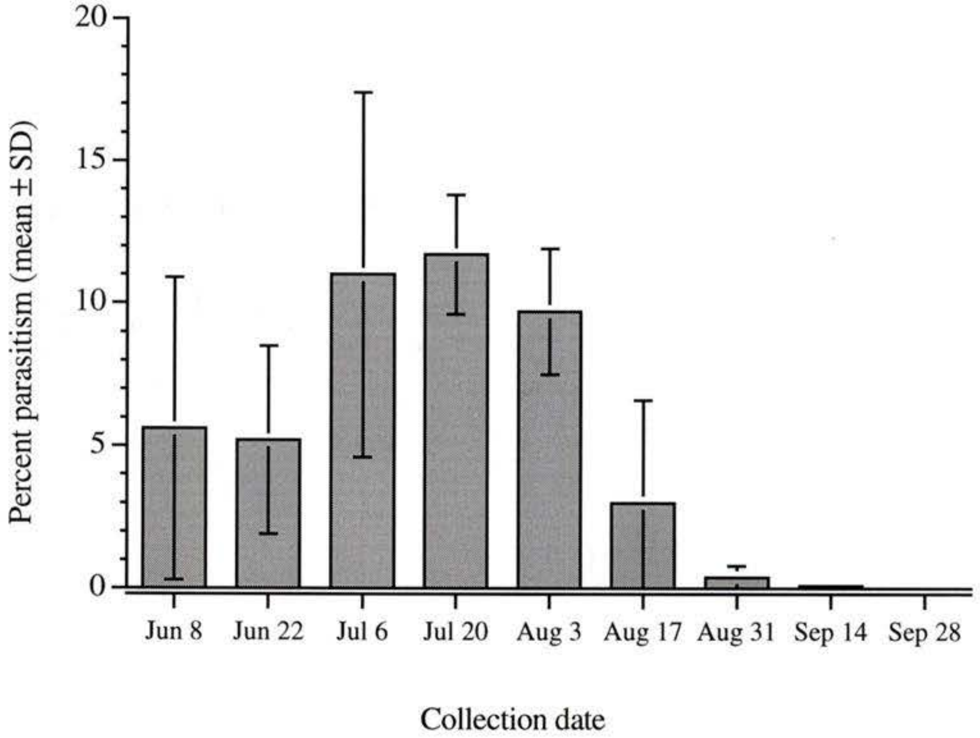

Figure 27. Mean percent parasitism of the agamic generation of *N. saltatorius* determined from the mass rearing of galls ($n \approx 4000$/week) collected at eight sites, 1992.

Table 10. Weekly percent parasitism of mature (>1mm) agamic galls of *N. saltatorius* collected from *Q. garryana* foliage and reared outdoors until October 30, 1992.

	% parasitism per site								
Collection Week	Mill Hill	Santa Anita	Mt. Douglas	Oak Bay	Blenkinsop	Beaver Lake	Mt. Newton	Tatlow	Overall mean (±SD)
Jun 08	8.7	.6	10.2	1.4	4.4	19.1	-	-	5.6 ± 5.3
Jun 22	6.5	.6	8.0	-	1.7	8.3	8.2	8.3	5.2 ± 3.3
Jul 06	19.9	1.6	4.0	6.9	7.3	18.5	9.5	20.0	11.0 ± 6.4
Jul 20	9.8	10.9	7.5	12.5	15.4	10.1	12.4	14.8	11.7 ± 2.1
Jul 27	11.1	8.0	-	7.1	14.1	7.4	10.2	-	9.7 ± 2.2
Aug 17	.8	4.0	1.3	16.5	.5	.5	.5	-	3.0 ± 3.6
Aug 31	-	-	-	.3	-	-	-	3.1	4 ± .7
Sep 14	-	.3	-	.8	-	-	-	-	-

Table 11 . Parasitism levels of agamic galls a) exposed to parasitoids for two week intervals June 7-October 4, 1993 and b) not exposed (controls).

Site	Galls collected	a) exposed		b) not exposed	
		Mean % Parasitism	No. galls	Mean % Parasitism	No. galls
Blenkinsop	Jun 21	0.0	353	0.0	80
	Jul 05	5.7	1795	-	
	Jul 19	13.0	6380	38.5	200
	Aug 02	16.2	4435	18.0	1040
	Aug 16	17.1	1335	17.1	1030
	Aug 27	3.4	1270	13.8	1040
	Sep 08	1.3	1807	11.8	1440
	Sep 20	0.1	1960	0.4	259
	Oct 04	7.4	907	4.7	1575
	Oct 27	2.4	3250	0.9	1710
Oak Bay	Jun 21	14.3	35	7.7	13
	Jul 05	50.6	79	0.3	320
	Jul 19	2.4	82	0.0	15
	Aug 02	37.5	301	27.4	190
	Aug 16	9.6	135	3.0	200
	Aug 27	2.2	45	0.0	14
	Sep 08	10.8	658	-	
	Sep 20	0.0	399	0.0	3
	Oct 04	19.0	253	0.0	4
	Oct 27	3.7	2500	0.0	65
Mill Hill	Jun 21	0.0	9	0.0	43
	Jul 05	6.6	351	0.0	8
	Jul 19	12.4	97	23.5	51
	Aug 02	11.9	84	12.4	510
	Aug 16	18.9	573	-	
	Aug 27	1.9	106	14.4	230
	Sep 08	1.0	193	1.5	200
	Sep 20	0.0	366	0.0	38
	Oct 04	8.9	305	0.0	19
	Oct 27	0.8	498	0.4	260

made from Mill Hill and Blenkinsop had greater levels of parasitism in the controls (e.g. July 19). Parasitism was greatest in galls collected from Oak Bay and lowest at Mill Hill, the oldest infestation area.

Parasitism in galls caught in funnel traps

Parasitism levels in agamic galls collected in funnel traps were highly variable and determination varied with the method used. Parasitism was observed to be greatest when galls were dissected however, neither rearings nor dissections seemed to provide an accurate indication of direct parasitism levels, particularly at Oak Bay (Fig. 28). Typically, parasitism was less than 20% in rearings but as high as 50-65% in dissections; often a four-fold difference in the estimate.

Gamic generation survivorship

The survivorship of adults at the end of the gamic generation (early June) was 89% at Mill Hill and 97% at Oak Bay (Fig. 29). Parasitism, gall desiccation and the presence of a secondary fungal pathogen in the gall were the primary sources of larval mortality. Chalcidoid parasitoids were responsible for <25% of the mortality on the foliage between June 23 and October 8, 1993. Parasitism levels slowly increased from 2.2 to 23.4% at Mill Hill between June 20 and August 1; at Oak Bay, they slowly climbed from 0.5% in early June to 22.5 % on August 29. Parasitism was almost twice as high in galls collected from the soil or in mature (>1mm) galls collected from the foliage (Fig. 30-32) than the general population of galls on the foliage.

Failed development accounted for most of the larval mortality on the foliage until the end of July. Subsequently, the greatest source of mortality was from fungal pathogens (*Discula umbrinella* (Berk. & Broome) Sutton) on the foliage that were infecting the

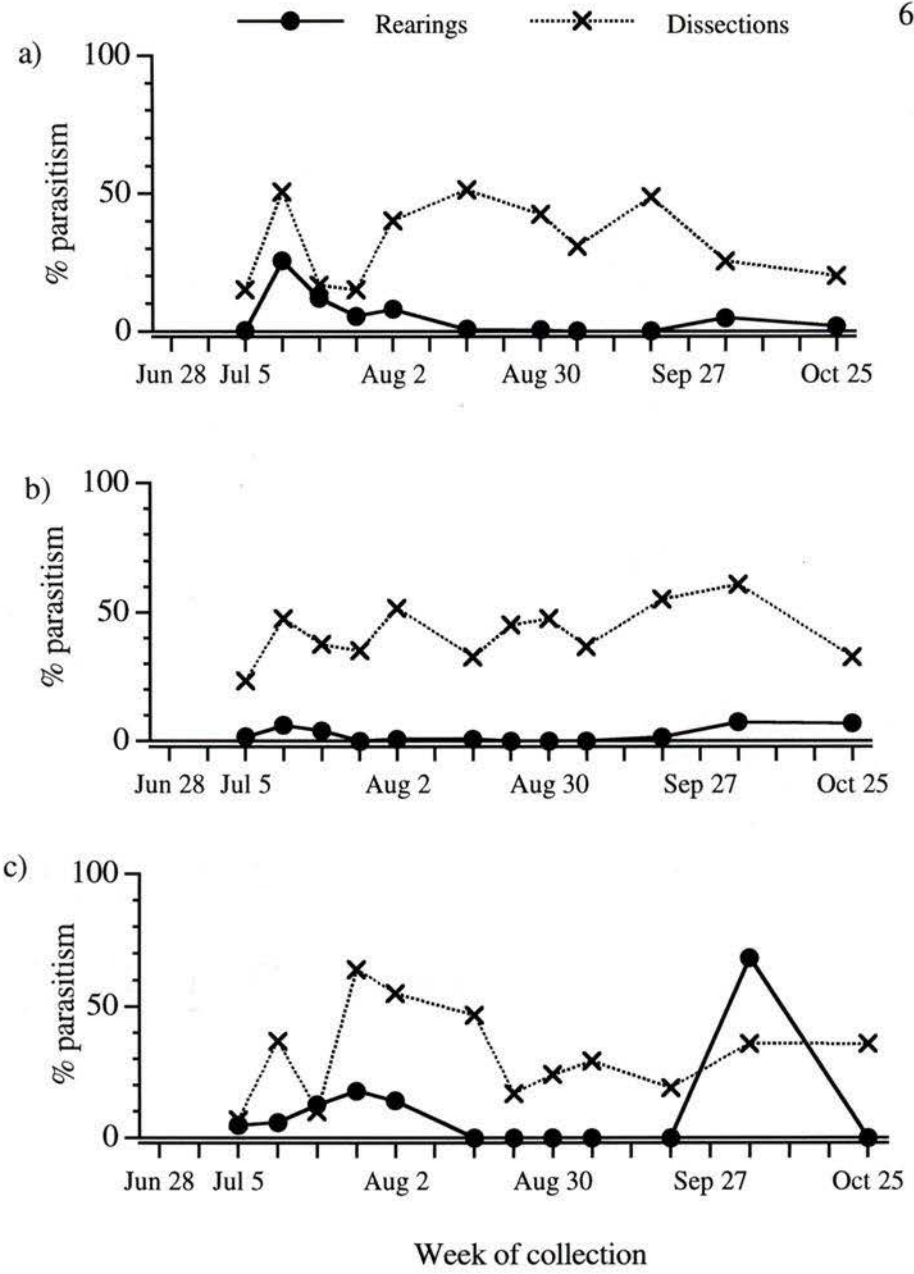

Figure 28. Parasitism levels found in dissections and rearings of agamic galls of *N. saltatorius* collected in funnels at three sites: a) Mill Hill, b) Oak Bay and c) Blenkinsop, 1993. Galls were reared indoors and dissections were done May 1994.

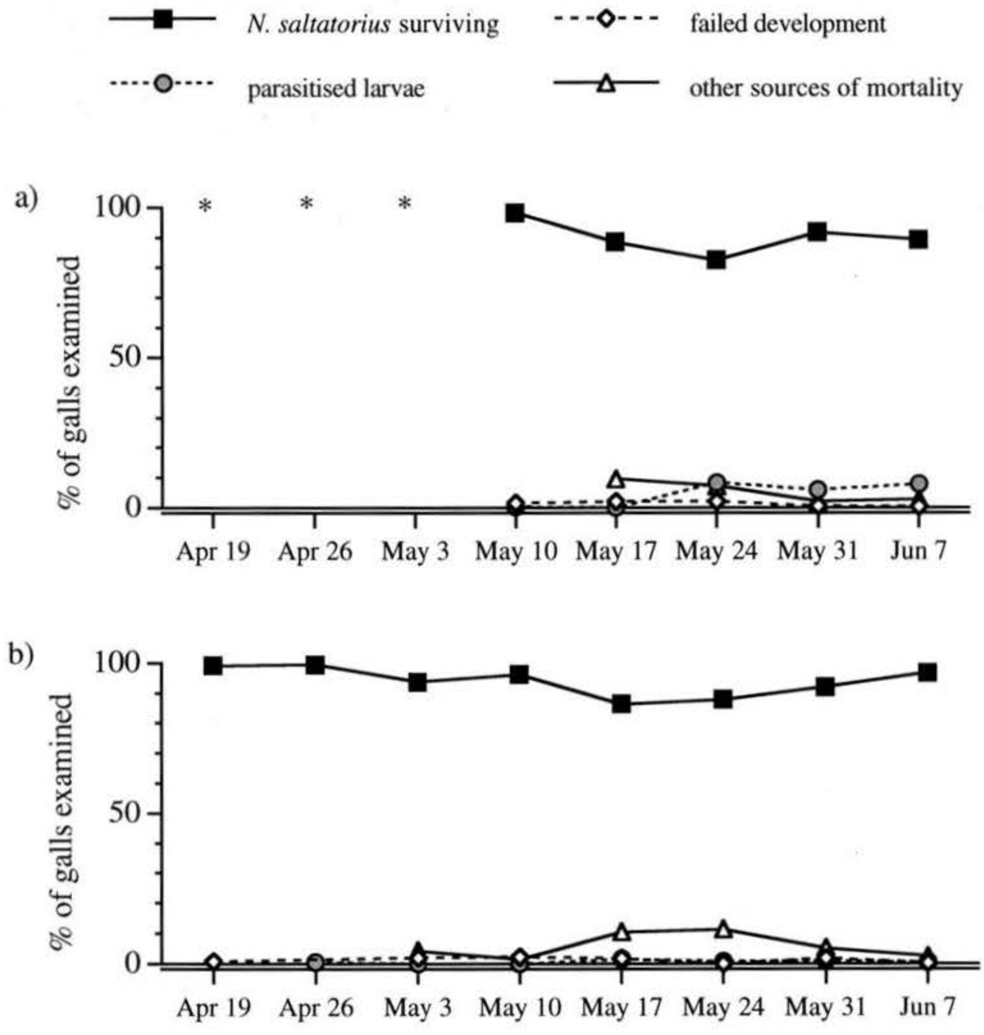

Figure 29 . Survivorship in gamic galls of *N. saltatorius* collected on the foliage at a) Mill Hill (*n*=2000) and b) Oak Bay (*n*=3195) 1993. (* indicates sampling dates missed).

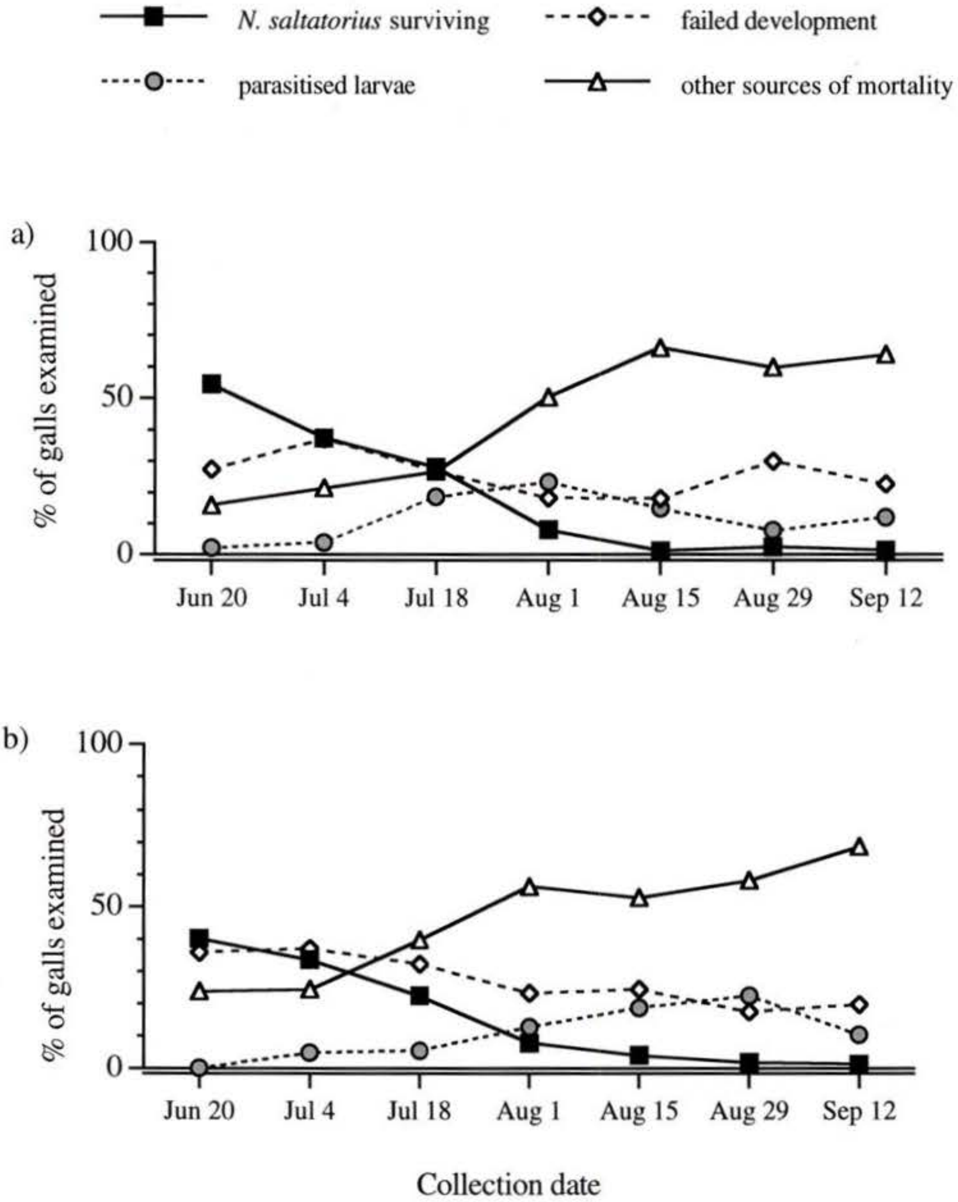

Figure 30. Survivorship in agamic galls of *N. saltatorius* sampled directly from the foliage at a) Mill Hill (n=2802) and b) Oak Bay (n=2794), 1993.

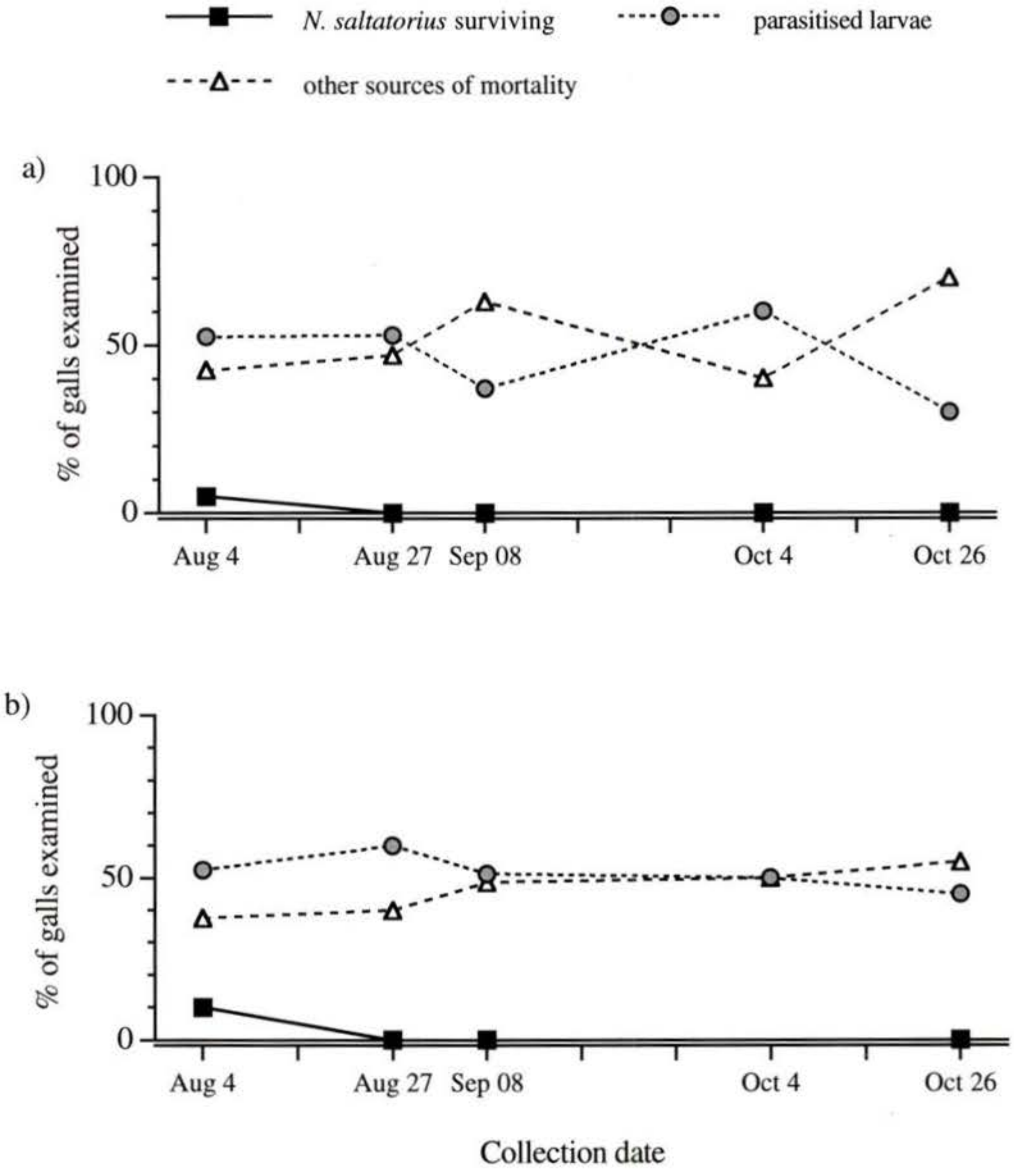

Figure 31. Survivorship in mature (> 1mm) agamic galls of *N. saltatorius* that were left on the foliage after peak gall drop and collected at a) Mill Hill (*n*=342) and b) Oak Bay (*n*=300), 1993.

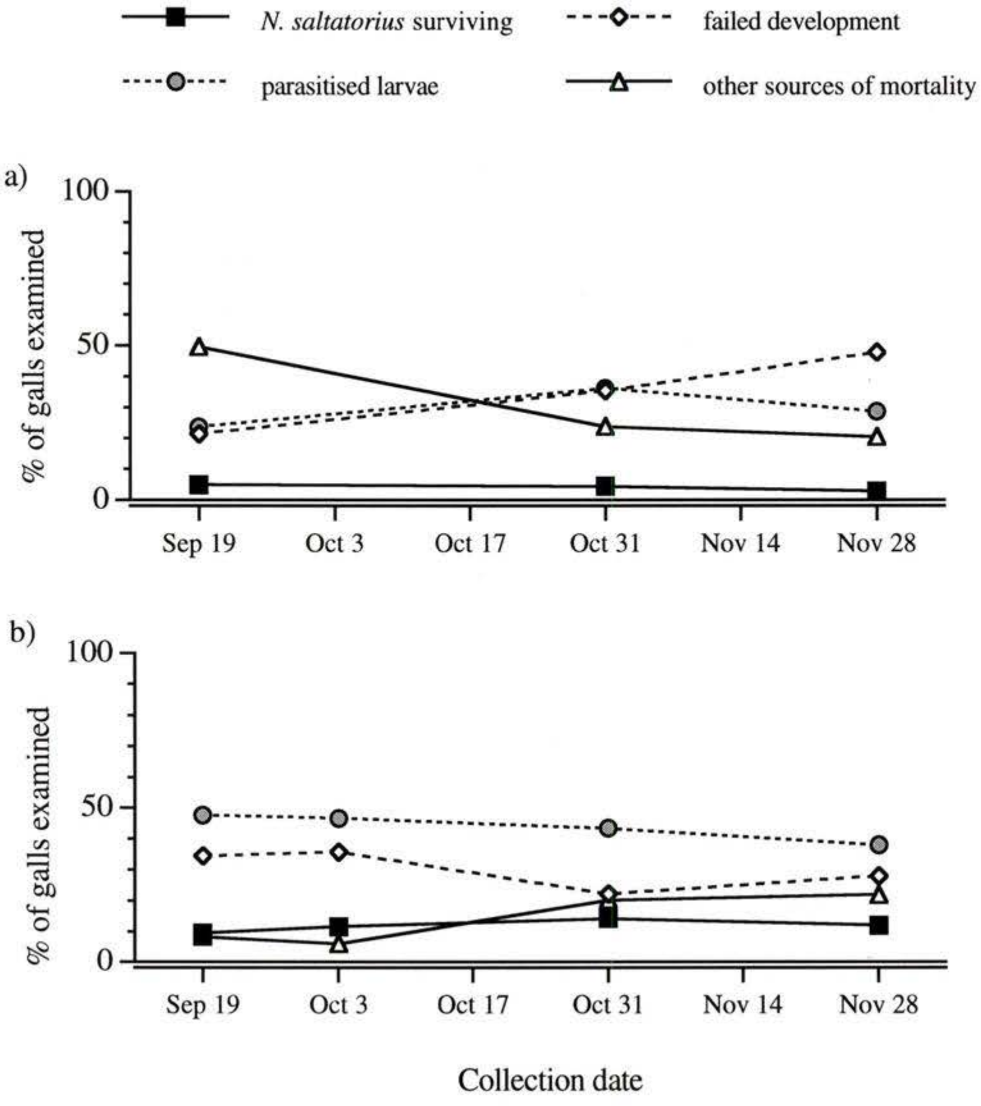

Figure 32. Survivorship in agamic galls of *N. saltatorius* collected from the soil at a) Mill Hill (*n*=1159) and b) Oak Bay (*n*=1601), 1993.

remaining galls. By September 8, most galls sampled from Mill Hill (52%) and Oak Bay (55%) had fungal infections (inside or outside) and Mill Hill generally had a higher proportion of galls affected by fungus. Mature galls (>1mm) on the foliage were empty or contained an amber-coloured liquid.

Agamic generation survivorship

Survivorship varied in the agamic generation depending upon the location of the gall (foliage or soil) and *Neuroterus saltatorius* survival was highest in soil collected galls. At the time of first sampling (June 20, 1993) larval survivorship on the foliage was < 60% at both sites (Fig. 30). By August 1, < 8% of the galls contained healthy larvae and on September 12, *N. saltatorius* larvae were found in only < 1.5% of the galls dissected. Between August 4 - October 26, survival of mature galls on the foliage ranged between 0 and 4.5% (Fig. 31). Galls collected from soil contained very low numbers of viable larvae although survival was slightly greater at Oak Bay, the newer infestation site (Fig. 32). On September 19, surviving *N. saltatorius* larvae were found in 5% and 9.5% of the galls at Mill Hill and Oak Bay, respectively. By the last sampling date, November 2, host larval survival was 3% at Mill Hill and 12% at Oak Bay.

Predation was a minor source of mortality for galls on the foliage or in the soil (generally <10%); a partial list of predators was established. The European earwig (*Forficula auricularia* Linn.) was a common scavenger found on the underside of leaves and laboratory trials confirmed that they ate agamic galls. Potential avian predators were the Chestnut-backed chickadee (*Parus rufescens* Towns.), Red-breasted nuthatch (*Sitta canadensis* Linn.) and Bushtit (*Psaltriparus minimus* Towns.) because they were repeatedly observed foraging on the underside of leaves during late June and early July. Beetles (carabids and tenebrionids) were observed to eat agamic galls in the lab.

Elevated parasitism levels were found in galls collected from funnel traps when compared to other dissections. Larval survivorship prior to or during peak gall drop was quite high, 80-90% but decreased sharply following peak gall drop at the end of June (Fig. 33). After the peak gall drop, parasitism rates increased to > 50% in galls collected from Mill Hill and Oak Bay. Other sources of mortality increased towards the end of the season to levels similar to those found in the other dissections. Interestingly, many of the galls examined during May 1994 contained hosts that had successfully matured to adults (although the adults were dead).

Cumulative survivorship

Due to an enormous amount of variation between and within sampling dates, a partial life table documenting the contribution of each mortality factor to the survivorship of *N. saltatorius* could not be constructed. The mortality rate (qx) varied greatly between sample dates, ranging from 9 to 93 percent (Table 12). Cumulative survivorship of agamic larvae on the foliage was .01% by August 27. The greatest mortality rate increases occurred in samples taken at the beginning of the agamic generation and one month after peak gall drop. After August 15, dropped galls had low survivorship and this is reflected in the large increase in the mortality rate (qx) on August 4.

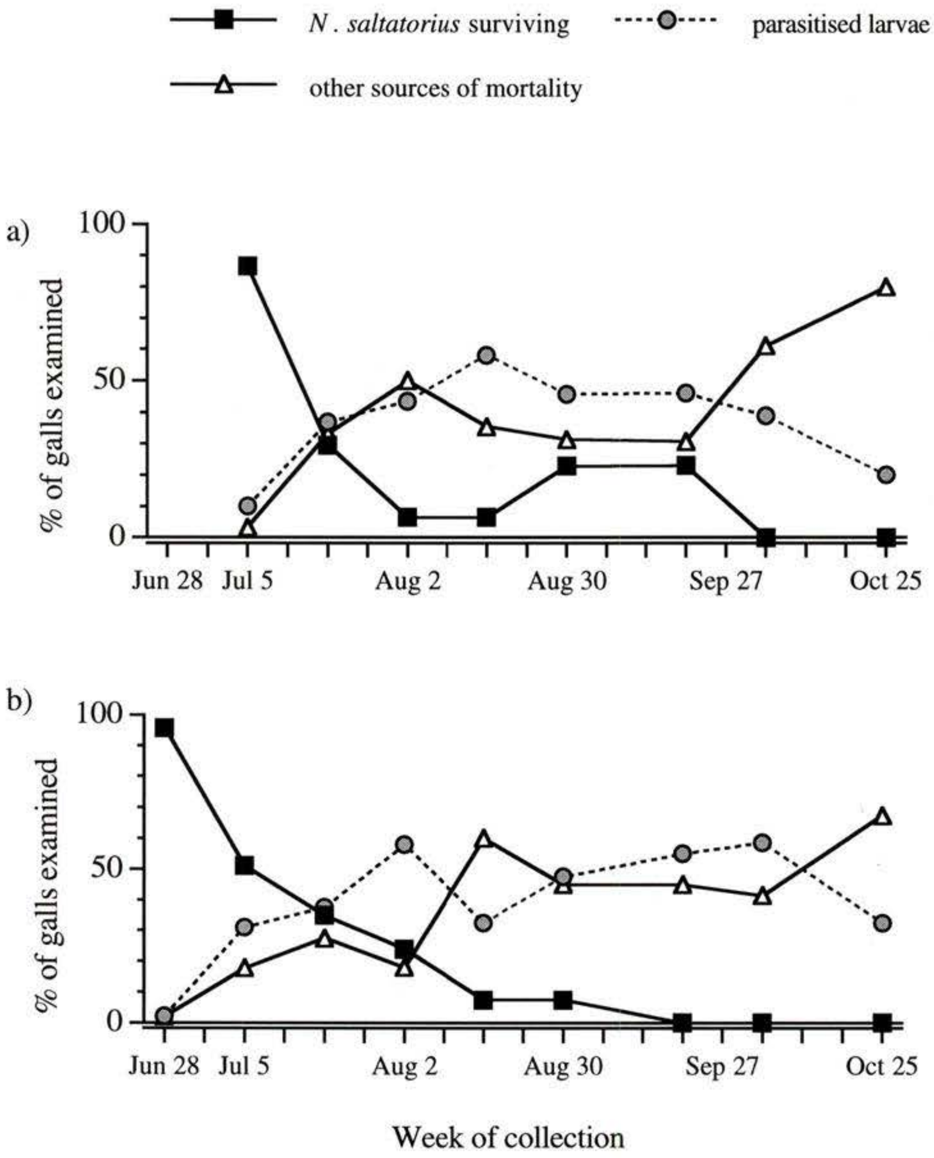

Figure 33. Survivorship in *N. saltatorius* in galls collected in funnel traps from a) Mill Hill (*n*=240) and b) Oak Bay (*n*=370) in 1993 and dissected in May 1994.

Table 12. Cumulative survivorship of *N. saltatorius* agamic generation larvae on Garry oak foliage sampled at two sites in Victoria, 1993.

Collection week	Week #	Life stage	Mill Hill			Oak Bay		
			zx	qx	1-Qx	zx	qx	1-Qx
May 3-16	0	"egg"	400	.42	.58	400	.52	.48
May 23	3	"egg"	2	.26	.43	34	.12	.42
		larva	216			126		
		dropped gall	14			31		
Jul 05	5	larva	150	.09	.39	133	.19	.34
		dropped gall	21			35		
Jul 19	7	larva	112	.53	.18	90	.31	.24
		dropped gall	44			46		
Aug 04	9	larva	32	.93	.02	31	.83	.04
		dropped gall	41			63		
Aug 16	11	larva	5	-	-	16	.56	.02
Aug 27	12.5	larva	10	.40	.01	7	.29	.01
Sep 08	14	larva	6			5		

† Qx (mortality) = $1- (1-qx)^n$

DISCUSSION

Life history and development

Several differences and similarities exist between the Vancouver Island populations of *Neuroterus saltatorius* and those found throughout the rest of its range. In southern California, galls begin to fall in August (Rosenthal and Koehler 1071a; Schick pers. comm.) and they continue to fall until the leaves have fallen from the trees. In contrast, in B.C., most of the galls will have dropped from the trees by mid -July. In the United States, population levels are rarely high enough to cause extreme foliar scorching. Chlorotic spotting was present on *Quercus garryana* in Washington, Oregon and northern California (pers. obs.) and occasionally, individual trees were heavily scorched. In areas of older gall wasp infestation in B.C. (e.g. Mill Hill and Beaver Lake) a similar trend was found and the amount of scorching from *N. saltatorius* appears to be decreasing over time (Bennett 1994).

Phenology can affect herbivorous insect densities on oak trees (Hunter 1992); a study of the distribution of *Neuroterus* spp. on *Quercus robur* L. indicated a correlation between leaf development and gall formation (Ejlersen 1978). Trees that flushed earlier had higher densities of herbivores and suffered more defoliation than those which flushed later. Although there was year to year variation in the flushing dates of individual *Q. robur* trees, the same trees were the first to leaf out and shed each year. The phenological variation within a host population will encourage a greater diversity of herbivores (Crawley and Akhteruzzaman 1988). In this study, *Quercus garryana* trees that flushed early generally had higher infestations of gamic generation galls and lower infestations of agamic galls (Smith unpub. results).

It has been suggested that trees, especially younger ones, can be temporarily harmed, disfigured, or even killed by repeated attacks of phytophagous insects (Evans 1972).

During this study, *Quercus garryana* trees with extensive defoliation and leaf necrosis might produce a second flush of leaves starting mid-July that was gall free. There was no indication that *Neuroterus saltatorius* caused mortality of Garry oak trees in Victoria but certain trees under repeated attack have exhibited some dieback or reduced vigor. The oak leaf phylloxera, *Phylloxera* sp. (Duncan pers. comm.) is the only species to have caused host tree mortality. Unlike the findings of Evans (1972) and Ejlersen (1978), young an mature oaks did not show appreciable differences in the scorching or infestation levels.

Population densities of certain insects may be higher in urban areas than in more natural habitats (Frankie and Ehler 1978). Human activities can influence insect population dynamics at small and large scales. For example, an insecticide applied to lower mosquito populations in California resulted in an increase in pine scale populations because it also eliminated the natural enemies and upset the ecological balance (Luck and Dahlsten 1975). Frankie and Ehler (1978) noted that isolated oaks in urban environments (e.g. parking lots) have greater infestations of a gall wasp *Disholcaspis cenerosa* (Bass.) than trees that occur in natural stands. Newly planted trees along boulevards and in shopping malls were essentially free of most insect populations. When they were colonised by gall formers, populations of these insects were able to increase without control from natural enemies because of the lag time associated with parasitoids locating these patches.

In contrast to the results found by Frankie and Ehler (1978), *Quercus garryana* found growing in parking lots in Victoria appeared to have lower levels of gall wasp populations than trees found in a more natural setting. Surprisingly, the trees were often greener and looked healthier. The reason for the lack of galls might be that the pavement surrounding the trunk reduces larval survival and minimizes the emergence of overwintering agamic females the following year. Additional mortality factors might include increased ground temperatures, presence of opportunistic predators and destruction of galls from human related activities.

Sex ratios were not consistent between the various methods of examination but results of dissections and rearings compared favourably with other published results. Rosenthal and Koehler (1971a) found a 3:1 female/male ratio for emerged adults in rearings; the same sex ratio found during the dissection of gamic galls in this study. Mass rearing of gamic galls in this study and by Sopow (1992) yielded an unbiased sex ratio (i.e. 1:1). The bias towards females in dissections in this study may be the result of an expanding population; in some of the parasitic Hymenoptera, more females are produced in newly colonised areas as a result of increased mate competition (Waage 1986). However, the greatest bias was found at Mill Hill, the oldest site. Sticky traps provided a ratio that favoured males (2:1). Traps may be more attractive to males or perhaps males are more likely to encounter a trap when searching for females.

Blackburn (1991) found no relationship between adult length and fecundity in some parasitic Hymenoptera. In this study, a weak linear correlation was found between adult length and potential fecundity (the number of ovum) that may be explained in terms of life history strategies. Generally a parasitoid will be more fecund if the chances of finding a host are high and the probability of egg survivorship low (r-selected reproductive strategies) (Price 1973). In the univoltine cynipid, *Diastrophus kincaidii* Gill. the ovaries of freshly eclosed females contain 211± 21 eggs (Jones 1983). The adult female is 2.0 - 2.5 mm and the egg size averaged 0.65 mm (Wangberg 1975). For its size, *Neuroterus saltatorius* appears to have relatively high fecundity.

On Vancouver Island, most agamic females overwinter as adults, rarely as larvae and the long developmental time of the agamic generation may be due to a period of arrested growth known as temperature-ruled parapause (Braune 1979). Low-temperatures during development were important for maturation and the prevention of adult emergence in *Neuroterus quercus-baccarum* (L.) and *N. numismalis* (Fourc.) (Braune 1979). Perhaps, pupae appearing later in the season in southern areas of California (Rosenthal and Koehler

1971a) and the delay in the drop of the agamic galls is the result of higher ambient temperatures through late summer and early fall.

Host-parasitoid community

Oviposition behaviour of parasitoids (Hymenoptera: Chalcidoidea) attacking cynipids is governed mainly by gall position, the time of year that the gall is found on the tree and the form of the gall (Askew 1961a; Shorthouse 1975). Also, biologically analogous host species will often share parasitoid species (Hails and Crawley 1991). The alternating generations of *Neuroterus saltatorius* function as two species since they are present at different times throughout the summer and differ in form and size. The gamic generation is present on the foliage earlier in the year and for a much shorter period of time. The galls of the first generation are somewhat flattened and ellipsoidal and agamic galls are circular. Lastly, the density of gamic galls on leaves is lower than agamic galls, therefore harder to find. The features of these two generations translate into differences in species composition of the parasitoid complex.

The shorter generation time of the gamic generation, coupled with fewer galls in the foliage suggests that the parasitoids of this generation may have greater searching abilities and generally may be more polyphagous than those of the agamic generation. Parasitoids reared from galls of the gamic generation provide some support for this hypothesis. The dominant species to emerge from gamic rearings was *Mesopolobus* sp. nr. *longicaudae* ; members of this genus parasitise a wide range of galls in the United Kingdom (Askew 1961b; Narendran 1985). *Mesopolobus* spp. larvae feed on the larvae, pupae and even the adults of gall makers. In the field, *M. fasciiventris* Westwood and *M. jucundas* (Walker) were observed to make wide searches of the foliage for galls and were even found searching trees on which no galls could be found (Askew 1961b).

Parasitoids attacking the agamic generation of *Neuroterus saltatorius* will likely have several alternate hosts to choose between. On Vancouver Island, several cynipids are present on the foliage at the same time and their position on the tree is similar that is, leaf gall formers (e.g. *N. saltatorius*, *N. washingtonensis* and *Besbicus mirabilis*). Since agamic larval development is slow, parasitoids will have an abundance of hosts to choose from. One of the dominant parasitoids of the agamic generation of *N. saltatorius*, *Aprostocetus pattersonae*, was reared from *N. washingtonensis, Bassettia ligni* and *Besbicus mirabilis* (Evans 1972). Evans (1985) considered *Aprostocetus pattersonae* the most common parasitoid of gall wasps and this species may have switched from other hosts to parasitise the *N. saltatorius* when it colonises a new area.

The second most prominent chalcidoid in the rearings, *Amphidocius schickae*, has no known alternate hosts on Vancouver Island. It appears from the parasitoid-exclusion sleeves that this might be the most host specific species. Askew and Shaw (1986) observed that "it is easy to investigate the parasitoids of a particular host but quite another matter to discover all the hosts of a particular parasitoid". An explanation for its absence in the rearings of other cynipids on *Quercus garryana* is that *Amphidocius schickae* was introduced with the jumping gall wasp and appropriate alternative hosts have not been established, or are not available.

Aprostocetus verrucarii, found in both generations of *Neuroterus saltatorius*, is a documented parasitoid of *Neuroterus* spp. (Balduf 1929). In Illinois, larvae were found overwintering in the galls of *N. verrucarum* and the adults emerged during May -July and a second generation developed on an alternate host, *N. niger* Kinsey. Parasitism from *Aprostocetus verrucarii* was high in Balduf's study (1929) and most adults of the second generation emerged later in the season. This parasitoid species does not contribute much to the overall level of parasitism of *N. saltatorius* on Vancouver Island because it may not have a strong host preference. *Aprostocetus verrucarii* may switch from other hosts, parasitising *N. saltatorius* later in the season, becoming become more generalised as the season progresses (Washburn and Cornell 1979).

Most descriptions of taxa associated with cynipid communities list a cynipid inquiline species (e.g. Evans 1972). In some cases, the inquiline was the only cynipid to emerge and was mistakenly identified as the gall maker (Krombein *et al.* 1979). On Vancouver Island, *Synergus pacificus* McCracken & Egbert was found in agamic galls of *Besbicus mirabilis* and both generations of *Neuroterus washingtonensis* (Evans 1967, 1972), *S. garryana* Gillette has been reared from other cynipids in B.C and *Synergus* sp. was reared from *N. saltatorius* in California (Heydon pers. comm.). No cynipid inquilines were noted in this study, perhaps a result of interspecific competition from chalcidoid parasitoids.

Many of the species in the parasitoid complex were found in low numbers but have been documented as parasites on gall formers. The family Ormyridae is represented by three species in Canada (Yoshimoto 1984) and is associated with cynipid galls on oak (Grissell and Schauff 1990). *Ormyrus distinctus* was a relatively uncommon parasitoid of the agamic generation of *Neuroterus saltatorius* during this study and another species, *Ormyrus* sp. nr. *brunneipes* Provancher, has been found in dissections from *Bassettia ligni* and *N. washingtonensis* (Evans 1972). I speculate that *Ormyrus distinctus* is an oligophagous species that is not particularly common on Vancouver Island and therefore, does not make a large contribution to cynipid host mortality.

In addition to species composition similarities, parasitoid - host relationships remain remarkably constant over wide geographical areas (Askew and Shaw 1986). Parasitoid species of the agamic generation of *Neuroterus saltatorius* have been found in galls collected from Vancouver Island, Oregon and southern California. Some species that occurred infrequently in rearings in B.C. (e.g. *Ormyrus distinctus*) are not known to occur in California and others have been found in low numbers in both locations (e.g. *Brasema* spp.) (Heydon pers. comm.). Heydon and Boucek (1992) observed that nearly every gall in California on *Quercus lobata* and *Q. douglasii* was parasitised and *Amphidocius schickae* was one of the most common parasitoids reared.

One of the anticipated results from parasitoid exclusion sleeves was clarifying the number of generations and phenologies for parasitoids attacking *Neuroterus saltatorius* . The analysis of adult emergence trends illustrated several peaks but they were not a clear indicator of generation times since one species dominated the rearings, *Amphidocius schickae*. This pteromalid was reared from galls of both generations collected on the foliage and agamic galls collected in the soil and has no known alternate hosts in B.C., possibly indicating a strong host preference for *N. saltatorius*. Duncan (pers. comm.) found that in dissections of mass collections of dropped galls from three sites in California, August 1994, < 3% of the galls were parasitised and *Amphidocius schickae* dominated the complex.

There are some difficulties associated with collecting galls for rearings or excluding parasitoids with sleeves. Evans (1972) found that it was almost impossible to exclude unwanted cynipids while using micro-mesh screening cages and concluded that *Quercus garryana* had cynipids present during most of the year. To illustrate this problem in this study, two parasitoid species, *Dibrachys cavus* and *Gastrancistrus* sp., were found only as a result of the sleeve experiment. *Dibrachys cavus* has 200 recorded hosts, including chalcidoid and (occasionally) cynipid hosts and the genus contains primary, secondary and tertiary parasitoids (Grissell and Schauf 1990). It may have emerged from *Lambdina* spp. and *Forficula auricularia,* two hosts present on *Quercus garryana* during this study or it may be a hyperparasite of chalcidoids attacking *Neuroterus saltatorius*. The relationship of *Gastrancistrus* sp. to *N. saltatorius* is unclear because it is recorded as parasitising willow gall formers (Diptera: Cecidomyiidae) and in this study it only emerged from sleeves (Krombein *et al.* 1979). As a result, only parasitoid species reared from gall material known to be free of contaminants were included in the list of parasitoid taxa attacking *N. saltatorius*.

Frequent, within generation sampling is necessary to establish a list of parasitoids that attack multivoltine hosts in temperate regions. Also, studies from a single site can be misleading (Askew and Shaw 1986). A study of the white admiral butterfly, *Ladoga camilla* (L.) in Britain found that the host was practically unparasitised at the edge of its expanding range (Pollard 1979). The low levels of parasitism at the Tatlow site would reflect a similar trend in *Neuroterus saltatorius*. It would have been interesting to rear galls from Duncan, Nanaimo of Saltspring Island to examine the parasitoid complex at edge of expanding range of the jumping gall wasp.

Askew and Shaw (1986) suggest that "arboreal hosts may support a richer parasitoid fauna in ancient and undisturbed habitats than altered ones". The richness of the parasitoid fauna was greatest at Blenkinsop and Mt. Douglas sites but these two sites reflect different disturbance levels. Blenkinsop is a heavily disturbed site, effectively an "oak island" surrounded by agricultural land but the Mt. Douglas site was just outside a park containing many native coniferous and deciduous trees. Certainly the Mt. Douglas area has been fragmented by urbanisation and none of the sites in this study could be considered undisturbed.

Factors affecting survivorship

Chalcidoid parasitoids are able to cause a considerable amount of host mortality and if each gall type was attacked by the same parasitoid species in the same proportion, then cynipids should compete to avoid parasitoid attack. This competition is reduced because each gall is specific to the species that induces the gall which permits the coexistence of a large number of similar species on the same host plant (Askew 1985). Additionally, the formation of different galls for each generation may reduce parasitoid competition for host larvae because each generation attracts a different complement of parasitoids (Askew 1961a); there was some overlap of parasitoid species attacking *N. saltatorius* in this study.

Askew (1985) was very interested in the diversity of oak gall communities and suggested that gall communities have evolved over a long period of time because diversity is found at the species, genus and family level. Initially, a parasitoid community might consist of a few polyphagous species which, after a lengthy association with the host, may become host specific. However, due to their (at least initial) wide host preference, polyphagous insects are continually being added to the communities and replacing some of those that were previously established.

Competition for gall sites also exists within the cynipid community. The presence of large numbers of *Neuroterus saltatorius* on *Quercus garryana* has likely increased interspecific competition among cynipids for oviposition sites on the foliage. *Besbicus mirabilis*, once a relatively common cynipid on southern Vancouver Island, has become increasingly difficult to find as *N. saltatorius* populations expand (Ring pers. comm.); other oak cynipids may have experienced a similar decline.

Outbreaks of the winter moth, *Operophtera brumata* and a leaf roller, *Pandemis cerasana* fluctuated between 1992-93 and individual trees were often more affected than entire stands (Bennett 1995). In 1992 at several sites (e.g. Mt. Douglas) had trees with more than two -thirds of the canopy defoliated and galls were few in number. Defoliation removes cynipid galls from the foliage and may also serve to increase interspecific competition within the phytophagous community due to a reduction in herbivory sites.

Askew and Shaw (1986) found that within a leaf mining community there were often greater levels of parasitism in late summer host generations. Similarly, in oak gall communities parasitism differs qualitatively according to the time of year and greater levels of parasitism are usually associated with late summer host generations (Askew 1961; Askew and Shaw 1986; Washburn and Cornell 1979). Parasitism levels of *Neuroterus* *saltatorius* were greatest in August, a qualitative difference or a greater number of galls available later in the summer.

Galls that develop rapidly are usually able to avoid parasitism by maturing before parasitoids are active (Askew 1985). Chalcidoid species infested young galls of *Acraspis hirta* Bass. (Washburn and Cornell 1979). Low levels of parasitism prior to gall drop in *Neuroterus saltatorius* may indicate that parasitoids were not active early in the agamic generation and galls fell before peak parasitoid activity. If galls fall to the ground, they might not be at risk from parasitoid attack because chalcidoids do not seem to search on the ground (Askew 1985); the occupation of cryptic subterranean habitat may reduce parasitoid discoverability and mortality (Askew and Shaw 1986). However, it is possible that *Amphidocius schickae* is a ground searching parasitoid because adults were found to emerge from overwintering galls collected 1993-94. Most *Quercus garryana* sites were characterised by rocky outcrops such that the galls are not well disguised when they fall.

Parasitic Hymenoptera have certainly been recognised as prominent natural control agents of oak gall formers. For example, larval survival of the cynipid wasp *Besbicus mirabilis* was limited by the presence of parasitoids; most of the larvae were destroyed by parasitoids or inquilines (Evans 1967). Other documented sources of mortality, unidentified miscellaneous causes and bird predation, accounted for approximately 15 percent of the mortality in a *Besbicus mirabilis* population on Vancouver Island (Evans 1967). No diseases were found but secondary fungal infections have been documented in other cynipid galls. *Acraspis* sp. galls on *Quercus prinus* L. were infected with fungus (3%) which was responsible for both parasitoid and host mortality (Washburn and Cornell 1979).

Failed development was common at all sites, most notable at Mill Hill. Larval failure (including desiccation) and empty galls may be the result of indirect parasitism (i.e. parasitoid activities that do not always involve oviposition). Sources of indirect parasitism include host-feeding by female parasitoids for the production (Gauld and Bolton 1988) and maturation (Doutt 1959) of eggs, oviposition trauma and the rejection of a gall and its occupant after penetration. Some individuals may follow host feeding with oviposition (Askew 1971) and therefore would not be considered indirect parasitism in this study.

Host mortality from indirect parasitism results from the piercing of the host to obtain a fluid meal or lay an egg. Injury to the host may leave it susceptible to infection and consequently, neighboring galls are affected by the resulting secondary fungal pathogens. Host feeding was not observed in the field but it has been observed in several families of parasitoids represented in this study, Pteromalidae, Eupelmidae and Eulophidae. The contribution of indirect parasitism to "other sources of mortality" is unknown and it is likely that the level of parasitism has been underestimated because of the inherent difficulty in measuring these values.

Another indirect source of mortality is venom injected into the host. Occasionally, venom may kill the host but the paralytic effect could expose the host to attack from a wide range of natural enemies, including other parasitoids, predators and scavengers. Parasitoids will usually consume the host before it can be attacked by scavengers or micro-organisms such as bacteria and fungi (Gauld and Bolton 1988) but if the parasitoid fails to develop, the source of mortality may not be obvious in the galls examined.

The presence of phenolic compounds in leaves (phenols and tannins) has been shown to inhibit the feeding behaviour of phytophagous insects (Feeny 1968; Parker 1977). In the pedunculate oak, *Quercus robur*, condensed tannins first appear in the leaves in May; condensed tannins are more harmful than hydrolysable tannins found earlier in the season (Feeny 1968). The source of larval failure could not be readily detected in this study because many of the immature galls were infected by fungus. Defoliation can also change the chemical composition of leaves. Repeatedly defoliated red oaks, *Q. rubra* Linn. were found to have higher levels of tannins and phenols than did leaves of undamaged trees (Schultz and Baldwin 1982).

Galls are thought to act as tannin sinks. Taper *et al.* (1986) suggested that tannins might serve a protective function for cynipids against fungal mortality because a positive correlation existed between cynipid densities and leaf tannin levels; leaf tannin levels were higher in areas of greater gall densities. Tannin levels of *Quercus garryana* were not measured in this study but many galls were found to contain fungi, even when present at high densities. The fungus that infested *Neuroterus saltatorius* , *Discula umbrinella* is characterised as a secondary fungal pathogen (B. Callan pers. comm.), attacking hosts that are dead or unhealthy. One possible explanation for high levels of fungal infection was damp, cool weather in 1993 which might have masked any protective function that tannins had.

Theoretically, if jumping gall wasp populations decline, chlorotic spotting should also decrease. However, in 1993, scorching levels remained the same as the year prior yet it was more difficult to obtain suitable sample sizes for rearings. The observed pattern was at least partly due to scorching from fungal infections. Fungal pathogens invaded both healthy and dead galls and the spread of disease to healthy tissue caused elevated levels of leaf necrosis. The decline in suitable galls could be attributed partly to the spread of infection over the leaf, preventing the maturity of agamic galls on the foliage.

Parasitoid fauna are also affected by fungal infections and numerous parasitoid larvae were found surrounded by fungal hyphae. The cause of mortality was categorised as "parasitised larvae" because the initial cause of host mortality was the result of direct parasitism. This interpretation of mortality does not account for the value associated with unsuccessful emergence of an adult parasitoid with respect to parasitoid population levels.

Lastly, the physical characteristics of a leaf might affect cynipid oviposition success and contribute to failed development. Newer leaves are more amenable to successful maturation due to a higher water content, softer texture and more available nitrogen (Feeny 1970). The hardening of the leaf tissue may prevent successful maturation of the agamic generation larvae.

The incidence of fragmentation may prevent natural enemies from spreading rapidly throughout an infested area (Frankie and Ehler 1978). The fragmented *Quercus garryana* habitat on Vancouver Island may have prevented parasitoids from reaching *Neuroterus saltatorius* populations quickly thus contributing to rapid population increases when *N. saltatorius* colonised a new area. This explanation supposes that parasitoid species are coming from other hosts that may or may not be nearby consequently, parasitoid caused mortality will be greatest at those sites that are the least fragmented or isolated. In this study, all sites were disturbed but discontinuous *Quercus garryana* stands (urban or "island" environments) suffered higher infestation levels than sites with continuous vegetation. For example, parasitism was greatest at sites surrounded by forested areas (Mill Hill, Beaver Lake and Tatlow) and lowest in heavily disturbed areas (Santa Anita). An exception was Mt. Douglas (a forested site) that suffered high levels of lepidopteran defoliation and therefore, had low parasitism levels during 1992.

The relationship between infestation levels and mortality factors can be evaluated with respect to the mechanics of host and parasitoid dispersal. On Vancouver Island, the prevailing southwest winds would aid the dispersal of *Neuroterus saltatorius* to the northeast as seen in the movement of *N. saltatorius* from the original infestation area west of Victoria to *Quercus garryana* stands to the northeast. Time is probably the greatest factor in the colonisation rate for a weak disperser. For example, an oak leaf phylloxeran, *Phylloxera* sp., was introduced to Vancouver Island from Europe in the early 1960's (Duncan pers. comm.) and over time it has gradually populated most stands of *Quercus garryana* and *Q. robur* on Vancouver Island and the adjacent Gulf Islands.

Human activities also influence the dispersal of *Neuroterus saltatorius*. The first record of *N. saltatorius* on a Gulf Island was in 1994 on Saltspring Island (Duncan pers. comm.). Saltspring is one of several Gulf Islands serviced by vehicle ferries and the *Quercus garryana* hosting *N. saltatorius* populations were adjacent to a ferry dock. Certainly, the northward spread of *N. saltatorius* to Duncan and Nanaimo was aided by individuals accidentally transporting galls, probably agamic generation galls that fell into pick-up trucks. Therefore, it will just be a matter of time before *N. saltatorius* is found on most of the Gulf Islands, especially those that are accessible by vehicle.

In conclusion, I predict that jumping gall wasp populations on Vancouver Island will gradually decline and stabilise at endemic, non-damaging levels. Populations in newly colonised areas will likely experience low levels of parasitism and high survivorship initially, resulting in explosive population increases. Following the initial epidemic, populations will decline as a result of increasing mortality due to parasitism, predation, entomopathogens and host resistance. Foliage scorching will always be present to a minor extent due to the effects of climatically induced infections of foliar fungal pathogens. Eventually, our oaks should resemble the populations south of Vancouver Island with only an occasional tree suffering visible mid-summer scorching.

Summary

1. Several life history characteristics separated the gamic and agamic generations of *Neuroterus saltatorius*. Gamic females were larger, had a greater number of eggs and emerged over a shorter period of time than agamic females.
2. Agamic larvae began to drop in the middle of June and peak gall drop occurred at the end of June - beginning of July.
3. In the agamic generation, fewer galls fell and survivorship was lowest at the oldest infestation site (i.e. Mill Hill).
4. In the gamic generation, *Mesopolobus* sp. nr. *longicaudae* was the most abundant parasitoid to emerge and *Aprostocetus pattersonae* and *Amphidocius schickae* were the most abundant parasitoids in the agamic generation.
5. The parasitoid complex of *N. saltatorius* has a high degree of overlap with other cynipid species in B.C. and is consistent with those found on *Quercus garryana* and *Q. lobata* in the United States.
6. *Amphidocius schickae* may be the most host-specific species in the parasitoid complex; other parasitoid species have several recorded alternate hosts.
7. Peak parasitoid activity on the foliage occurs after most *N. saltatorius* larvae have fallen from the tree. I concluded that parasitoid activity was not synchronous with *N. saltatorius* development.
8. At all sites, failed development and entomopathogens (not chalcidoid parasitism) were the primary causes of host mortality on the foliage after the peak gall drop.
9. Rearings were not a useful indicator of mortality because they relied on the successful emergence of adult parasitoids and host larvae may suffer from re-parasitism if the parasitoids are not removed promptly after emergence.

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APPENDIX I. Property owners and street addresses for the eight sites used 1992-94 to survey for the jumping gall wasp, *Neuroterus saltatorius* (Edwards).

Site No.	Site	Property owner and street address
1	Mill Hill	Vagelsang, 2642 Selwyn Rd.
2	Santa Anita	Stack, 4119 Santa Anita Rd.
3	Mt. Douglas	Mt. Douglas X Rd.
4	Oak Bay	Mitchell, 2171Granite St.
5	Blenkinsop	Galey Brothers Farms, Lohbrunner Rd.
6	Beaver Lake	Yanuzzi, 621 Beaver Lake Rd.
7	Mt. Newton	Kitridge, Mt. Newton x Rd.
8	Tatlow	Cummings, Tatlow Rd.

APPENDIX II. Survey and collection locations in Washington, Oregon and California for *Neuroterus saltatorius* (Edwards) agamic galls, June - July 1993.

Date	No.	Location	Collection	Other cynipids
June 28	1	Memorial Park, Sequim, WA	-	*N. washingtonensis* *Disholcapsis eldoradensis*
June 29	2	Willamette University, Salem, OR	Y	
	3	Rickreall, Or	Y	
June 30	4	Walnut Park, Corvalis, OR	Y	*Andricus californicus*
	5	Peavy Arboretum, Corvalis, OR	Y	*Besbicus mirabilis*
	6	n. Eugene on I5, OR	Y	
	7	s. Eugene on I5, OR	Y	
July 1	8	Roseburg, OR	*	
	9	Azalea, OR	Y	
	10	Sexton Pass, OR	Y	*B. mirabilis*
	11	Oregon -California border	-	
July 2	12	Whiskeytown Lake, CA	**	
	13, 14	Oak Bottom, CA	-	
	15	Bella Vista, CA	**	
	16	Dumois, CA	-	
	17	Grenada, CA	-	
July 3	18	Phoenix, OR	*	
	19	Oregon City, OR	Y	*Besbicus mirabilis* *A. californicus*
	20	Kalama, OR	-	*Besbicus mirabilis*

Legend:

Y	agamic galls collected and brought back for rearing
-	no galls found
*	agamic galls found in low numbers; no collection
**	agamic galls found; no collection permit

APPENDIX III: Description of ectoparasitoids (Hymenoptera: Chalcidoidea) recovered from bisexual and agamic generation galls of *N. saltatorius*.

Family ORMYRIDAE

Ormyrus distinctus Fullaway

Biology / habit: Genus currently under revision. Family associated with cynipid galls on oaks. *Ormyrus* sp. may act as primary or secondary parasitoids. Ormyridae is represented by three species in Canada and one genus (Yoshimoto 1984). Two individuals were reared from the agamic generation in 1993.

Male: 9 funicular; 5 tarsi; post-marginal and stigmal veins; blue-green metallic; setae on mesoscutum; setae on gaster; brown antennae; small antennal segments; brown legs; hind tibial spur; 1.2-1.5mm.

Family EUPELMIDAE

Brasema sp.

Biology / habit: Variable hosts. Several species attack gall formers and may be primary or facultatively secondary parasites. Found in mass and sleeve cage rearings of agamic galls.*Brasema* sp.

[35] [36] Female: 8 funicular; 5 tarsi; faint post-marginal, stigmal veins; few setae at speculum; metallic green; setae on mesoscutum; green-yellow femur; brown tibia; yellow legs; brown antennae; 2 rows setae on tarsi of mid leg; 1.4-1.6mm.

Male: 8 funicular; all same as above [35] except 2 rows setae absent on mid tarsal segments; 1.0-1.2mm.

[34] Male: 7 funicular; 5 tarsi; post-marginal, stigmal veins and uncus present; metallic green; brown abdomen; setae on mesoscutum; setae on wings numerous; brown antennae; brown legs; < 1.0 mm.

Family PTEROMALIDAE

Amphidocius schickae (Heydon and Boucek)

Biology / habit: Newly described species (Heydon and Boucek 1992). The exact host relationship to *N. saltatorius* in the USA is unknown. However, it is thought to be one of the most abundant parasitoid species that emerge. Considered to be closely associated with the agamic generation in B.C. as no alternate hosts have been identified. May be a primary and hyperparasitoid. Reared from bisexual and agamic generations, as well as soil-collected galls. Females were observed ovipositing on mature galls, usually > 1mm in size. Females used their antennae to detect the *N. saltatorius* larvae in the gall and (presumably) determine whether an oviposition attempt should be made. This species does not appear to be attracted to light sources since they were rarely found at the top of the funnels or rearing containers. *A. schickae* was one of the first species observed in the field on the foliage. In 1992, males and females were both observed in May. In 1993, males were found first and females were not observed until mid -June. *A. schickae* was most numerous in rearings at sites that were infested between 1988 and 1990.

Female: 5 funicular; 5 tarsi; no post-marginal vein; stigmal vein; may have wash present on forewing below stigmal vein; dark metallic green; setae on mesoscutum; yellow/amber antennae; black legs; > 1mm usually

Male: 5 funicular; 5 tarsi; wash on forewing; yellow band on brown abdomen, amber legs

Amphidocius n. sp.

Biology / habit: Emerged from bisexual rearings and agamic galls that were collected and screened from the soil.

Female: 6 funicular; 3 club segments; 5 tarsi; post-marginal, stigma vein and uncus; slight wash on wings sometimes; dark metallic head and thorax; yellow legs; > 1.2 mm

Mesopolobus sp. nr. *longicaudae* Doganlar

Biology / habit: Species of the genus *Mesopolobus* make up a large fraction of the chalcid species that inhabit cynipid oak galls. *Mesopolobus* spp. are polyphagous and attack a wide range of gall formers, acting as either primary or hyperparasitoids (Askew 1961b). In Britain, field captures of *M. fasciiventris* and *M. jucundus* revealed at least three generations per year with perhaps a partial fourth (Askew 1961b). Identification to species depends on characters found only in other sex. Found in mass rearings of bisexual and agamic galls.

Male: 8 funicular; 5 tarsi; weak sub-marginal vein; weak/absent post-marginal and stigmal vein; band around brown abdomen; yellow funicular segments, club segments black; leg segments yellow.

Dibrachys cavus Walker

Biology / habit: Long list of chalcid hosts and occasionally parasitoids of cynipids. Found in sleeve cage rearing of agamic galls.

Male: 5 funicular; 5 tarsi; metallic blue; amber antennae; amber legs. (specimen lacks wings).

Gastrancistrus sp.

Biology / habit: Known hosts are Cecidomyiidae. Genus needs revision and species characters are not worked out. Found in sleeve cage rearings of agamic galls.

Male: 7 funicular; 5 tarsi; post-marginal, uncus and stigma veins; numerous setae on wings; metallic green; setae on mesoscutum; brown antennae; brown and amber legs; 1.2mm.

Family Eulophidae

Aprostocetus pattersonae (Fullaway)

Biology / habit: =*Tetrastichus spilopterus* Fullaway or *Aprostocetus spilopterus* (Burks). Parasitoids of cynipid galls on oak (LaSalle, pers. comm.). Found in rearings of agamic galls of *N. saltatorius*. During courtship, males approach females from behind and quickly mount them. Males grasp the head of the female with their antennae and proceed to rock her head from side-to-side. Females remove males by flapping their wings and "shaking" them off. On occasion, several males would attempt to mate with more than one female.

Female: 3 funicular; 4 tarsi; post-marginal and stigmal veins; no setae basal to speculum; occasional spot on wing; metallic green -blue; setae uniformly scattered over entire mesoscutum; yellow tibia, tarsi and coxa; brown femur; red eyes.

Male: 4 funicular; dark spot on forewing; funicle segments without whorls

Aprostocetus verrucarii (Balduf)

Biology / habit: = *Tetrastichus verrucarii* Balduf. Northern New World. Parasitoids of cynipid galls on oak. Found in rearings of bisexual and agamic galls.

Female: 3 funicular; 4 tarsi; post-marginal vein small/absent; numerous setae basal to speculum creating wash; dark with some metallic shine; setae uniformly scattered over entire mesoscutum; antennae with short setae; white tarsi; all leg segments brown ; < 1.5 mm some specimens > 2mm.

Aprostocetus sp.

Biology / habit: Genus under revision by LaSalle, International Institute of Entomology, London. Identification to species requires characters found in the other sex. All parasitoids of cynipid galls on oaks. Found in rearings of agamic galls.

Female: 3 funicular; 4 tarsi; post- marginal vein absent; stigmal cell; no/little setae at speculum; brown and green, slightly metallic body; setae confined to a single row just median to notaulus; distal 3 tarsi darker.

Male: 4 funicular; forewing without a dark spot; antennae with dorsal whorls

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July 14, 1995