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**THE POTENTIAL ABILITY OF *Stethorus bifidus* (Kapur) TO
REGULATE POPULATIONS OF *Tetranychus*
lutearius (Dufour)**

A Thesis presented in partial fulfilment
of the requirements for the degree of
Master of Science in Ecology
at Massey University.

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1993

PLATE 1: Gorse as a problem in forestry

KOPURIKI NEAR TE PUKE



Silviculture practices are restricted or prevented by gorse.

ABSTRACT

Tetranychus lintearius Dufour (Acar; Tetranychidae) was released in New Zealand, in 1989, to assist in the regulation of gorse (*Ulex europaeus*). The present study was initiated to determine why colonies of GSM are consistently failing to establish above parallel 39°S and the possibility that *Stethorus bifidus* may be regulating populations of *T.lintearius* (GSM).

Predation by *S.bifidus* was investigated by examining both numerical and functional responses to prey density.

- Development of *S.bifidus* is described by a linear relationship with temperature between 8.5°C and 27.5°C (numerical response). Oviposition and temperature are linearly related and independent of GSM density. Measurements of temperature under GSM webbing showed an elevation of 1-2°C above ambient.
- The feeding rate of *S.bifidus* increased in a non-linear fashion between 6.5°C and 32.5°C (functional response).
- Handling time decreased with increasing prey density demonstrating that *S.bifidus* is an effective predator at high mite densities.

This investigation suggests that the role of *S.bifidus* in regulating GSM is more important in northern regions of New Zealand.

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CHAPTER ONE: INTRODUCTION

Part one: Regulation of gorse in New Zealand - The plant, the biocontrol agents, the policies/procedures and the complications.

Gorse - The options for regulation of a noxious plant:

Gorse (*Ulex europaeus* L.) is a fast growing woody legume capable of establishing rapidly from seeds or stumps. It thrives particularly in low fertility soils where the competitive ability of other 'more favoured' plants is reduced. Although gorse is found throughout Europe, it is only considered a major weed of agriculture and forestry in North America, South Australia, Tasmania, New Zealand and at high altitudes in Hawaii. A warm, moist climate free of temperature extremes and exposure to cold winds appears to suit gorse. Control is difficult and expensive. In 1977, chemical control of gorse in New Zealand cost approximately \$7 million and this did not include the cost of lost production (MacCarter & Gaynor 1980). According to Miller (1970; cited in Hill & Gourlay 1990), gorse plants can be found on over 3.5% of the land area of New Zealand, however long-lived seed is buried in the soil over a larger area.

The first attempts to control gorse biologically began in the 1920's when the only agent introduced was the seed-feeding weevil, *Apion ulicis* Forst. Because of the importance of gorse as a hedging material damaging plant foliage was not desirable. *A. ulicis* did not control the spread of gorse, but it did establish successfully (MacCarter & Gaynor 1980). MacCarter (loc cit.) considered that the good establishment of *A. ulicis* argued well for introductions of further biocontrol control agents for gorse. Consequently, DSIR's Entomology Division began to investigate several agents for biological control of gorse, including the stem boring weevil *Apion scutellare* Kirby and a leaf feeding moth, *Agonopterix ulicetella* Stnt. (MacCarter loc cit.). This research recognized that even if many introductions of biocontrol agents were to be made, eradication of gorse would be unlikely, instead, the probable effect would be to reduce its vigour to a situation where gorse is merely part of the natural succession, and no longer a serious weed (MacCarter loc cit.).

In 1984 the value of lost production on gorse infested lands exceeded \$150 million per annum (Monsanto 1984). Current gorse regulation practices are largely ineffective because of the extreme vigour and competitive ability of the weed. According to Monsanto (*loc cit.*) the herbicide applied to gorse infested land each year is enough to kill 25% of the gorse in New Zealand, yet the problem remains as severe as it was 30 years ago.

A report by Monsanto in 1984 clearly identified gorse as a major weed. Hackwell (1980) however, pointed out that gorse also has beneficial effects, including a role as a soil improving species and as a nurse plant for regenerating native forest.

Sandry's (1985) economic analysis considered both detrimental and beneficial effects, and concluded that current benefits of gorse were unimportant apart from beekeeping. Sandry also suggested that control of gorse may undermine the unrealized potential of goat farming. A subsequent review by Longworth (1986) also concluded that the benefits of biological control of gorse outweighed the costs.

Hill (1986) summarized opinions expressed in 49 submissions on a proposal for biological control of gorse. Thirty submissions supported the proposal to use biological control agents to control gorse, nine opposed the proposal and ten did not express a strong opinion. Responses from the various organisations contacted allowed a balanced assessment of some non-economic questions which were beyond the scope of Sandry's (1985) report. Strongest opposition to the proposal came from those concerned about the possible impact of successful control on regeneration of native forests in New Zealand. Hill (*loc cit.*) considered that biological control of gorse, even at its most effective level, would probably have no adverse effect on the rate of succession of native forest species. He pointed out that effective biological control might be beneficial in other respects for native plant communities. Other major concerns expressed included those to do with the use of gorse as fodder and the fear of increased erosion. Hill (*loc cit.*) concluded that both concerns were unlikely to eventuate in practice.

Clearly public debate was necessary to uncover all arguments for and against biological control of gorse. This debate was summarised and analyzed in a

subsequent cost-benefit analysis (Hill & Sandry 1986). Key points of this report include, firstly that it is not possible to predict the amount of damage that biological control agents could do to gorse in New Zealand; and secondly that beekeepers were the major group which could suffer economically, but only if gorse vigour was reduced by more than 50%.

These reports by Sandry (1985), Hill (1986), and Hill & Sandry (1986), together conclude from an overall perspective that a biological control programme against gorse in New Zealand is desirable.

Ninety four species of invertebrates attack gorse in Europe; of these only 16 appear sufficiently host specific to show promise for introduction into New Zealand as biological control agents (Hill 1983). Five of these attack reproductive structures and 11 feed on green shoots. There are no suitable agents which attack roots, crowns or woody stems. The four species with the greatest potential to damage gorse are *Tetranychus lintearius* Dufour (Acari; Tetranychidae), *Agonopterix ulicetella* Stat. (Lepidoptera; Oecophoridae), *Dictyonota strichnocera* Fieber (Lepidoptera; Tingidae) and *Aplon scutellare* Kirby (Coleoptera; Curculionidae) (Hill loc cit.). Of these *T.lintearius* the gorse spider mite (GSM), can severely damage gorse in Europe, and offers the only prospect of causing lethal damage to gorse by itself. This species was the first to be selected for introduction during the 1980s, **see plate 2**. Subsequent introductions of other species aim to increase the biotic pressures on gorse. The net effect should be to reduce gorse vigour, improve the susceptibility of gorse to existing control measures, and reduce the extent of regrowth. Some agents may further reduce gorse seed production throughout the year (Hill 1983).

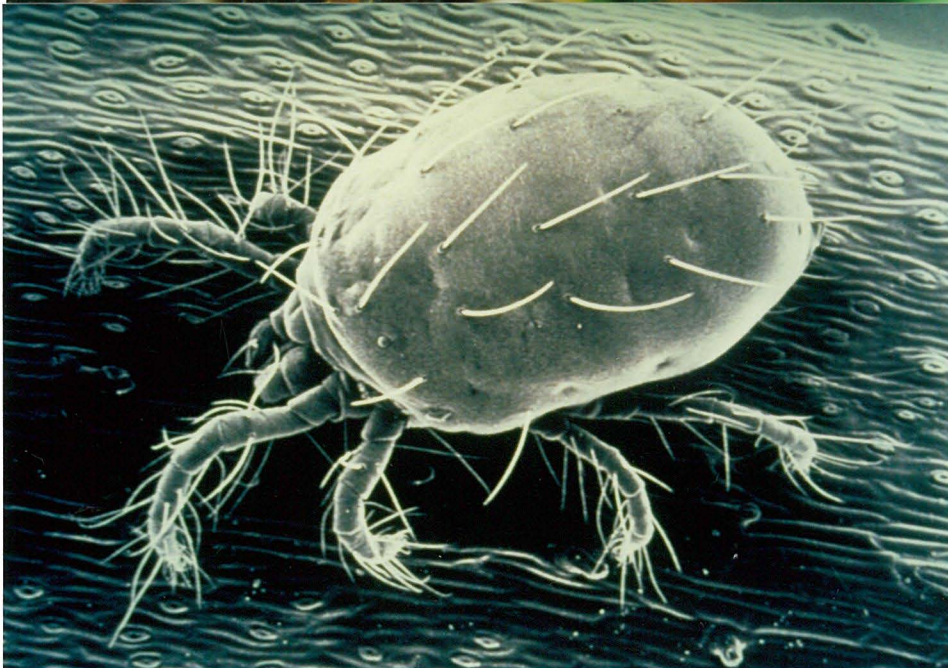
Hill (1987) prepared an Environmental Impact Assessment (EIA) which considered the potential for biological control of gorse, the suitability of GSM as a control agent for gorse, and the possible impact of biological control of gorse to the environment and primary production in NZ. This EIA ties together Sandry's (1985) ex-ante evaluation of biological control of gorse, Hill's (1986) implications for the natural environment report, media response, goat farming considerations by Sandry (1987) & farming organisations in general including the beekeepers association submissions. It also includes draft papers describing the host range of GSM and the inability of GSM to

PLATE 2: *Tetranychus lintearius* - the biocontrol agent

a- *T.lintearius* the gorse spider mite (a colonial tetranychid mite)
(Magnification X 1)

b- *T.lintearius* feeding on a gorse (*Ulex europaeus*) spine
(Magnification X 25)

c- Electronmicrograph of *T.lintearius* Photo: Lynley Hayes
(Magnification X 150)



breed with other species. These draft papers, which were eventually published elsewhere (Hill & O'Donnell 1988), showed that *T.lintearius* is a distinct species incapable of crossing with either *T.urticae* or *T.turkestanii* and that it is entirely host specific to *Ulex* species. *T.lintearius* does not feed and reproduce on native legumes.

T.lintearius was finally introduced into New Zealand from Porthowan, Cornwall, England in 1988 (Hill et al. 1989). The first four shipments of mites arrived at Christchurch on 22 July. The mites were reared in strict quarantine at DSIR, Lincoln, for two generations. *T.lintearius* was first released near Christchurch on 22nd February, 1989. Mites successfully transferred from shoots onto gorse plants (30 April, 1989) (Hill loc cit.).

By 1990 *T.lintearius* had been released at over 100 sites (Hill 1990). It overwintered successfully and is regarded as established. Its effect on gorse is currently being evaluated in Otago, Canterbury and Southern Hawkes Bay (P.McGregor & R.Hill pers comm.). Hill et al. (1991) recorded the establishment success of *T.lintearius* at over 170 sites. The mite established poorly above latitude 39 degrees south where only 22% of colonies released became successfully established on gorse. Conversely 87% of colonies successfully established below this latitude (poor establishment success on the west coast of the South Island was also noted). This pattern of establishment demonstrates the difficulty in predicting the outcome of an introduction for biological control, even when great effort is directed at forecasting the result. Analysing the outcome of an introduction therefore depends on post hoc. research. My research contributes to this analysis by examining the potential effects of predation by an endemic insect *Stethorus bifidus* (Kapur) (Coleoptera; Coccinellidae) on *Tetranychus lintearius* populations. The importance of predation in regulating gorse spider mite populations is not known.

New Zealand has two families of common predatory invertebrates that may significantly affect *T.lintearius* populations. *Phytoseiulus persimilis* (Acari; Phytoseiidae) Athias-Henriot and three species of *Stethorus* (Coleoptera; Coccinellidae) which have been recorded in the literature as regulating tetranychid mite populations. Successful establishment of GSM colonies in the field has been recorded despite the presence of *P.persimilis* (Hill et al. 1991). This suggests that *P.persimilis*

alone is unlikely to cause widespread establishment failure of GSM. This information on *P.persimilis* coupled with a lack of knowledge on *Stethorus* predation in New Zealand, indicated that research needed to focus on GSM predation by coccinellids. In line with 'major factor analysis', as opposed to a study of the predator complex, the potential regulatory ability of *Stethorus* species alone is addressed in this thesis. *Stethorus bifidus*, the most common endemic *Stethorus* species in New Zealand, was taken as the study predator in association with *T.lintearius*.

***S.bifidus* an endemic predatory insect:**

There are three New Zealand species of *Stethorus*. *S.bifidus* (Kapur), *S.griseus* (Chazeau) and *S.histrio* (Chazeau). *S.griseus* and *S.bifidus* are endemic to N.Z. (both with an earliest record of February 1912) and their closest relatives are in Australia, *S.nigripes* and *S.vagans*, respectively. *S.histrio* is native to Australia, New Caledonia, Chile and Mexico. It has been present in NZ since at least 1932, while the earliest Australian record is 1892 (Houston 1990).

The importance of coccinellid predators in New Zealand orchards has long been recognized. This is indicated by Collyer (1964) who sees *S.bifidus* as the only important predacious insect in New Zealand. This statement, while not to be taken literally, does indicate the importance of *Stethorus* species as predators (especially of phytophagous mites).

Chapter three provides information relating to predatory performance of *Stethorus* species in general as well as specific information on the taxonomy and biology of *S.bifidus*.

Part two: Objectives, hypotheses and how the problem was investigated

Previous research:

Debach (1950) working on population fluctuation in *Paratetranychus citri* (citrus red mite) comments on the controversial nature of published work regarding the relative importance of regulatory factors, especially predatory and climatic variables. Debach (1950) reviewed a variety of methods to evaluate the effectiveness of predators feeding on citrus red mite populations. These methods involved the correlation of quantitative data on mite and predator population changes and the effect of predator exclusion on mite development rate. The possible influence of climate variables on mite population regulation were also considered by following two procedures; attempting to correlate climatic extremes in temperature and humidity with mite population fluctuations and secondly mite population fluctuations with prior climatic extremes (Debach loc cit.). This type of data can be very useful if consistent trends are uncovered though collection of data is labour intensive and often impractical.

Looking at variables within the predation process Tanigoshi loc cit. (1977b) considers predation pressure as the compilation of many predatory species. The importance of this is stressed by the study done by Tanigoshi loc cit. (1977b) on the dynamics of predation of *S.picipes* and *Typhlodromus flordanus* on the prey *Oligonychidae punicae*. It was noted here that 'phytoseiid mites were the most effective predators in maintaining *O.punicae* populations at low levels and that *S.picipes* was the most effective predator in suppressing high spider mite populations and that the impact of the two predators together resulted in a numerical suppression of the prey which was 3.0 and 6.7 times greater than that for *T.flordanus* and *S.picipes*, respectively, acting alone.' Finally Putman (1955) noted that 'although *S.punctillum* alone cannot alone control severe infestations of mites it is an important member of the biological complex that limits mite populations.'

It is clear that *Stethorus* species have the ability to exert considerable predation pressure on prey populations under certain conditions. However *Stethorus* species are consistently referred to as merely one of the components of the overall predation pressure shaping pest population dynamics. *Stethorus* is often considered as having

a reduced regulatory potential if present in isolation from other predators. This point stresses the importance of adopting a 'multi-factor' approach to this type of problem in order to uncover the underlying importance of various interactions. In other words caution is needed when interpreting results dealing with a predator taken from its surroundings.

The objective of this study is to determine the potential ability of *Stethorus bifidus* to regulate populations of *Tetranychus lintearius*. To do this it is necessary to learn about the predators Phenology (activity cycle) and consumption rate. Phenology and consumption rate are therefore used as starting points for the examination of wider interactions.

Objective A: What is determining *S.bifidus* phenology?

- Physiological State in relation to temperature
- Development rate in relation to temperature
- Prey quantity (density) measured by development speed/fecundity of *S.bifidus*
- Prey quality (colony age structure) measured by the fecundity of *S.bifidus*
- Substrate

(NB: A high fecundity is the ability to produce offspring frequently and in large numbers)

Objective B: What are the primary Influences on consumption rate?

- Activity tempo (or speed) in relation to temperature
- Prey density measured by search distance
- Interference measured by webbing & competition

The approach to addressing each of these 'variables' associated with *S.bifidus* phenology and consumption rate is given below. Abbreviations are used in each case to describe the way in which each question was investigated.

Obs= observations

Ref= key reference(s)

Exp= experiment

Objective A: What is determining *S.bifidus* phenology?

Temperature

- aim** - PHYSIOLOGICAL OR ACTIVITY STATE: At what times of the year/season is *S.bifidus* an active predator having the potential to regulate *T.lintearius*?
- obs.** - To address this question *S.bifidus* populations in the field will be observed. A review of the literature will also be used.
- ref.** - (Collyer, 1964)

Temperature

- aim** - DEVELOPMENT RATE: The rate of development will depend on temperature. Experimental work and a literature review will be used here.
- ref.** - Putman (1955)
- exp.** Experiments will be run to determine the duration of development at different temperatures when excess food is available. An estimate of threshold temperatures will be made. Incorporating this information with work done by Stone (1986; looking at development rates of *T.lintearius*) will allow development rates of both predator and prey to be plotted and compared as temperature changes, **see Chapter four: part one.**

Prey quantity

- aim** - DEVELOPMENT SPEED/FECUNDITY: How is development time/fecundity affected by prey density. Past evidence will be used here in conjunction with oviposition testing.
- ref.** - (Bailey 1986; Collyer 1964; Houck 1991; Putman 1955; Smith 1965).
- exp.** - Measure oviposition in relation to prey density **see Chapter four.**

Prey quality

- aim** - FECUNDITY: How is the availability of mite stages influencing *S.bifidus* fecundity. A literature review will be used.

- ref. - (McMurtry et al. 1974; Scriven & Fleshner 1960; Putman 1955; Orr & Obrycki 1990)

Substrate

- aim - SUBSTRATE: Can *S.bifidus* carry out it's life cycle on gorse? Evidence and observation will be incorporated here.
- ref. - (McMurtry et al. 1970a; Collyer 1964).
- obs. - Observation of eggs being laid on gorse in the field or laboratory by *S.bifidus* will be made. Development while feeding on GSM alone will be followed and the laying of viable eggs on gorse will be used as a final check.

Objective B: What are the primary influences on consumption rate?

Temperature

- aim - ACTIVITY TEMPO OR SPEED: How is temperature affecting consumption of GSM by *S.bifidus*. Evidence and experimentation will be used here.
- ref. - (Hull 1974; Hull et al. 1976; Hull et al. 1977a)
- exp. - Experiments will determine the number of mites consumed by *S.bifidus* feeding at different temperatures. GSM distribution in relation to temperature will be important (if the mites clump as temperature drops prey consumption may be maintained or even increase). However this will not be determined (as the tests will be carried out in artificial arenas) but this point must be kept in mind.

Prey density

- aim - SEARCH DISTANCE: Determine how prey density will affect predation. Literature and experimental findings will be incorporated here.
- ref. - (Putman 1955; Hull et al. 1977b; Putman 1950; Chant 1961; Readshaw 1973,74; Charles et al. 1985).
- exp. - Testing individuals under varying prey densities will be used to determine if

S.bifidus' functional response has characteristics necessary for effective regulation of GSM populations. This will be done by measuring the handling time variation as prey density is altered, **see chapter four: part 2, section 2.**

Interference

aim - WEBBING: Does the presence of webbing affect consumption rate?
Evidence and observation will be relied on here.

ref. - (Tanigoshi & McMurtry 1977a; Putman 1955; Davis 1952)

obs. - check for obstruction to feeding in GSM web throughout experimentation.

aim - INTRASPECIFIC COMPETITION: Is intraspecific competition likely to be occurring? Use evidence here.

ref. - (Hattingh & Samways 1990; Putman 1955; Raros & Haramoto 1974)

The above information will be integrated to predict the potential ability of *Stethorus bifidus* to regulate *Tetranychus lintearius* in various regions of New Zealand, **see Figure 8 for a summary of the above considerations.**

CHAPTER TWO: BIOLOGY AND LIFE HISTORY OF *Tetranychus lintearius*

The following table summarizes the use of abbreviations for the common or Latin names of *Tetranychid* mites.

Common name	Latin name(s)	abbr.
Gorse spider mite	<i>Tetranychus lintearius</i> (Dufour)	GSM
-	<i>Eotetranychus sexmaculatus</i> (Riley)	
Two-spotted mite	<i>Tetranychus urticae</i> (Koch)	TSM
	or <i>Tetranychus telarius</i> (McG)	TSM
European red mite	<i>Panonychus ulmi</i> (Koch)	ERM
Citrus red mite	<i>Metatetranychus citri</i> (McG)	CRM
	or <i>Paratetranychus citri</i>	CRM
Fruit tree red		
spider mite	<i>Metatetranychus ulmi</i> (Koch)	
Pacific spider mite	<i>Tetranychus pacificus</i> (McG)	
Avocado brown mite	<i>Oligonychus punicae</i> (Hirst)	
Banks grass mite	<i>Oligonychus pratensis</i> (Banks)	BGM
Spruce spider mite	<i>Oligonychus ununguis</i> (Jacobi)	
-	<i>Tetranychus turkestanii</i> (Ugarov & Nikolski)	

NB. *T.telarius* refers to TSM here, however earlier in the literature to describe closely related species within the genus *tetranychus* including *T.lintearius* and *T.urticae* (Hill, 1987).

General characteristics of *Tetranychidae*:

Mite damage:

The *Tetranychid* mites, commonly known as spider mites due to their ability to produce webbing, are an important family of the Acarina with the ability to become highly destructive in many agricultural crops. Van de Vrie et al. (1972) state that 'spider mites may cause such severe injury that very heavy losses result, in such crops as citrus, avocado, beans, cotton, apples, pears, plums, tea, and a great many others.' Damage is caused by mite feeding which involves puncturing plant cells and extracting

the contents which causes 'bronzing' and eventual death of foliage, **see plate 3**. Van de Vrie (*loc cit.*) goes on to say that 'spider mites do not commonly cause widespread damage in natural or semi-natural environments little influenced by man. An extensive literature suggests two different explanations, both of which undoubtedly contain much truth. The most common view has been that in these undisturbed situations, natural factors, such as predators and diseases (parasites are unknown), commonly hold mites in check. In environments where broad-spectrum pesticides are used, however, the enemies are more adversely affected than the spider mites, and an outbreak of the latter occurs. Much recent work has shown that some conditions, eg., the use of fertilizers, better crop management, and, in fact, application of pesticides, enhance the intrinsic power of increase of the mites, and may occasion outbreaks, regardless of the influence on mite enemies.'

Early reports of large spider mite outbreaks were linked to the introduction of DDT in the 1940's as an insecticide to control the codling moth, mealybugs, mosquitos, and walnut pests. Two schools of thought developed relating the appearance of DDT and the outbreak of spider mite populations that followed (Readshaw 1975). These include the hypothesis that DDT was killing important predators of spider mites leaving populations relatively unchecked, and the hypothesis that DDT had a direct stimulatory effect on mites such as increased oviposition rates. Although the question of a direct or indirect effect of DDT on mite population increase is not resolved, the evidence suggests that the greatest cause of mite population increase following DDT is the destruction of predators (Pielon 1962; cited in Boudreaux 1963).

Huffaker & Spitzer (1950) have however, demonstrated an increase in population density of spider mites associated with DDT treatments. They comment that some of the results were consistent with the idea of a physiological stimulus to reproduction under DDT influence, although this tendency was erratic in occurrence and only of secondary importance as an explanation of the problem. In the past the common practice of using oil as a 'spreader', which is toxic to all mite stages, appears to offer a plausible explanation for the sudden rise in mite damage with the shift from lead arsenate (sprayed with oil) to DDT.

PLATE 3: GSM feeding damage to gorse

Damage (light green
appearance)

Undamaged

When considering the other main hypothesis it is found that tetranychid mites are preyed upon by a large number of arthropods represented by the following groups listed from Boudreaux (1963). Thysanoptera, Anthocoridae, Lygaeidae, Capsidae, Reduviidae, Chrysopidae, Itonididae, Syrphidae, and Coccinellidae; and among Acarina, principally Phytoseiidae. According to Boudreaux (1963) there appears to be a connection between the large number of predators of *Tetranychid* mites and their high reproductive potential.

Life history:

Van de Vrie et al. (1972) reports that 'as with many arthropods, the pattern of oviposition in tetranychids generally consists of a short preoviposition period, a rapid increase to a peak a few days later, followed by either a slow or a rapid decline. In unmated females the peak may be delayed until after mating.' Borror et al. (1989) notes that spider mites generally lay eggs which hatch in 4-5 days on host plants during summer. Growth through four instars from egg to adult usually requires about three weeks.

'The life cycle of tetranychids is a typical epimorphosis, the stages are each followed by a quiescent stage: nymphochrysalis, deutochrysalis and teleiochrysalis. There is a marked difference between male and females in the rate of development. The early maturing males locate by contact and remain near the female teleiochrysalis until the females hatch. Copulation takes place almost immediately after hatching of the young female. This explains why, in a normal bisexual population the females are nearly always mated. Unfertilized eggs produce only males; fertilized ones only females. But a mated female may still produce both sexes, because not every egg receives a spermatozoan' (Van de Vrie et al. 1972). In general, a single impregnation will suffice to provide a female with diploid eggs (females) for the rest of her life, to be used in combination with unfertilized haploid eggs (males) (Helle 1967). Borror et al. (1989) note that most species overwinter in the egg stage.

Tetranychids cover leaves with a mass of silken webbing which is produced by glands opening on the enlarged epinathidium on the tarsus of the pedipalp (Evans 1961). According to Evans (loc cit.) the main function of webbing appears to be protective but

it may also aid dispersal which is accomplished in a manner reminiscent of ballooning in spiders. Carter (1956; cited in Evans, 1961) has described the massing of *Eotetranychus tiliarum* on lime trees in Hertfordshire. In early September millions of mites producing large quantities of webbing were seen swarming on the bark of the trees. The webbing was easily blown away from the trees and converted into matted masses containing large numbers of mites. All the mites aggregating on the trees were females. Flesher (1956) observed ERMs dropping on web lines from foliage when chlorophyll was nearly depleted, however drift appeared to be limited. Gilliatt (1935) concluded from orchard studies that there was no large scale wind drift of the ERM, however it seems that more mites are transported by light or moderate winds than by gales. Like spiderlings, it appears that mites only aggregate for dispersal when air movement is slight and avoid becoming airborne in strong winds.

Foott (1963) suggests that spider mite webbing is involved in interspecific competition as seen with *Tetranychus telarius* and *Panonychus ulmi*. Georgala (1955; cited in van de Vrie et al. 1972) found that *Bryobia rubrioculus* on fruit trees was restricted to web free areas on leaves where *Tetranychus urticae* was present. Rota (1967; cited in van de Vrie et al. 1972) is of the opinion that the webbing of *T.urticae* on fruit trees in Northern Italy is an advantage for this species in its competition with *P.ulmi*. Webbing is discussed further below.

Factors determining spider mite abundance:

Firstly it must be stated that an independent analysis of any influential factor in isolation is purely academic. This is demonstrated by Van de Vrie et al. (1972) who state that 'weather and nutrition are interrelated in that weather may have a direct affect on increases or decreases in the food supply, or an indirect effect through its influence on natural enemies.' Jeppson et al. (1957) observed populations of the citrus red mite *Metatetranychus citri* (McG.) over a three year period and commented that 'low humidities and moderate to high temperatures were unfavourable for mite development, and low humidities accompanied by high temperatures and winds appeared to make new plant growth less favourable for mite population development.' This indicates complexities whereby interrelationships between nutrition and weather influence mite growth potential.

These indirect effects are also mentioned by Force (1967) who illustrates how temperature effected the role of *Phytoseillus persimilis* in the regulation of *T.urtica*. In plant growth chambers, *P.persimilis* was seen to regulate prey numbers only over a given temperature range.

Temperature, humidity and photoperiod:

Kramer & Hain (1989) found temperature to be the overriding influence in the development of *Oligonychus ununguis*. Outbreaks of *Oligonychus pratensis* may also be due to high-temperature environments stimulating growth and in turn the reproductive response, according to Perring et al. (1984). Feese & Wilde (1977) also working with *O.pratensis* found they developed most rapidly when temperatures were high, the effects of relative humidity were not statistically significant.

Boudreaux (1963) describes the interesting phenomenon whereby moderate, as opposed to high, temperatures, while not allowing the most rapid completion of the life cycle, result in individuals that are longer lived with the net result of increasing the overall intrinsic rate of increase.

According to Van de Vrie et al. (1972) 'low winter temperatures cause mortality in overwintering stages, and represent a prime challenge which has been met in many species by development of cold-tolerant or diapausing stages, commonly eggs or adult females.'

Investigation by Kramer & Hain (1989) demonstrated how variable humidity regimes, either alone or with variable temperature regimes, had no significant effect on the development period of the immature stages of *O.unungius*. Survival was marginally decreased under variable temperature regimes. Mori & Chant (1966) comment on how *T.urticae* avoided high humidities in experiments on hygrotaxis (orientation response to a given humidity gradient) and became sluggish in moist air experiments on hygrokinesis (level of activity as indicated by movement after exposure to a given humidity). On the other hand, *P.persimilis* did not avoid high humidity in its tactile behaviour, though its level of activity declined rapidly in high humidity and the mites became almost immobile. In dry air, both the prey and predator moved continuously

in the arena. With both species, activity was always higher in low humidity, and lower in high humidity. The number of prey consumed by *P. persimilis* was higher in dry air than in damp air (Mori & Chant loc cit.).

Relative humidity has little influence on the egg incubation time but is of major importance in determining the number of eggs which hatch (Harrison & Smith 1961). Extreme humidities reduce the number of eggs hatching and 100% relative humidity delays hatching time so long that the embryo usually dies (Harrison loc cit.).

Boudreaux (1958) working on various spider mites notes that hatching of eggs is not greatly affected by extremes in humidity however newly hatched mites survive poorly in moist atmospheres. According to Boudreaux (loc cit.) ovipositing mites lay more eggs at a higher rate and live longer than mites ovipositing in a near saturated atmosphere.

To avoid desiccation in 'dry' environmental conditions Van de Vrie et al. (1972) suggest that 'tetranychid mites feed on moisture-laden plant tissue, and thus make up for loss of water to the atmosphere. The egg stage, however, may become rapidly desiccated in dry air.'

Rain represents another abiotic factor with an uncertain influence on the biology of tetranychids. Van de Vrie et al. (1972) comment on how 'heavy rains might be expected to cause severe losses, particularly in species that inhabit the upper surfaces of leaves and are not heavy webbers, and the effect may be intensified if heavy rains are accompanied by turbulent wind, which would also tend to expose the lower surface of the foliage.' Thomas (1990) collected data in conflict with the traditional belief that plant stress and the occurrence of heavy driving rains are important factors in spider mite population dynamics. According to Thomas (loc cit.) other factors associated with drought conditions require consideration to explain spider mite population dynamics in soybean such as increased development rates, inactivity of predators and pathogens and rate of immigration from deteriorating food sources may be the most important precursors for the development of spider mite epidemics.

Huffaker & Spitzer (1950) conclude that 'wind was shown to be a major factor

influencing the rapidity of development of two-spotted mites on pears,' (strong wind inhibiting the early development of a two-spotted mite population).

The above considerations suggest temperature is of crucial importance to mites with humidity being regulatory only at extremes. Factors such as wind and rain still are controversial and should not at this stage be dismissed as unimportant. This information has relevance to the current situation. Temperature should be seen as an important factor determining the survival of *T.lintearius*, whereas rainfall also appears to be very important. Work looking at the effects of rainfall is in progress.

Host suitability/availability:

Jeppson et al. (1957) noted while working on the citrus red mite (*Metatetranychus citri*) that mite population fluctuations were correlated with seasonal growth cycles of the tree and with periods of high temperature and low humidity. It was found that citrus red mite populations on lemon trees tend to be highest during periods when there is the maximum amount of foliage growth. Lemons, however, produce sufficient new growth to sustain relatively high populations most of the year if weather conditions are favourable.

Van de Vrie et al. (1972) conclude that 'a number of other factors related to the host-plant and agricultural practices may influence rather directly the actual increase of tetranychids. Among such factors are differences in species, variety or biotype of the host-plant, sources of alternate hosts, soil-mineral-water relations, biochemical composition of the leaves, dispersal pressure and impact of pesticides, and other management features.'

More intricate features such as host architecture are mentioned by Van der Vrie et al. (1972). The notion 'that leaf surface texture, vestiture and contours (ridges, depressions) are important in the reproductive potential of a resident tetranychid has long been recognized. Such features may serve as tough impediments to feeding, as surfaces for attachment of webbing or direct protection from disturbing or harmful microweather on the leaf surfaces. The degree to which vestiture may be an advantage, or even a disadvantage varies with the species, particularly with the

amount of webbing it forms. Strong webbers, like *T.urticae* and *E.sexmaculatus*, will develop more uniform heavy populations, and more quickly on smooth plant surfaces if they are covered with a lint or floc than if left untreated (van de Vrie et al. 1972).

Predation:

Chapter three summarises spider mite predation.

Dispersal:

In the past natality and mortality have received substantial study while movements into or out of an area have generally been neglected. With species like tetranychids dispersal may be very important. Some species form 'ballooning threads' by which they lower themselves from a leaf, and are picked up by air currents and carried for some distance (Van de Vrie et al. 1972). Fleshner (1956) intercepted such drifting mites on aluminium strips, bordered with 'deadline,' at the top of a 20 foot pole. Studies on the avocado brown mite, *Oligonychus punicae*, revealed that 'when the air was calm females began spinning and drifting activities soon after sunset. When weather permitted, these activities continued throughout the night' (Fleshner loc cit.). Fleshner (1958a; cited in Van de Vrie 1972), also makes the comment that population decreases resulting from mass emigration may be as striking as those from predation.

Morphology and biology of *Tetranychus lintearius* the gorse spider mite.

Limited work has been carried out on *T.lintearius*, but Stone (1986) examined the average development rate at 25, 23, 20 and 15°C, fecundity, longevity, sex ratio and extent of diapause. It was found that *T.lintearius* has a slower rate of development than other related tetranychid species (Stone loc cit.). In Britain, Hill and Stone (1986) report that *T.lintearius* continues to reproduce throughout the year and can produce up to six generations/year.

Before introducing GSM into New Zealand, Hill & O'Donnell (1988) looked at its reproductive specificity. Results of a long series of crosses between males of *T.urticae* or *T.turkestani* and *T.lintearius* females yielded no female progeny at all, (females are

only produced in spider mites via fertilized eggs, hence a test for true fertilization). Hill & O'Donnell (1988) conclude that '*T.lintearius* is biologically different from other tetranychids. It forms discrete, long-lived colonies which live within a tent-like web and move around the host plant en masse. This behaviour is rare among tetranychid species. The mite has never been recorded from any host plant other than gorse. Stone (1986) has shown that its growth rate, fecundity and life span are very different from these of related pest species. The biology of this mite, coupled with its inability to hybridize with other tetranychid species, suggests that *T.lintearius* is a discrete species.'

The host specificity of GSM was also tested prior to its introduction by Hill & O'Donnell (1988). Here preliminary experiments showed that *T.lintearius* colonies were easily transferred from one gorse plant to another but that mites chose to migrate from unacceptable plants rather than to settle and form a colony. More detailed experiments examining the performance of individual mites on various host-plants showed that *T.lintearius* adults survived poorly and laid fewer eggs on test plants other than gorse. In most cases hatched larvae died without feeding. None of the non-leguminous species tested were suitable hosts for the mite. These included species such as apple and strawberry, which are susceptible to attack by closely related tetranychid mites such as *T.urticae*.

Hill and O'Donnell (1988) and Stone (1986) have shown that *T.lintearius* is a distinct, recognisable species which is reproductively isolated from its closest relatives in the tetranychids. Hill (1988b) concludes that 'this study has used accepted methodology (Wapshere 1974) to show that *T.lintearius* has a very narrow host range and in the field is almost certainly restricted to *Ulex* species. In fact, the host range determined under laboratory conditions is narrower than that of some insects which have been successfully and safely used for biological control of weeds in the past. On the basis of the host-range tests reported here, *T.lintearius* is safe to introduce into NZ.'

Following introduction of GSM, measurements to determine its establishment success were taken. After noting that establishment success was consistently reduced above latitude 39 degrees south investigation into variables influencing GSM establishment and growth was seen as being potentially important. Of these variables it seemed

necessary to collect data relating to predation pressure in the field. An account of the predator considered in this work is given in the next chapter. Although the study predator in this case is a coccinellid, acarine predators may also prove to be of considerable importance, particularly *P.persimilis*.

Predacious tetranychids:

Phytoseiulus persimilis was found to exert a remarkable control over *T.telarius (urticae)* and eventually eliminated it in the greenhouse environment (Chant 1961a). This finding, coupled with a consideration of the theoretical requirements of an efficient predator of phytophagous mites (Chant 1960; Chant & Fleshner 1960; cited in Chant 1961a), leads to the conclusion that '*P.persimilis* largely meets these: it is voracious, rapidly reproducing and developing, highly mobile and largely dependent on its prey for food. Its distribution on the host plant is well integrated with that of its prey: it does not establish itself except where the prey is present and its activity is directed toward these favourable places. The female predators do not feed to any extent on prey eggs and move to new prey infestations when all the active prey are eaten, leaving behind their own eggs in a colony of prey eggs, both of which hatch at about the same time. This favours wide dispersion of the predator over prey inhabited areas and ensures that the predacious larvae will not hatch on a leaf from which all prey have been removed and consequently starve to death.'

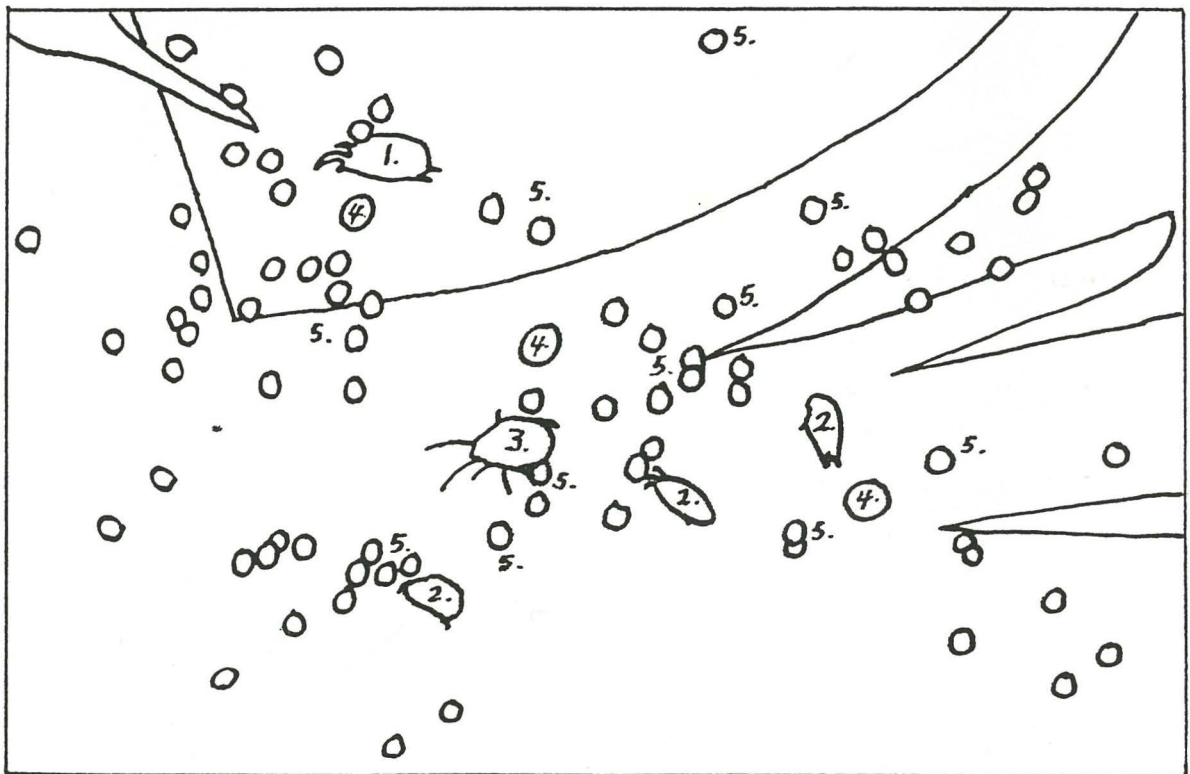
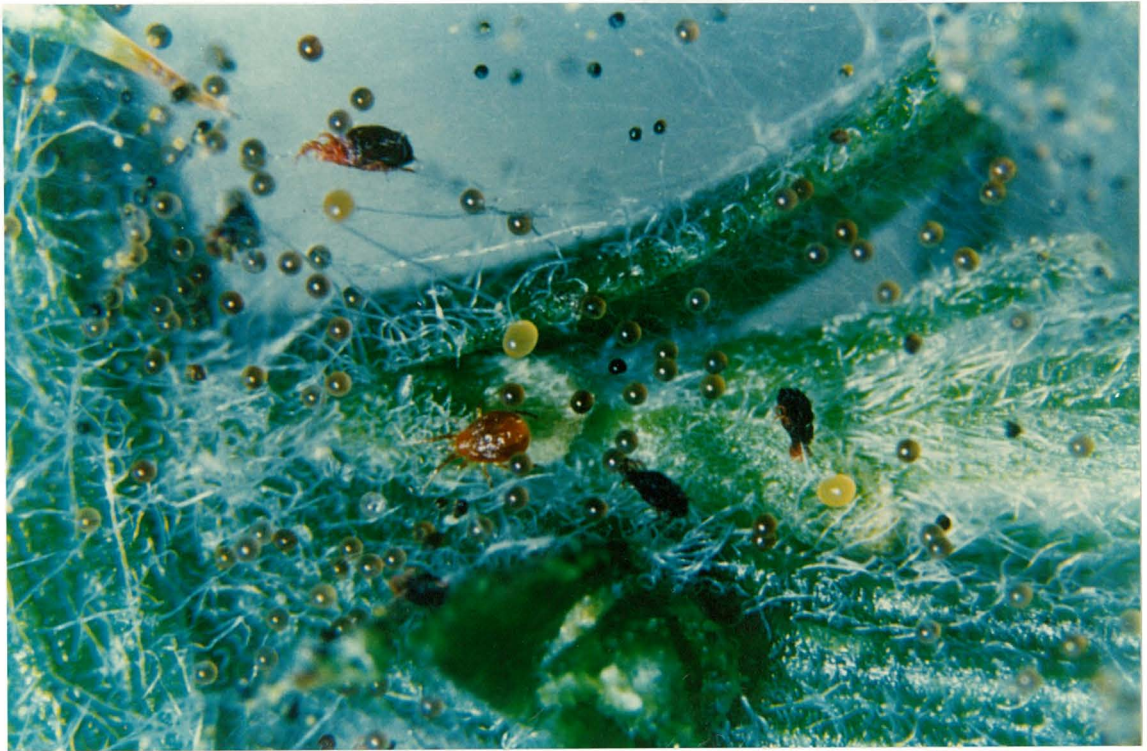
Although the elimination of *T.urticae* populations has been recorded in the greenhouse and *P.persimilis* appears to meet the criteria of an efficient predator, the potential for GSM regulation in the field has not been studied, **see plate 4**. The importance of this is stressed in **chapter three** where the notion of a predator complex having a much greater regulatory potential than an individual predator species is supported.

PLATE 4: *Phytoseiulus persimilis* a predatory mite that feeds on GSM

a- *P.persimilis* moving amongst a GSM colony eating gorse spider mites and laying eggs
(Magnification X 25)

b- Diagram illustrating features of importance

- 1- *T.linzei* (GSM)
- 2 - Dead GSM (eaten by *P.persimilis*)
- 3 - *P.persimilis*
- 4 - *P.persimilis* eggs (X3)
- 5 - GSM eggs (not all labelled)



CHAPTER THREE: BIOLOGY AND LIFE HISTORY OF *Stethorus bifidus*

The genus *Stethorus*:

Collyer (1953b) states that 'species of the genus *Stethorus* are important throughout the world where red spider mites occur.' In most instances the beetles have been found feeding exclusively on mites and are regarded as one of the more important predators. In fruit orchards of South-Eastern England *S.punctillum* feeds entirely on mites, principally the fruit tree red spider mite (Collyer loc cit.).

The family Coccinellidae are extremely diverse in their habits. The majority of species are beneficial because of their predacious nature, but some are injurious being phytophagous on agricultural crops (Hagen 1962).

Due to the importance of *Stethorus* species in connection with spider mite control their feeding and phenology has been widely studied. Colburn & Asquith (1971) working on *S.punctum* and *P.ulmi* found that there are three generations a year of *S.punctum* in Southcentral Pennsylvania. An average period from the time the egg is laid to the appearance of the adult is 23 days. About 25 days from the time the adult emerges from the pupal case it begins to lay eggs. The adults overwinter in duff near the trunk of apple trees, entering overwintering quarters in late October (North America) and emerge into the trees in mid-April of the following year (Colburn loc cit.).

Copulation takes place a few days after emergence and is usually repeated several times during adult life, even though for most species (except *S.punctillum* which lacks a spermatheca) one copulation is enough to give the female life long fertility (Hodek 1967). Eggs are laid in the vicinity of prey apparently because oviposition occurs where the adults have been feeding on essential prey (Hodek 1967). The reason eggs are laid in areas of high prey density is due to the reduced locomotion of the adults in this situation and the increased oviposition rate when food is abundant (Gilliat 1935; Dixon 1959; Putman 1955).

Longevity in *Stethorus* species is high and the adult beetles are highly mobile eg. in the field they were observed searching up to twenty leaves/hour, running rapidly over

the leaves and flying from leaf to leaf (Readshaw 1975).

Consumption rates of *Stethorus* species are high and they are known for their ability to regulate mites at high density (Putman 1955; Huffaker 1969). Food consumption is usually maximal in ovipositing females, however less in non-ovipositing females and minimal in males (Hodek 1967). This was also demonstrated by Putman (1955) who found ovipositing females of *S.punctillum* ate an average of 40 two-spotted mites/day compared with 19.9 by males. Data from Putman (1955) suggest that the adult is the main predatory stage in *S.punctillum*.

Although feeding characteristics of *Stethorus* species have been studied by various workers the question of how these predators find prey populations in an orchard or field situation is only now becoming apparent (Turlings et al. 1990). Fleshner (1950) with *S.picipes* larvae, as did Putman (1955) with *S.punctillum* adults, found that *Stethorus* species did not perceive prey presence until physical contact was made. Once contact was made searching immediately commenced in the surrounding area. Although Thompson (1951; cited in Hodek 1967), states that 'predators can perceive their host at a distance,' all the experimental evidence implies that these predators are guided by phototaxis and geotaxis so their search can only be random (Hodek 1967). Vision in *Stethorus* has been dismissed as unimportant in the past by such workers as Fleshner (1950) and Banks (1957). However according to Houck & Strauss (1985) vision may be an important stimulus to the final stages of predation. This is also backed by Stubbs (1980), who found prey perception prior to contact in adult coccinellids through vision and in fourth instar larvae through scent.

A possible answer to this confusion has been discovered by Turlings et al. (1990) who worked on the cues used by a parasitic wasp *Cotesia marginiventris* (Cresson) to locate caterpillar prey. It was discovered that an active chemical release by corn seedlings being attacked by caterpillars was exploited by host searching parasitoids. This chemical (a terpenoid) may be produced in defense against herbivores but may also serve a secondary function in attracting the natural enemies of these herbivores (Turlings loc cit.).

Stethorus species are susceptible to most insecticides and therefore are not present

in commercial orchards until late summer when in the absence of insecticides become very numerous if mites are abundant (Readshaw 1975). This particular study by Readshaw (loc.cit.) lead to the firm conclusion that the problem of mite outbreaks was caused by the lethal effects of pesticides, for example DDT, on predators.

Factors influencing phenology and feeding of *Stethorus* species:

Temperature, humidity and photoperiod:

Much of coccinellid phenology and feeding is primarily regulated by temperature. Putman (1955) showed that development and food consumption of *S.punctillum* were positively correlated with temperature. Hull (1976) demonstrates how temperature even influences the ability of *S.punctum* to find its prey, *P.ulmi*, with an increased predation efficiency at high temperatures. Hull et al. (1977a) again demonstrated this behaviour by recording a change in the feeding characteristics of *S.punctum* throughout the day, 'feeding increased as temperature rose during the day with maximum consumption occurring during the warm afternoon hours.' A combination of cold temperatures low reserves and sluggish functioning are probably the main factors contributing to the poor predator/prey interactions early in the season as opposed to a rapid response to low prey densities late in the season (Hull 1976). According to Hodek (1967) an increase in development rate accompanying a rise in temperature naturally results in a higher daily feeding rate. Therefore temperature will not only determine consumption but may alter the predators' searching effectiveness by controlling its' activity tempo ie. speed of movement.

Humidity or photoperiod, or both, do not appreciably affect coccinellid development rate and humidity causes increased mortality only at high and low extremes as does temperature according to Hodek (1967).

Prey preference/availability:

Collyer (1953b), with respect to *S.punctillum* feeding on *Metatetranychus ulmi*, found that all stages of the coccinellid showed a definite preference for the larger mite stages, but that mite eggs are devoured especially by the larvae. In contrast to this

McMurtry et al. (1974) has shown how oviposition rate (in relation to prey quality) indicated that eggs and larvae of *Tetranychus pacificus* McGregor were more favourable as food than other stages of prey to *S.picipes*. Scriven & Fleshner (1960) when working with *S.picipes* found that young larvae must have an abundant supply of mite (*T.pacificus*) eggs, larvae and nymphs. The first instar beetles are very weak and slow and cannot overpower adult mites. Mites should also be readily available to the larvae prior to pupation or considerable mortality will result in the first few hours after emergence (Scriven loc cit.).

Collyer (1964) found that development rates were dependent on prey availability. The minimum number of *P.ulmi* females for 1st, 2nd, 3rd and 4th *S.bifidus* preimaginal development were 5, 10, 10 and 20 mites/day respectively. This is backed by Bailey (1986) working with *S.nigripes* who notes that high rates of reproduction and survival only occur when mites are abundant.

Collyer (loc cit.) also examined the oviposition performance of *S.bifidus* feeding on *P.ulmi* and found a positive correlation between mites eaten and eggs laid. Putman (1955) noticed prolonged activity in starved *S.punctillum* accompanied by a reduction in eggs laid and Gilliatt (1935) found that well-fed adults of *S.punctum* tend to remain at rest on leaves for periods of 1/2 to 1 hr. Dixon (1959) suggests 'that *Adalia decempunctata* oviposit close to aphids because they are less active when well fed and consequently remain in the vicinity of their own food supply. The chance that eggs will occur close to aphids is further increased as more eggs are laid when food is abundant.'

Findings by Orr & Obrycki (1990) demonstrate how prey preference can influence coccinellid development. Preimaginal development of *Hippodamia parentheses* reared at 22° C on pea aphids was significantly shorter than that on a diet of greenbugs.

Obrycki & Tauber (1982) working with *Hippodamia convergens* suggest that annual variation in temperature and food availability interact to determine the number of generations actually produced each year and the degree of importance of these two factors varies geographically. Hagen (1962) concluded that prey availability influences the voltinism of *H.convergens* populations more than abiotic factors. This refers to

poor food supply triggering aestivation. This point, although not tested in this work, may have relevance to *S.bifidus* in southern regions of New Zealand.

However, Orr & Obrycki (1990) conclude that thermal and dietary requirements for population increase would alone not account for its population fluctuation relative to other coccinellid species in the midwestern aphidophagous guild. Further studies are needed on biotic and abiotic factors that influence coccinellid populations, for example, parasitism or the effects of relative humidity or rainfall on survival of early instars (Orr & Obrycki loc cit.).

Alternative food supplies:

From feeding experiments Putman (1955) concludes that the frequent acceptance of alternative food by coccinellids only serves as an energy source and does not allow development. Despite the complete dependence of many *Stethorus* species on mites, Putman (1955), has repeatedly observed adult *S.punctillum* feeding on the secretion of peach leaf glands (extrafloral nectaries) in the orchard. According to Hagen (1962) pollen and fungi frequently make up part of the diet of many predacious coccinellids.

Cannibalism, another alternative food source, does not appear to be of any great importance among *Stethorus* according to Putman (1955). Raros & Haramoto (1974) found no evidence of cannibalism among the larvae of *Stethorus siphonulus* but adult beetles ate some of their own eggs. Cannibalism among *S.bifidus* was observed here when other food was not available. Both newly hatched larvae and adults consumed *S.bifidus* eggs however cannibalism of eggs by other larval instars was not tested.

Interference:

Davis (1952) notes how certain spider mites in concentrated populations accumulate great masses of webbing and live in or under this canopy. The webbing was repeatedly observed to entangle and delay certain predators such as lacewing larvae. In addition the webbing acts as a protective device against disturbing natural factors such as wind, rain and anthropogenic unnatural factors such as spray particles. According to Davis (loc cit.) the protection provided by the webbing may be great

enough to compensate for much of the adverse effect due to crowding.

Webbing appeared to limit the movement of *S.bifidus* 1st and 2nd instar larvae especially, but was not seen as a barrier to adults, **see plate 5**. According to Putman (1955) the larvae of *S.punctillum* showed few problems penetrating and venturing beneath the webbing spun by the two-spotted mite, loosening it by forward and upward thrusts of the head, and concludes that webbing is an inefficient barrier to predation; implying it would have small influence on the consumption of prey by *S.punctillum*. The extent of *T.urticae* webbing is limited compared with that of *T.lintearius*.

Putman & Herne (1966) note, 'webbing gives considerable protection against general predators but the specialized predators *Amblyseius fallacis* (Garman) and *S.punctillum* penetrate the webbing and remain beneath it, feeding and reproducing, till the colony is often exterminated.' Tanigoshi (1977a) also observing feeding behaviour within ovipositional cells and on *Persea indica* (avocado) leaves revealing that little difficulty was experienced in penetration of *Oligonychus punicae* webbing by any stages of *S.picipes*.

Intraspecific interference, was considered by Hattingh & Samways (1990) who conclude that the three predatory ladybirds tested, *Chilocorus nigritus*, *C. bipustulatus* and *C.infernalis*, did not decrease their feeding rate or disperse with increased predator density; no significant behavioural interference was observed either. This was not tested here though precautions were taken to avoid any possible intraspecific competition.

Variables influencing Coccinellid development:

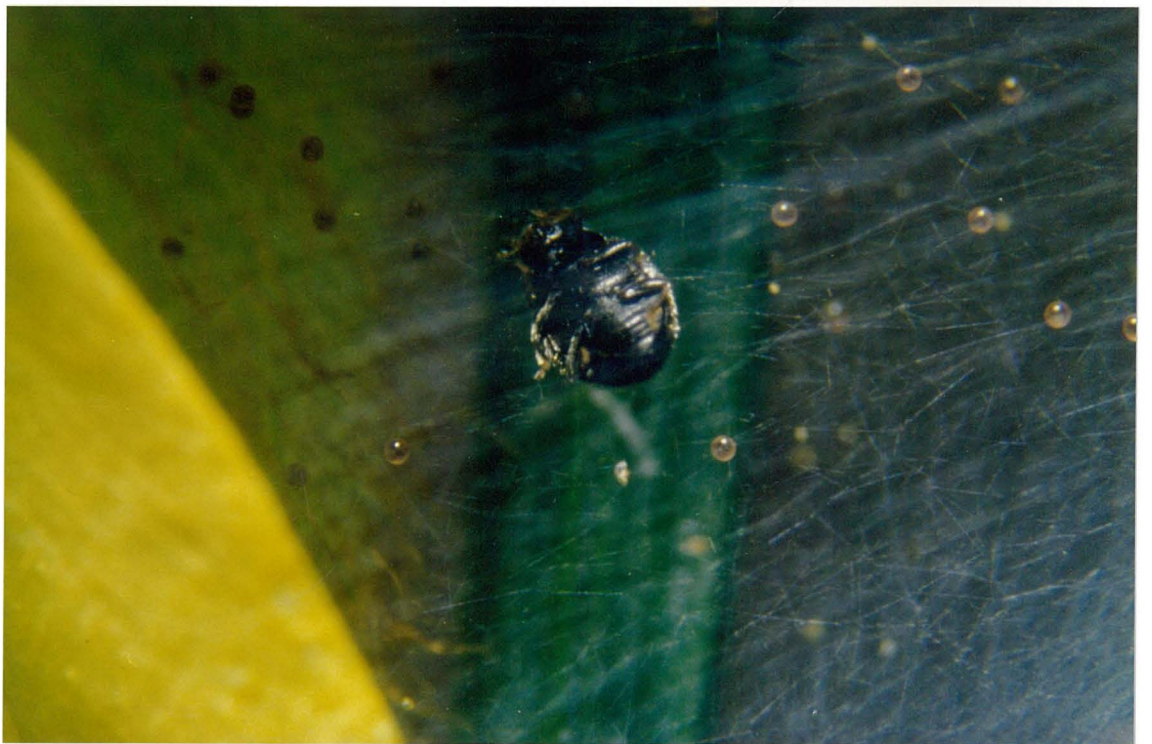
The literature reveals that temperature is a major factor influencing coccinellid development (Congdon & Logan, 1983; Orr & Obrycki 1990; Butler & Dickerson 1972; Miller 1992; Obrycki & Tauber 1982). Orr & Obrycki (1990) however, investigated the 'state' of adult *Hippodamia paretthesis* by weighing individuals after emergence over a range of temperatures. It was found that although development was fastest at 26°C the heaviest individuals emerged at 18°C and 22°C (Obrycki loc cit.). This has interesting implications when speculating about optimum developmental temperatures.

PLATE 5: GSM web interfering with predator mobility?

(Magnification X 25)

a- Larvae often become entangled in GSM webbing and die unable to escape

b- Adult GSM move over and through GSM webbing without becoming entangled



A summary of factors influencing predatory development, survival and oviposition, some of which are mentioned above, may include:

Abiotic

- temperature
- geography (altitude)
- humidity
- photoperiod
- substrate

Biotic

- webbing
- prey availability
- parasitism
- disease
- interspecific competition
- intraspecific competition

***Stethorus* as a predator of mites:**

Putman (1955) working in peach orchards in the Niagara peninsula, Ontario, found *S.punctillum* (a European native) to be one of the more important predators of tetranychid mites. Colburn & Asquith (1971) has shown that *S.punctum* is an important native predator of the European red mite *Panonychus ulmi* in southcentral Pennsylvania.

Hodek (1967) points out that if the attributes of an effective enemy are taken as the criteria for estimating the effectiveness of coccinellids (as controlling agents of coccids, aphids and mites) it is clear that coccinellids possess only some of the required characteristics. Their searching activity is high, they occupy all the habitats of their prey, they survive well, are amenable to culture, oviposition is high, development rate and number of generations is favourable relative to the prey in most cases except in aphidophagous coccinellids (Hodek loc cit.). Some species are also able to adjust their rate of development and adult weight according to the prey quantity (Smith 1965), and quality, (Orr & Obrycki 1990).

Hodek (1967) notes that coccinellids are not strikingly host-specific in their feeding, inferring that their regulatory potential is reduced because of this. Bailey & Caon (1986) however state that specialized predators may have limited regulatory affect, whereas the combined effects of several species can give good control. Bailey & Caon (loc cit.) provides the example of *S.nigripes* which is an important predator of

mites but its increase in numbers tends to lag behind those of the mites which is a consequence of it being an obligate mite predator/consumer.

Predation by *Stethorus* species can be described by two innate responses. These, the functional and numerical responses, are described separately to clarify the predation process.

Among other workers, Holling (1959b), found that as the prey density increased, consumption rate/individual predator increased. This describes the functional response.

The numerical response is divided into a reproductive and aggregative response. The reproductive response is related to the number of prey eaten, and the aggregative response is related to predators congregating in areas of high prey density and dispersing from areas of low prey density (Readshaw 1973).

In reality both the functional and numerical response have importance when considering a predator's overall potential to regulate a prey population (Holling 1959b; Fleschner 1950 & Putman 1955; Hull 1977a). However in dense colonies of prey the functional response of predators will reach a limit after which the numerical response (delayed) may be of greater significance (Huffaker, 1969). Whether this will be as effective with the slower developing *Stethorus* as it is with phytoseiid predators is of interest.

Functional response:

Within certain limits, consumption of food is positively correlated with the density of the prey (Holling 1959b; Putman 1955). A characteristic of the genus *Stethorus* is that it is an effective predator at high mite densities. This is supported by Huffaker et al. (1969) who state that '*Stethorus* thrives at high mite densities and in many cases, probably does not become abundant enough to exert a suppressive effect on mite populations until the economic level is exceeded (Clancy & Pollard 1952; Putman 1955). *Stethorus* however may be important predators of species that do not cause severe injury at moderate densities (McMurtry & Johnson 1966), or in cases where the

prey is locally concentrated on the host plant, before the average density on the entire plant is high (Putman 1955; Putman & Herne 1966).’ Putman (1955) observed that where two-spotted mites occurred the populations were most susceptible to attack by predators at the beginning of the season where dense localized populations were present. Unlike the more colonial two-spotted mites the European red mite is less susceptible to attack hence less well controlled by *S.punctillum*.

Mechanisms behind the functional response include two major time consuming predatory activities. ‘Attack rate’ and ‘Handling time’ (Holling 1959b).

Fleshner (1950) working on one mechanism of the functional response, attack rate (the area searched by a predator in a given time), found searching larvae ‘work harder’ after encountering prey, searching in tighter turns in the immediate vicinity. This behaviour has also been witnessed by Fleshner (1950) where an adult that has not recently fed, runs rapidly often in one direction for some distance. If it encounters a mites it stops, eats it and then proceeds much more slowly with frequent turns as it searches the area in the immediate vicinity. This suggests that the mechanism for the functional response here is an increase in the attack rate/orientation.

Although an experimental confirmation of variation in attack rate was not attempted with *S.bifidus* feeding on *T.lintearius*, the other main mechanism mentioned as driving the functional response, handling time, was investigated. This phenomenon is also described by Houck (1991). Houck (1991) found that starved *S.punctum* females spend a greater proportion of time feeding, with an increase in handling time/prey item. The increase in handling time was due to a more complete extraction of body fluids from individual prey, while satiated beetles were observed to pierce prey, initiate feeding and then abandon the prey. Putman (1955) writes that the increased opportunities for feeding give rise to a situation where prey is only partially consumed, perhaps explaining why predatory larvae appear to consume considerably more than the minimum required for their development if prey is abundant.

An indication that the functional response also varies seasonally is given by Hull (1974; cited by Hull 1976) who has noted that overwintering adults do not respond functionally to increasing mite densities compared with second and third generation adults. Again

according to Hull (loc cit.) this combination of factors such as cold temperatures, low reserves and sluggish functioning probably contribute to the predators slow response to increasing prey numbers early in the season.

numerical response: (reproductive or aggregative)

Readshaw (1973) examined the numerical response by predators to prey density and stated that it is of critical importance in natural control.

The aggregative response, which has been neglected in the literature, is likely to have application to a wide range of problems where the exploitation of one species by another is involved. Readshaw (loc cit.) however states that, 'the numerical response by *Stethorus* to *T.urticae* was largely the result of reproduction by the beetles in response to increased supplies of prey.' Although the aggregative response was also seen in *Stethorus* (driven by behavioural alterations in searching pattern) it was not seen as the primary reason for local increases in their numbers (Readshaw loc cit.). Readshaw (1975) comments that large numbers of adult *Stethorus* can occur suddenly on trees more than 100m downwind from a source population. Hull (1977b) appears to support an aggregative response as the major factor determining the overall numerical response in *Stethorus* in contrast to the reproductive response supported Readshaw (1973).

As mentioned earlier Putman (1955) has shown that while temperature directly influences the development rate of *S.punctillum*, high temperatures actually accelerate the development of the mite more than that of the predator (*S.punctillum*), so that the relative growth potential of the predator is negatively correlated with increasing temperature. This point illustrates how careful consideration of the prey species is also necessary when predicting the potential ability of a predator to regulate its prey. The data used for predicting this regulatory potential should be flexible so that in any set of specific biotic and abiotic conditions an independent prediction can be made. This relates to the situation where a predator may regulate one species of mite whereas another similar species is not regulated. Putman (1955) gives an example of this (illustrated earlier in the section addressing the functional response) whereby the different clumping behaviour of *T.urticae* and *P.ulmi* is one factor determining how

each is regulated to a different extent by *Stethorus*.

Charles et al. (1985) does not differentiate between reproductive and aggregative responses, but states that *S.bifidus* shows a clear numerical response to TSM.

The delayed numerical response, via reproduction, will also be of importance for coccinellids where dispersal from an outside location is minimal. This is discussed by Chant (1961b), working with the predatory mite *Typhlochromus occidentalis*, who states 'at prey densities greater than those permitting maximum predator oviposition, the prey would be freed from the density dependent check imposed by the predator unless the immature predators that hatched from the eggs could mature and start to reproduce at a faster rate than that of the prey.' Here Chant (loc cit.) is emphasizing the within-generation effect. It appears that in most situations, an enemy can certainly compensate for a levelling off, or even a decline in functional performance of the individual through increase in numbers (the delayed numerical response; Huffaker 1969). Some offspring of phytoseiids may be consuming prey within four days or less hence the delay in effective numerical response is not so great (Huffaker loc cit.). This is confirmed by Tanigoshi (1977a) who looks at the relative life tables of the predatory coccinellid *S.picipes* and prey *Oligonychus punicae*. Although *O.punicae* had the highest intrinsic rate of increase early in the reproductive period due to high fecundity, short development time and generation times, the greater longevity and longer oviposition period allowed *S.picipes* to have a higher overall potential for increase. Subsequently the reproductive response to prey density will be an important part of the overall numerical response in *Stethorus* species.

Again despite the notion that the reproductive response is perhaps more important than the aggregative response in *Stethorus*, this is not supported unanimously.

Hull et al. (1976) observed searching behaviour within an apple orchard and showed that *S.punctum* adults were able to increase to high densities in one area of the apple orchard and then move to other areas of the orchard preventing mites from reaching levels of economic injury; effectively searching out areas of the tree where the mite populations were the highest. According to Hull (loc cit.) the aggregative response of *S.punctum* (to the changing distribution of a *P.ulmi* population) is very important to the

success of the Pennsylvania integrated pest-management-within-apple-trees programme because female beetles deposit eggs on leaves on which prey is present.

Although Hull's (*loc cit.*) work did not disprove that searching of *S.punctum* is random, it did suggest that there may be some stimulus other than random searching to find mites in orchards. All these cases fail to address the stimuli which allow *Stethorus* individuals to find and aggregate in areas of high prey density. Turlings (1990), as mentioned earlier, provides a mechanism for this behaviour in predatory mites which may prove to have wider significance.

In summary the literature suggests that an aggregative response could be primarily important followed by a stronger reproductive response in *Stethorus* species.

***Stethorus* as a predator in the field and its' role as a control agent in a predatory complex:**

Charles et al (1985) found that the predators *P.persimilis* and *S.bifidus*, especially the former, were able to limit TSM populations to acceptably low levels in commercial berryfruit gardens under pesticide regimes that provided high quality fruit for export markets.

Putman & Herne (1966) conclude 'that endemic densities of *Panonychus ulmi* are maintained in that state by predators, chiefly *Typhlodromus candigans*, that subsist to a considerable extent on other sources of food, whereas epidemics are reduced largely by other predators, chiefly *Haplothrips faurei* and *S.punctillum*, that increase by feeding on the mite during its period of rapid population growth but exert their greatest effect through later destruction of winter eggs.'

Tanigoshi & McMurtry (1977b) also support the notion that predators are more effective as a complex rather than independently. Data collected by Tanigoshi (*loc cit.*) 'indicated that phytoseiid mites were the most efficient predators in maintaining *O.punicae* populations at low levels and that *S.picipes* was the most effective predator in suppressing high spider mite populations.'

Extrinsic factors limiting the predatory potential of insects such as coccinellids include insecticides. Hull et al. (1985) reporting on the integration of biological and chemical control tactics for apple pests note that selective timing and choice of synthetic insecticides indicate that certain synthetic pyrethroids decimated *S.punctum* populations resulting in higher ERM populations. Cypermethrin and flucythrinate completely suppressed *S.punctillum*, whereas permethrin allowed substantial survival of the predators (Hull loc cit.).

Hoy & Smith (1982) report on the failure of *Stethorus nigripes*, from Australia, to establish in Californian almond orchards where it was to assist in the control of *Panonychus ulmi* and *Paratetranychus citri*. Two reasons for this failure were the sensitivity of *S.nigripes* to pesticides and the requirement for prey during winter (eggs of *P.citri* or *P.ulmi* were not fed on).

The study insect *Stethorus bifidus*:

Morphology and distribution of *S.bifidus*:

Stethorus bifidus is a small black coccinellid endemic to New Zealand, see plate 6. McMurtry et al (1970a) notes that *S.bifidus* in NZ. can be found in all stages and in high numbers on certain plants during winter. According to Hill (pers comm.) *S.bifidus* are uncommon until early summer in the South Island. Collyer (1964) found that *S.bifidus* was the most abundant insect predator in New Zealand, 'being particularly common near Auckland and in Hawkes bay and somewhat less common in the Nelson District. In March 1960 it was present in small numbers near Blenheim and abundant near Christchurch and in central Otago; in these South Island areas the higher populations were often in association with *T.urticae*.' '*S.bifidus* and other *Stethorus* species are distributed throughout the country' (Charles et al 1985).

The only study looking at the seasonal activity cycles of *S.bifidus* throughout the year has been made by Collyer (1964). It was found that *S.bifidus* has two generations in summer on deciduous trees before leaf fall and was also active on citrus and other evergreens where it fed and reproduced during the winter. It feeds entirely on mites of several species and probably hibernates in colder conditions (Collyer loc cit.).

PLATE 6: The Coccinellid *Stethorus bifidus*

(Length \approx 1.2mm)

a- An adult *S.bifidus* searching on gorse

(Magnification X 25)

.

b- *S.bifidus* a ventral view

(Magnification X 50)



The attractiveness/suitability of the host plant to predators is of importance. Although it is known that certain species of predators may colonize some types of plants but not others, there is almost no information about the factors involved (McMurtry 1970a). Determining the factors that influence the colonization of gorse by *S.bifidus* is therefore difficult. From observation it appears gorse is suitable for *S.bifidus* reproduction and development. This is perhaps an indication that another factor such as prey availability is 'more' important. Evergreens may suit *S.bifidus* by allowing all year round feeding and reproduction on the one host plant where climate and prey availability allows. This implies a lack of dispersal from winter to summer feeding areas. According to Hull et al. (1976), *S.punctum* not only found trees in an orchard that had increasing mite populations but also sections of the tree that had the highest TSM density. Movement from one plant to another would appear not to be a factor limiting the predatory potential of such a mobile insect. The advantage of a year round food supply on one plant type is questionable if the searching ability and subsequently the aggregative response in *Stethorus* is strong. Work on the parasitic wasp *Cotesia marginiventris*, Turlings et al. (1990), needs to be paralleled by similar work on coccinellids to clarify the aggregative response.

Houston (1990) provides a key to New Zealand species of *Stethorus* *weise*. Main features used in this work to separate *S.bifidus/histrio* came from Houston (loc cit.) and include the presence of:

- long sparse semi-erect pubescence in *S.bifidus*, compared with elytral pubescence short dense & decumbent (lying along surface of body) in *S.histrio*.
- femoral line complete in *S.bifidus* as compared with an incomplete femoral line in *S.histrio*.
- metasternum distinctly convex posteromedially in *S.bifidus* compared with a relatively flat posteromedially metasternum in *S.histrio*.

The easiest way to distinguish between the two species is by comparing the shape of the metasternum. The metasternum of *S.histrio* is cube shaped with a square cross-section. In *S.bifidus* the metasternum has a rectangular section with a flaring of the anterior edges under which the front legs protrude.

Another characteristic, for males only, is the presence of a notch in the ventral sclerite

of *S.bifidus* not found in *S.histrio*. Also chelicerae are shorter and thicker in *S.histrio* than in *S.bifidus*.

Feeding and developmental characteristics of *S.bifidus*:

Collyer (1964) recorded *S.bifidus* as feeding entirely on mites of several species, where the larval development and number of eggs laid by females was related to food supply. This has been noted by Smith (1965), where the size of adults could be related to the availability of food during development.

Collyer (1964) found that most *S.bifidus* larvae in Auckland were grey in colour, and hatched from pale yellow eggs. In addition, dark brown broader larvae hatched from red eggs. Adult *S.bifidus* collected during this work were only seen to lay pale yellow eggs though some eggs were more white than yellow. Both eggs gave rise to grey coloured larvae. **See plate 8** for the life stages of *S.bifidus* and **chapter four: part a**, for more information on the development and feeding characteristics of *S.bifidus*.

CHAPTER FOUR: THE PREDATORY ABILITY OF *Stethorus bifidus*

Part one - The Reproductive Response

Introduction

The potential ability of a predator population to regulate a prey population can be examined by dividing the predatory response into two main components, the functional and numerical responses (first described by Solomon 1949). The functional response describes an increased rate of predation per individual predator as the prey density increases. The numerical response describes an increase in predator abundance in relation to prey density.

The numerical response has two subcomponents, the reproductive and the aggregative responses (Readshaw 1973). An increase in predator abundance due to reproduction is termed the reproductive response while the aggregative response describes an increased predator abundance due to immigration of predators from an 'outside location'.

Chapter four, part two, addresses functional response components of *Stethorus bifidus* as a part of its potential ability to regulate GSM populations. **Part one** looks at a subcomponent of the numerical response influencing predator abundance, namely, the reproductive response.

The reproductive response provides important information regarding a predator's potential to increase in numbers in various climatic regimes and geographic zones. This aspect of predator abundance is crucial to the estimation of a predators success in a given area and therefore its likely potential in regulating pest populations. The relationship investigated here, (*Stethorus bifidus* predatory on *Tetranychus lintearius*) is novel in that these two organisms are 'new' to one another, and the outcome of this interaction may hinge on the ability of the foreign organism, *Tetranychus lintearius* (GSM), to effectively out-reproduce the endemic predatory ladybird or vice versa.

Stone (1986) defined GSM development rate in relation to temperature. These data will be used in conjunction with the present work to compare the relative development rates of GSM and *S.bifidus* over a range of temperatures.

Several workers have recorded development duration of mites and coccinellids. Past work addressing mite development is summarized in **chapter two**. Variables driving coccinellid development and reproduction are summarized in **chapter three**.

This section represents an investigation into temperature as a factor regulating the development and oviposition in the coccinellid *S.bifidus*.

Materials and Methods

Development:

- Development rate in relation to temperature

Experiments were conducted in temperature controlled rooms set to 8.5, 12.5, 17.0, 21.0, 24.5, and 27.5°C under a fluorescent light (33 cool white cg instant start 40w) set to a 16L/8D photoperiod. NaCl was used to regulate relative humidity (Buxton & Mellanby 1934; Winston & Bates 1960). To ensure humidity regulation was maximized, air tight chambers were constructed from cardboard box ends connected with light framing timber, and then covered in clear plastic bags (drum liners). The dimensions of the chambers were 400mm x 450mm x 750mm. Relative humidity was kept between 65 and 80% at all times using this method. Humidity was recorded from humidity dials every 12 hours and a hygrothermograph was rotated throughout the temperature control rooms to check the extent of humidity fluctuations.

Colonies of *T.lintearius* were reared (using the shoot culture technique) in preparation for *S.bifidus* development (Hill et al. 1989). Gorse shoots, 150mm long excluding the stalk, were kept alive in plastic capped test tubes which were pierced by a gorse stem. The apparatus was water-tight, allowing inspection of the shoot on its side under a dissecting microscope. The water in the test tubes was changed regularly to ensure the shoot did not deteriorate before termination of the experiment.

GSM colonies were initiated by introducing 100-200 adult and deutonymph mites onto each shoot. GSM colonies were placed in warmer temperatures to speed mite development or cooler temperatures to preserve initial populations, as appropriate.

GSM eggs for developmental trials were laid at the appropriate temperature except in cases where split temperature developmental regimes were employed (**note 1**).

Prior to egg laying, female test beetles were left for a 12 hour period at the appropriate temperature. This was a precaution taken to control for 'carry-over' effects from one temperature to another, ie. the influence of temperature on egg development before oviposition may be important.

Eggs were laid until enough were collected in one 12 hour period for use at that temperature (at 8.5 & 12.5°C this was not possible so eggs were collected over a longer time period and kept in chronological order). Eggs were either placed onto shoots or transferred to cells (**note 2**).

Each *Stethorus* egg was placed onto a shoot containing a full complement of GSM stages. This method of individual development (one predator/shoot) prevented confusing individual larvae of different ages and eliminated the possibility of intraspecific interaction/competition.

Six shoots were used at each temperature. After each group of six shoots was inoculated with a predator egg, observation followed every 12 hours (**note 3**). Development was followed for all preimaginal stages of *S.bifidus*, **see plate 8**.

Note 1 - At 8.5°C a split development technique (**McGregor 1989**) was used to speed data collection. This involved partial development of a given stage at 8.5°C then relocation to a warmer temperature (where expected development duration is already known) to complete development. To estimate the total time for development at 8.5°C the proportion of development that took place at 21°C was calculated (ie. 'h'). From this measure the proportion of development to take place at 8.5°C (ie. 1-h) and therefore the total time for development at 8.5°C could then be calculated. This method proved convenient though should be treated with caution. No indication of mortality (which is probably linked to the amount of time spent at a cold temperature) was found. Another source of error could include the time taken to adjust to the second temperature after being moved. Shifting individuals from 8.5°C to 21°C may be accompanied by a developmental response lag.

Surplus eggs were put into cells at the appropriate temperature and kept alive on GSM (eggs and larva for first instar, protonymph, deutonymph and adults for second to fourth instars). Mites were added periodically when required to prevent starvation. Although excess prey was not always provided for 'surplus larvae' (also reared individually) any effect on development duration proved negligible, **see table 1**. The cells used to raise these surplus larvae were identical to those used for first instar development at 8.5°C and in feeding experiments, **see plate 10**. The extra larvae were used as replacement individuals when larvae died on experimental shoots. In these cases development duration pertaining to shoots was only recorded after the replacement larva moulted and started feeding as the next instar on the shoot. Following preimaginal development adult beetles were sexed after emergence and a sample of females was mated at 20-22°C to check for viable offspring production.

- Development thresholds

Development thresholds were found by solving the development rate regression equations for temperature = 0.

Mortality:

The death of preimaginal *S.bifidus* was observed throughout experimentation so that general comments on the possible causes of death could be made.

Note 2 - Cells were used exclusively at 8.5°C for 1st instar larval development due to the very high mortality rate if left to hatch and feed on the shoot. McMurtry et al. (1974) type cells were modified as follows: 100mm x 100mm x 3mm perspex x 2, cell drilled had a 15mm diameter and ventilation holes on the bottom layer an 8mm diameter, (see plate 10).

Note 3 - Due to my positioning of *Stethorus* eggs on the gorse shoots the majority of larvae hatched in the vicinity (not more than ten body lengths away) of *T.lintearius* eggs. Whether this is a representation of what occurs in the field is not known, however, *S.bifidus* eggs found on potted plants were seen amongst GSM eggs (see plate 7).

PLATE 7: Beetle egg found amongst GSM eggs

Coccinellid egg $\approx 0.3\text{mm}$

Tetranychid egg $\approx 0.1\text{mm}$

(Magnification X 12)



PLATE 8: Development stages of *S.bifidus*
(Magnification X 50)

a- Egg; length \approx 0.3mm

b- 1st instar; length \approx 0.6mm

c- 2nd instar; length \approx 0.8mm



PLATE 8: cont..

(Magnification X 50)

d- 3rd instar; length \approx 1.2mm

e- 4th instar; length \approx 1.8mm

f- Pupa; length \approx 1.2mm



Oviposition:

Oviposition rate data in relation to temperature and GSM density was collected concurrently to feeding experimentation. Each female *S.bifidus* was given a predetermined GSM density at 6.5, 11.5, 15.5, 20.5, 24.5, 27.5 and 32.5 °C. These, unlike development experiments were checked every 24 hours. After 24 hours a visual count of eggs was made which was then rechecked by destructively searching the cell with a fine brush. Data relevant to feeding was also recorded **see Part two, section one**. These experiments were run in temperature control rooms. Humidity was not controlled but was monitored every 24 hours by checking both humidity dials and a continuous read out given by a hygrothermograph.

Field observation:

Field observations to investigate *S.bifidus* reproduction were made every three weeks from February through to October near Palmerston North. A visual search for beetles was conducted on arrival at a site. After finding a beetle(s), approximately 30cm of gorse either side of the beetle was cut from the bush. This was repeated until 4-6 beetles were located or until beetles were no longer found. The gorse cuttings, approximately 50-60cm in length, were taken to the laboratory where a close inspection was made of each cutting under a microscope. A record of all mites seen was made along with a note of both GSM and *S.bifidus* preimaginal and mature stages. All *S.bifidus* adults were sexed. Due to the method of locating beetles; namely finding GSM colonies first, samples always contained gorse spider mites.

GSM establishment success in relation to temperature:

Here a possible relationship between the average annual air temperatures (throughout NZ.) and GSM establishment success was investigated. Air temperatures were obtained from a map drawn by department of Lands and Surveys and published by N.Z. Meteorological Service, Miscellaneous Publication 175, Part 4(v), Edition 1 1985), **see appendix 1**. The failure/success locations recorded by Hill et al. (1991) were matched to the annual average temperature nearest to each site. Each temperature was given a tally of successes and failures. From these a percentage establishment

success at each temperature was calculated.

Temperature under spider mite webbing:

To estimate the actual temperature experienced by gorse spider mite colonies at each site a temperature probe was placed inside a 'tent' of webbing. This experiment was run in Palmerston North on three year old potted gorse plants approx 1.5m high. Probes measured less than 5mm across and were connected to a data logger. Three probes were used. One was placed in an exposed position above gorse plants. The second was attached to a gorse bush at approximately the same orientation and height as that of the test probe. The test probe was placed beneath well-established GSM webbing approximately 1 meter from the ground, **see plate 9**. Measurements were taken from 11am till 10:30pm.

Results

Development: - Development rate in relation to temperature

Development data (from eggs to the 4th instar) in cells and on shoots over all temperatures tested were compared. To retain an overall (experiment-wise) error rate = 0.05, individual tests were adjusted by the Bonferroni procedure, **see Appendix four**. Thus, because there were five shoot/cell comparisons, the error rate was set at $\alpha=0.05/5 = 0.01$. Using this criterion, none of the shoot vs cell comparisons was significant (**table 1**).

Table 1: A comparison of development rates of *S.bifidus* in cells and on shoots

Stage	F	df.	p
egg	3.8208	1, 135	.05269
1st	0.2477	1, 95	.61984
2nd	6.5173	1, 67	.01297
3rd	0.2040	1, 60	.65317
4th	0.2930	1, 46	.59092

PLATE 9: Probe used to measure temperature under GSM web



The data from development experiments are summarized in **Figure 1**. Development of *S.bifidus* is approximated by a linearly relationship with temperature between 8.5 and 27.5°C. For development rate of individual instars in relation to temperature **see figure 1a** and for total development rate in relation to temperature **see figure 1b**.

An analysis of co-variance was run to test the null hypothesis that there is no difference between the slopes of development rate curves for feeding stages (1st - 4th instar). The null hypothesis can not be rejected ($F = 1.94$, $p = 0.312$, $df. = 5, 291$).

Total development time was calculated by summing the average time to develop for each instar, at each of the temperatures tested. Note that this estimate of total development time differs from that which would be obtained by summing development times for each individual beetle. The latter method was not possible because at some temperatures specific individuals were not followed throughout their entire development.

- Development thresholds

The threshold temperatures for development of each coccinellid stage (estimated by solving the regression equations for temperature with development rate = 0) are shown in Table 3. Theoretical thresholds for the development of *S.bifidus* lie between 9.2°C (3rd instar) and 11.4°C (4th instar).

Table 2: Threshold temperatures for development of *S.bifidus*

Stage	Threshold temperature °C
egg	9.5
1st instar	9.7
2nd	10.3
3rd	9.2
4th	11.4
pupa	8.8

FIGURE 1A: Development rate of *S.bifidus* in relation to temperature (eggs, instars 1 - 4 and pupa)

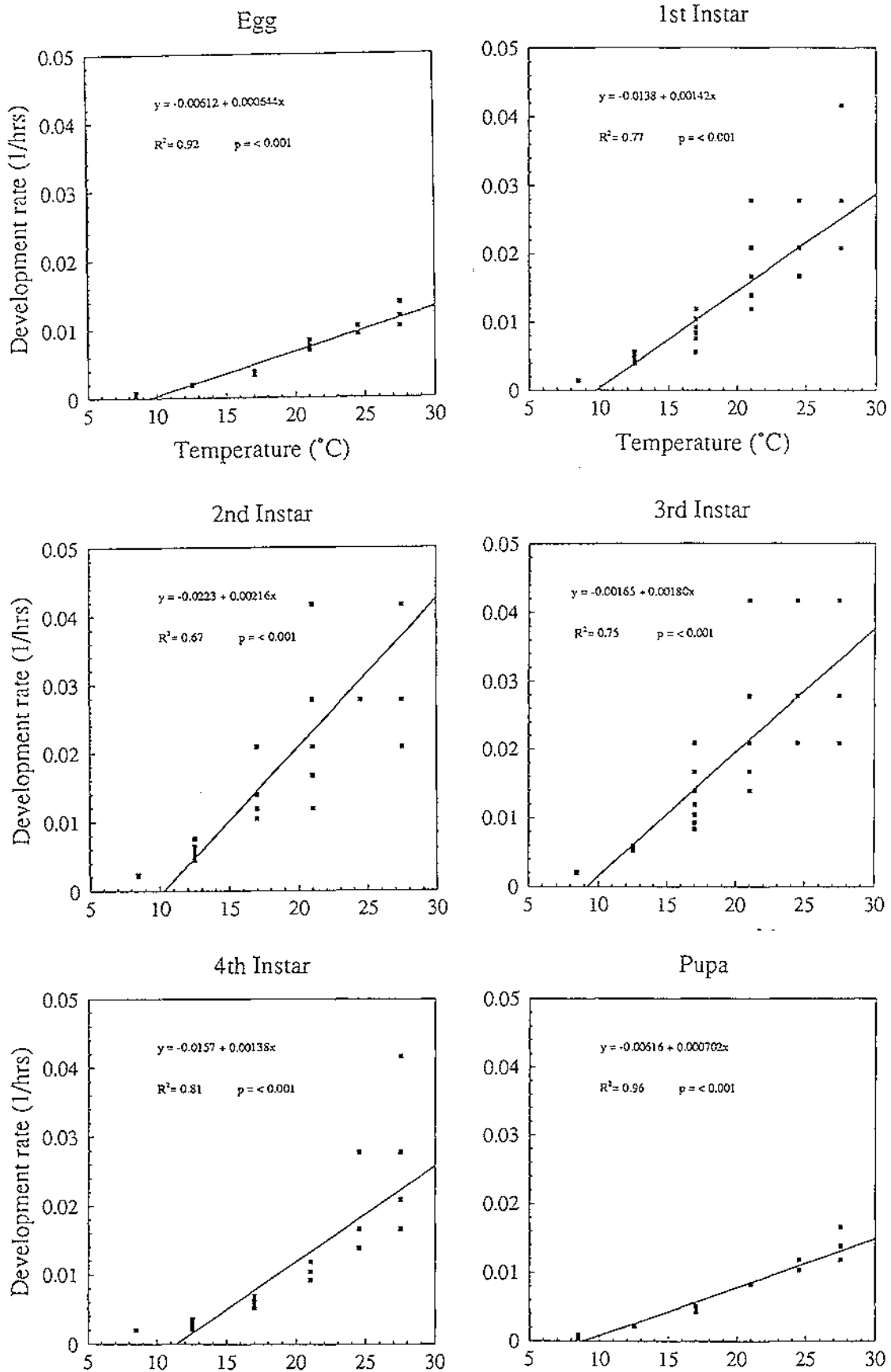
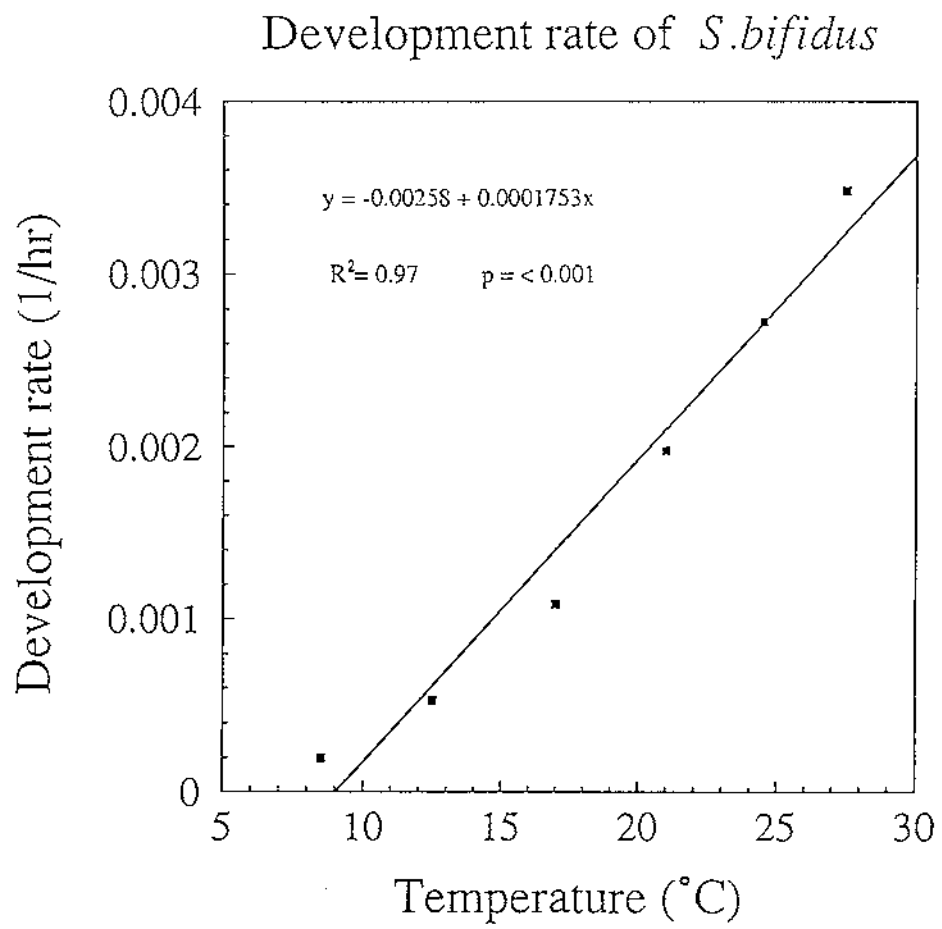


FIGURE 1B: Total development rate of *Stethorus bifidus* in relation to temperature



Mortality:

Mortality of preimaginal *S.bifidus* was observed on shoots and in cells. Because experiments were not designed to determine mortality itself the findings are presented only as possible trends.

Mortality appeared to be higher on shoots as opposed to cells which may be due to webbing as an interference in the former situation and not the latter. Mortality also appeared to increase as temperature decreased. This may be due to the inactivity of early instars at cold temperatures (8.5 & 12.5°C).

Oviposition:

Oviposition significantly declined with decreasing temperature and egg laying ceased at 6.5°C. The number of eggs laid was independent of prey density **figure 2a**. Therefore total oviposition in relation to temperature was calculated by taking the average number of eggs laid at each temperature over the densities tested, **see figure 2b**.

Field observation:

Field observations are summarised in **appendix 2**. Larvae (second and third instar) were found on the 1/5/92 and an emerging adult was found on the 24/5. No immature stages were found after these dates. During late August, September and early October persistent rainfall (approx 63 out of 66 days had some rain) appeared to drastically reduce gorse spider mite abundance and clumping. Very few mites were found from the first week of September through until the middle of October. Although during this time no large GSM populations ($\approx >200$) were found, some old webbing was seen and collected. Many colonies were dead with individuals gummed together, perhaps trapped by the water tension as they became wet. Subsequent escape would appear impossible if rain is persistent. R.Hill (pers comm.) noted how GSM that are temporarily wet can escape when dried. Finding mites in the field after rain was always more difficult due to lack of visible webbing. This prevented the monitoring of *S.bifidus* reproductive activity during spring as they also were extremely hard to find.

FIGURE 2A: Oviposition of *Stethorus bifidus* in relation to GSM density between 11.5°C and 32.5 C

At all temperatures except 15.5°C the sample size (female *S.bifidus*) at each density was 16. At 15.5°C 32 females were measured for egg production at each prey density

Standard errors are plotted at 95% confidence intervals

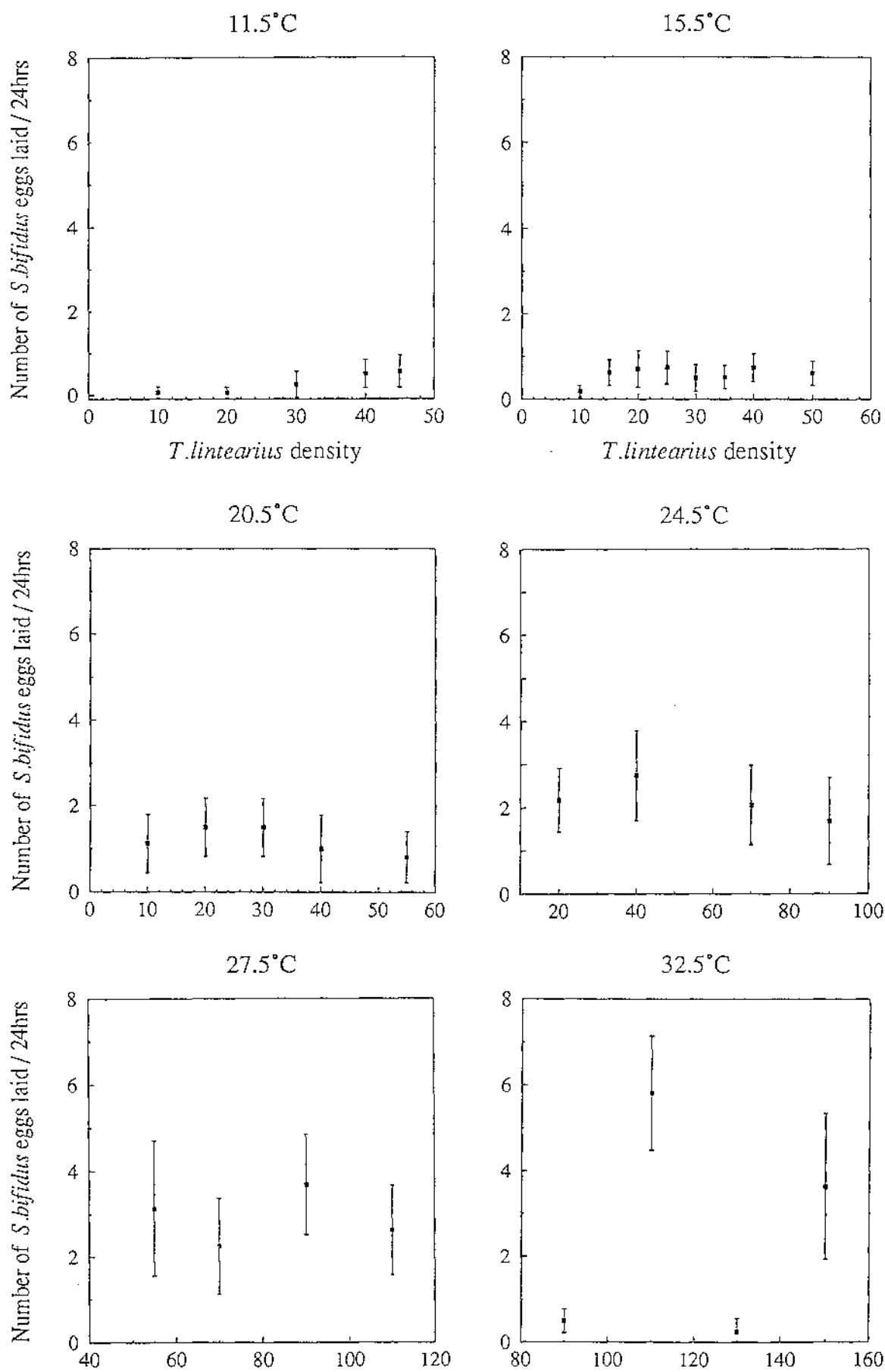
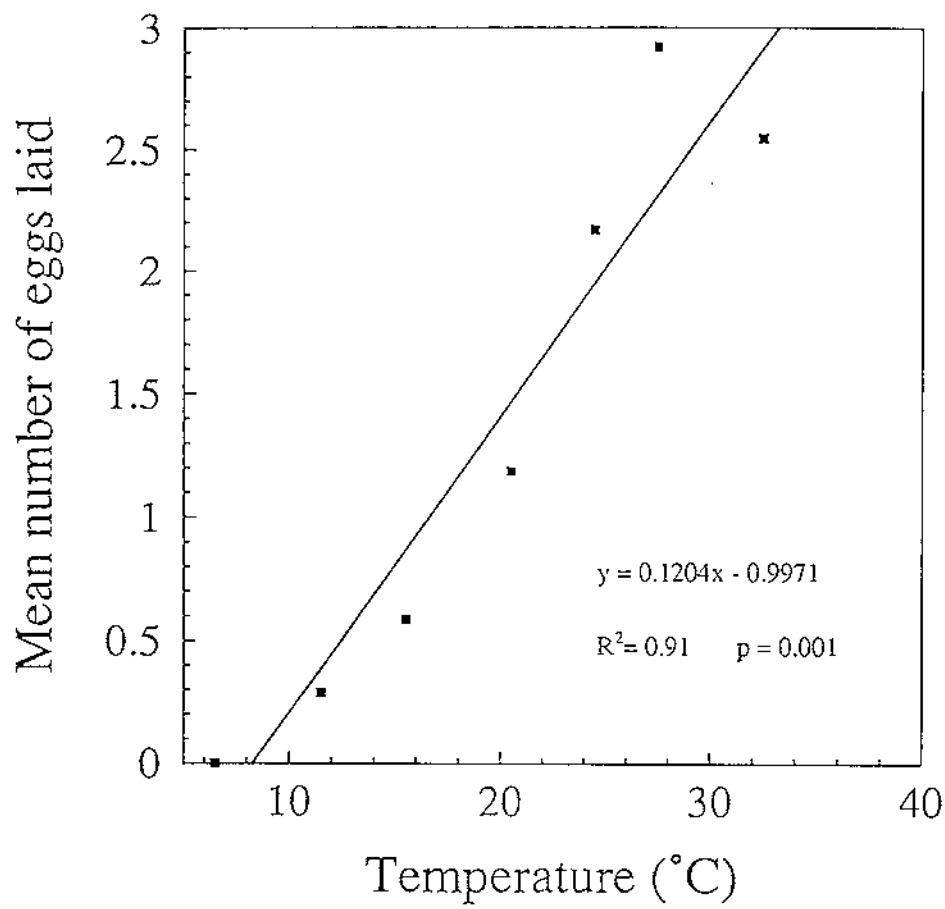


FIGURE 2B: Oviposition of *Stethorus bifidus* in relation to temperature

Oviposition of *S.bifidus* in relation to temperature



Although the start of reproduction was not seen it is estimated that *S.bifidus* would start to lay between mid and late September in Palmerston North. Observation of laboratory reared beetles on potted plants outside the laboratory confirms this estimate.

T.lintearius populations found prior to the August-October wet weather were found in all stages while *S.bifidus* probably ceased ovipositing early in May. Adult coccinellids were found in GSM colonies throughout the field observation and appeared to continue feeding. Other species found included *Phytoseiulus persimilis* which was collected on nearly every occasion before the rains in August. *Anystis baccharium* (whirling mite), *Bellodes viveti* (snout mite) and *Eupodidae* mites were among the other invertebrates found on gorse samples.

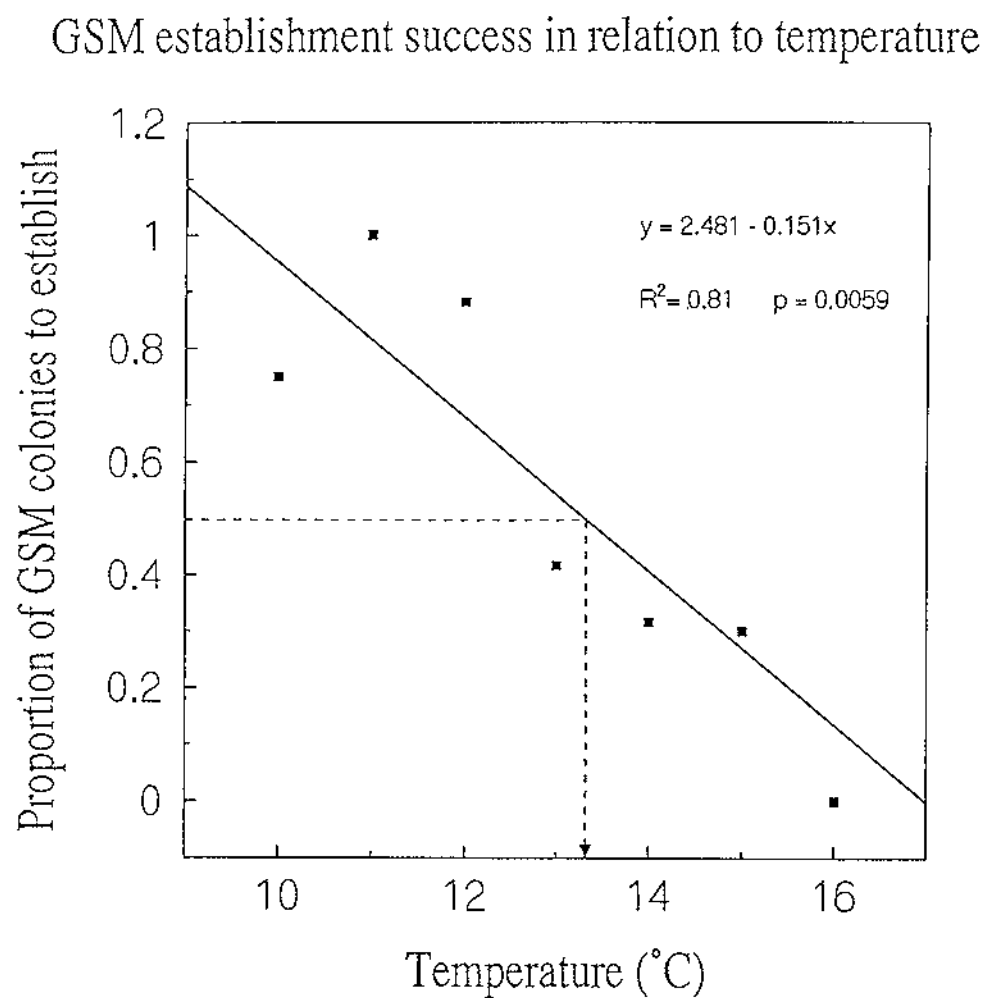
GSM establishment success in relation to temperature:

Table 3 displays temperature in relation to the percentage establishment success of GSM. The proportion of successful mite establishment at each temperature is plotted in **figure 3**.

Table 3: GSM establishment success in relation to temperature data obtained from the N.Z. Meteorological Service (see methods).

Temperature (°C)	No. of successes	No. of failures	% success
10	3	1	75
11	1	0	100
12	15	2	88
13	5	7	42
14	6	13	32
15	3	7	30
16	0	1	0

From **figure 3** at $\approx 13.5^{\circ}\text{C}$ 50% of GSM colonies establish successfully.

FIGURE 3: GSM establishment success in relation to temperature

Temperature under spider mite webbing:

Temperature under webbing reached a maximum of 11°C greater than the equivalent temperature outside the webbing. On average between 11am and 1pm in direct sunlight, temperature was 4°C greater inside webbing than outside. In shadow, this difference decreased to about 1-2°C (Appendix 3). Not surprisingly, temperatures were similar in the two positions at night and in the late afternoon, **see figure 4a**.

Figure 4b gives the regression for temperature under web in relation to temperature on gorse. As the ambient temperature rises the increase in temperature under the web is approximated by a log relationship: $\log(10)y = 0.6901 + 0.0324x$.

Discussion

Experiments were undertaken to determine how development and oviposition vary with temperature along with other indicators of the numerical response i.e. development thresholds, mortality and actual thermal microclimate in the field. In the lab temperature was controlled through the use of temperature control rooms and humidity was regulated with saturated salt solutions. Humidity suitable for *Stethorus* development is not strictly defined though values close to 79% relative humidity appear satisfactory (Putman 1955). Stone (1986) suggests a relative humidity of 70% for GSM development.

Thermal requirements for the development of *S.bifidus*:

Development rates of all stages of *S.bifidus* are adequately predicted by the linear model found between 8.5°C and 27.5°C. Development however did continue at 8.5°C despite the estimates for development thresholds being above this value. This suggests that at lower temperatures either the non-linear nature of the curve is borne out or the method used at 8.5°C has some significant errors **see note 1, page 47**. Development thresholds estimated from development rate linear regressions altered between stages of *S.bifidus* and ranged between 9.2°C and 11.4°C.

Mortality observation suggests that early instars of *S.bifidus* may be more likely to die if reared on shoots as opposed to rearing in cells. The observation that death in

FIGURE 4A: Effect of GSM webbing on temperature

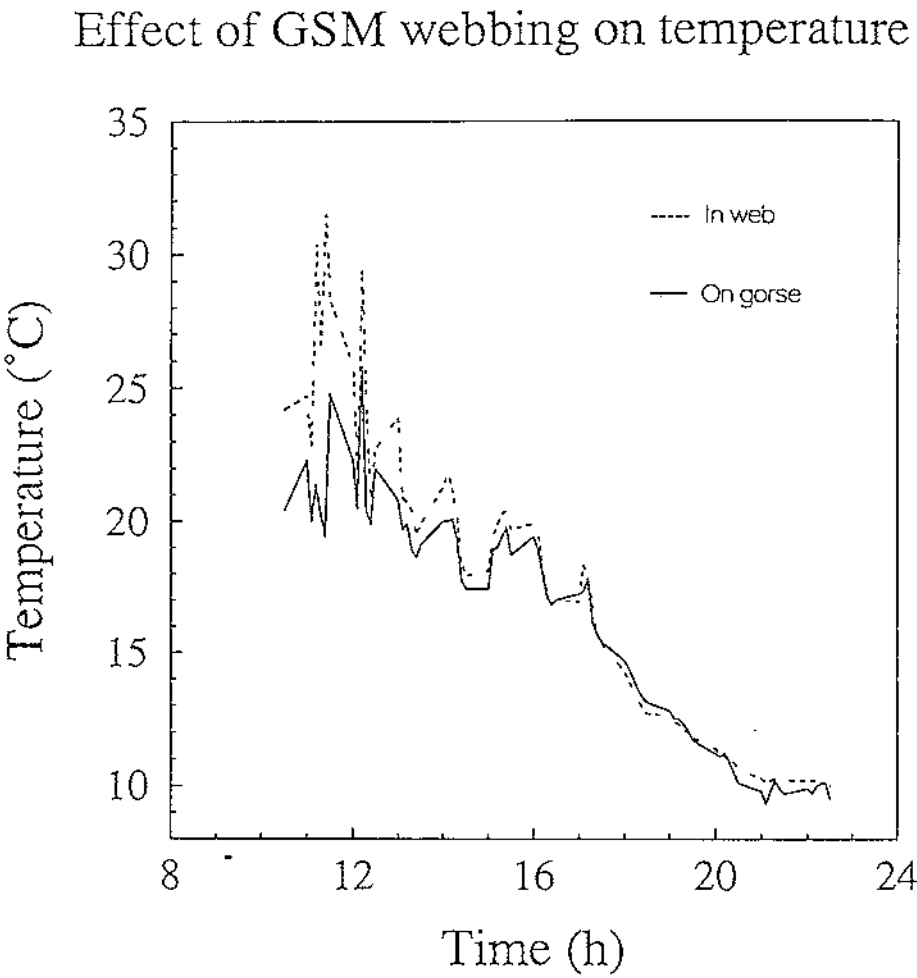
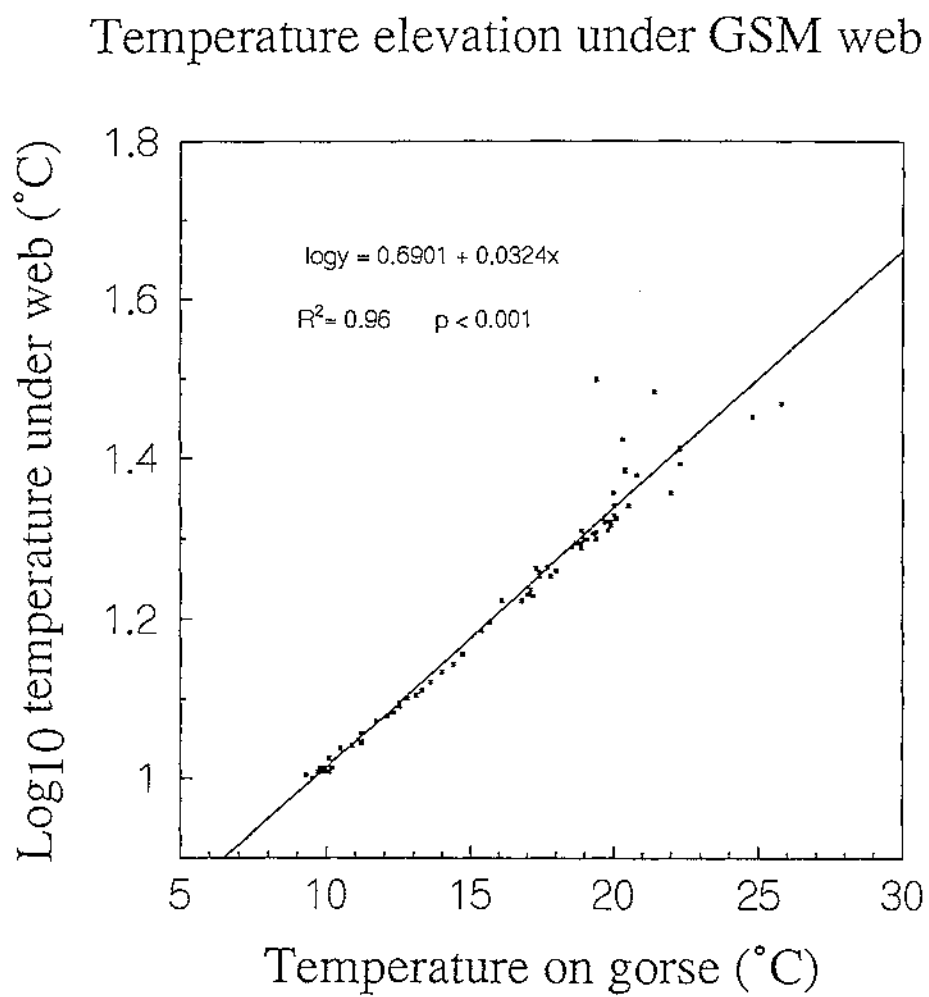


FIGURE 4B: Temperature under GSM web in relation to temperature on gorse



most cases occurred while larvae were tangled in webbing, suggests the cell environment was perhaps favourable to larvae development due to the absence of large amounts of web which was seen to restrict movement. It appears that *S.bifidus* larvae may also have a reduced chance of survival as temperature decreases. 1st instar larvae which are supposedly already vulnerable to becoming tangled in web due to their small size ($\approx 0.6\text{mm}$). The observation that low temperature appeared to increase the risk of death in 1st instar larvae especially, may be due to the increased duration of an already vulnerable stage.

Mortality observation were made systematically during development experiments and were not part of an experiment designed to investigate mortality. These findings should be interpreted cautiously and are only included to illustrate trends that became obvious as the work proceeded. Further work needs to be continued in this area to determine the extent of larval mortality in *S.bifidus* when exposed to various factors in isolation.

Oviposition data suggest there is no significant relationship between GSM density and *S.bifidus* oviposition at any of the temperatures tested. Collyer (1964) has collected data opposing this view. It needs to be noted here that the range of GSM densities tested is restricted and possibly bias to higher GSM densities. It is suggested by Hassell (1977; see part 2: section one - introduction) that results describing the outcome of predation in simple arenas with only large preferred prey present give a false indication of a predator/prey interaction. ie. the same amount of food supplied in an arena may be many times harder to secure in the field. If this is the case then relationships such as that between prey density and oviposition may be largely misunderstood. Accordingly data collected here implying that oviposition is not dependent on prey density should be treated with reservation. **Figure 2b** demonstrates the relationship between temperature and oviposition over the range of temperatures tested.

Field observations suggest GSM reproduce throughout the winter in Palmerston North whereas the last preimaginal stages of *S.bifidus* were found late in May.

Findings from investigation into actual temperatures under GSM web (see figure 4a)

suggest that ambient air temperatures underestimate the actual thermal environment in which the mites and their predators are developing. The estimated ambient temperature value of 13.5°C at which 50% of GSM colonies have established (see figure 3) should be adjusted accordingly. The limited data collected mean that this correction for temperature can only be a rough estimate.

Summary

The development rate of *Stethorus bifidus* (Kapur) was determined over a range of temperatures from 8.5°C - 27.5°C. Gorse spider mites, *Tetranychus lintearius* (Dufour), were available in all stages in excess of *Stethorus* larval development requirements. The development stage of each individual of *S.bifidus* was recorded every twelve hours. Development rate increased with temperature showing no apparent reduction over the range of temperatures tested. Relative development rates of *T.lintearius* (GSM) and *S.bifidus* in relation to temperature suggest that *T.lintearius* is adapted to a cooler climate than *T.lintearius*. This has important implications in relation to the predator/prey relationship existing under various thermal regimes.

Conclusion

- Development of all stages of *S.bifidus* is approximated by a linear relationship with temperature from 8.5°C to 27.5°C.
- Development thresholds for each instar lay between 9.2°C and 11.4°C from linear regression extrapolation.
- Mortality of *S.bifidus* appeared to occur more often in early instars at cool temperatures and on shoots as opposed to cells.
- Prey availability had no significant influence on the oviposition rate of *S.bifidus* between 11.5°C and 32.5°C.
- Field observation suggests that *S.bifidus* reproduction stops late in May at Palmerston North while GSM reproduction continues throughout the winter.

- Data indicate that the thermal environment under GSM webbing varies from ambient at night up to 11°C above ambient in direct sunlight. A probable mean temperature elevation of 1-2°C/ 24hrs is predicted.

CHAPTER FOUR: THE PREDATORY ABILITY OF *Stethorus bifidus*

Part two - Components of the functional response

General introduction

Putman (1955) and Hull (1974; cited in Hull et al. 1976) have both commented on the importance of temperature as a variable determining the feeding ability of coccinellids and on the importance of prey density in driving the functional response. Shipp (1991) states that 'the response of a predator is a complex series of events involving the length of time that a prey is exposed to the predator, the rate of successful attack and the handling time required for each prey by the predator.'

The following work includes consideration of both temperature and GSM density in relation to feeding by *S.bifidus*. Relevant background material is summarized in **chapter three**.

Putman (1955) states that 'where two-spotted mites occurred the populations were most susceptible to attack by predators at the beginning of the season where the dense localized populations were present.' A combination of results from **section one** and **two** of this chapter provides reasons why predators respond to prey in this way. The first section addresses the direct relationship between temperature and prey consumption. The second section involves an indirect relationship between prey density and feeding rate.

SECTION ONE - Feeding rate of *Stethorus bifidus*

Introduction

Two ways in which a predator can respond to prey density are functionally and numerically. Part one of this chapter addresses the numerical response. Here I am primarily concerned with the functional response. It is customary to divide functional responses into one of three types defined by Holling (1959a; cited in Hassell et al. 1977). Type one describes a linear increase in feeding with prey density, type two a feeding rate that increases at a decreasing rate to some maximum value in relation to prey density and the type three or sigmoid shaped curve where feeding rises at an increasing rate over a certain range of prey densities. It has been noted that the importance of distinguishing between type 2 and type 3 functional responses rests on their different contributions to stability (Holling 1959a, cited in Hassell et al. 1977; Murdoch & Oaten 1975). Sigmoid functional responses infer density dependent feeding over given prey densities whereas the type 2 functional response cannot contribute to the stability of a predator-prey interaction (Hassell et al. 1977). Here I discuss experiments designed firstly to investigate the effects of temperature on maximum consumption rate by *S.bifidus*; and secondly to determine whether *S.bifidus*' functional response has characteristics necessary for effective regulation of GSM populations.

Difficulty was experienced when distinguishing between the type 2 and type 3 curve by simple curve fitting techniques. Trexler et al. (1988) showed that standard curve fitting procedures cannot reliably distinguish between type 2 and type 3 functional response curves. Hassell (1977) demonstrated how the shape of the functional response curves in many cases may be an artifact of experimental design. Hassell et al. (1977) states that 'the normal practice of doing experiments in relatively small, simple laboratory universes using large preferred prey may have produced a very distorted picture of the full range of behaviour which invertebrate predators are capable of showing. If the arena complexity is increased or predators are presented with small unpreferred prey often type three functional response curves result when earlier type two curves were found. Hull et al. (1977a), with *S.punctum*, has demonstrated that functional response curves may not only vary between life stages but also between the sexes. The complexities when analysing functional response

data for predictions in the field are numerous. For these reasons another method to test for density dependent feeding was incorporated. The prerequisites implicit in the disc equation include the assumption that handling time is constant at any one temperature and independent of prey density, Hassell (1976a). In **section two** an attempt is made to demonstrate that handling time is density dependent therefore suggesting that a type two functional response as defined by the disc equation is unlikely to describe the feeding relationship between *S.bifidus* and GSM (Collins et al. 1981).

This section will focus on the ability of *S.bifidus* to consume mites under laboratory conditions in relation to temperature. According to Chazeau (1974) the prey consumption rate of *Stethorus madecassus* doubled with each 5°C temperature rise between 20°C and 30°C. A similar interpretation of consumption rate will be given in this work providing relative values of *S.bifidus* feeding throughout the country. Oviposition in relation to temperature and prey density will also be measured.

Materials and Methods

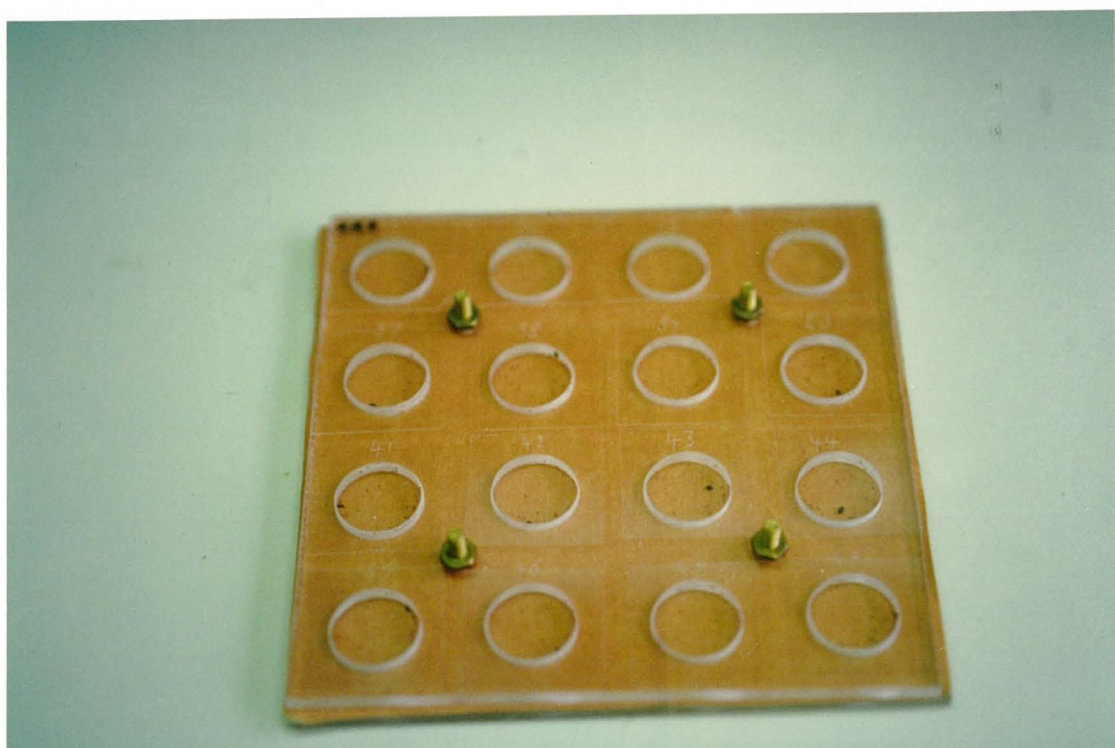
S.bifidus adults were collected from the Levin Horticultural Research Centre at Shannon and from a GSM release site on the outskirts of Palmerston North. The generation or age of these beetles was not determined.

40 beetles were split into two groups, 16 females and 4 males in each group. Only ovipositing females were used in this experiment for two reasons. Firstly they represent the stage and sex of *Stethorus* species that has the highest consumption rate (Putman 1955), and secondly oviposition performance was to be measured.

'Cell pads' were used for feeding/oviposition tests, **see plate 10**. Dimensions were modified from McMurtry et al. (1974), as follows: 2 squares of perspex 100 x 100mm x 3mm x 2, cells drilled were 15mm in diameter, ventilation holes had an 8mm diameter, perspex sheets were separated by builders paper to allow for air circulation in the cells.

Mites were taken from colonies reared in the laboratory or collected from the field.

PLATE 10: 'Cell pad' used for feeding experiments (beetles and mites included)



They were brushed from gorse spines or webbing onto a white tray, and placed into cells. When cells had been filled with the appropriate number of mites the number was re-checked. Most mites were adults but some deutonymphs were also used.

After the 16 test cells and one control cell were prepared the female beetles were taken from their 'resting containers' (**see note 5**) and one female placed into each cell other than the control.

All feeding/oviposition experiments were conducted in the 'walk in' temperature control rooms where humidity was monitored. DSIR Plant Protection, Palmerston North, (changed to CRI Landcare in 1992-1993).

After 24 hours cells were checked for eggs laid and mites still alive. Both these measurements were recorded (Oviposition rate in relation to GSM density is analyzed in **Chapter one, part one**). Every 24 hours the alternate group of 16 adult females were tested at a predetermined mite density and temperature. All beetles were given at least 24 hours to readjust to a new temperature before feeding data were collected. No adjustment or habituation period to prey density was allowed, however beetles were not starved and were assumed to be at a similar hunger level at each test, **see note 6**. This procedure was carried out at 6.5, 11.5, 15.5, 20.5, 24.5, 27.5, 32.5°C under a 16L:8D photoperiod.

Each 'pad' of 16 test cells was paralleled by one control cell where mites alive after 24 hours were also counted. Two identical cell pads were used side by side in temperature rooms. One contained the 16 beetles + mites, the other cell pad one control with mites only. To compensate for a lack of control data a model was fitted to the control data over all temperatures and densities. This model was derived using a stepwise multiple regression.

Note 5 - Rest containers were 500g vegemite jars (plastic) topped with fine netting. These containers each contained a gorse shoot, gorse spider mites and two male coccinellids. The 'rest day' (24 hours) was used in an attempt to bring beetles to a standard hunger level. Although two groups of 16 females were used on alternate days for testing, during rest days each group of 16 was again split into two groups of 8 to reduce crowding in rest containers. Males were shared accordingly.

The best fit to the pooled control data is given by:

$$^*Control\ mortality = .134036(D) - .262118(T) + .016828(T^2)$$

R = 95.4% p = < 0.001 D = mite density T = temperature (°C)

The formula below was used to calculate the number of mites eaten by *S.bifidus* after correction for control mortality at each temperature and GSM density:

Number eaten = Initial density - number dead - control mortality.*

These values are plotted in relation to GSM density at each temperature, **see figure 5a.**

To approximate maximum consumption by *S.bifidus* the highest value at each temperature was used. Effectively, this data point at each temperature is a best estimate of maximum consumption (without fitting a functional response curve) regardless of prey density.

During these experiments it was assumed that all mites were available to the beetle in the arena at all times. Several experiments showed this to be the case when the maximum number of mites were killed.

Note 6 - To standardize food quantity in the 'rest container' frequent observation to determine GSM numbers was made. GSM were maintained at between 50 and 100 adults and deutonymphs. This method required a more frequent prey addition to 'resting' beetles at higher temperatures. One advantage of this method over starvation is pointed out by Houck (1991) who noted that starved beetles may kill less mites due to a more complex extraction of contents from prey caught. With this in mind the procedure above was used so that no beetle tested was starved. This ensured beetles would not 'hold' mites for long periods giving an underestimate of their potential to 'kill' prey. Another advantage related to standardization of hunger levels over a wide range of temperatures is illustrated by the following example. Mites starved for similar periods of time both at 8.5°C and 32.5°C will be at very different hunger levels when finally presented with prey.

Results

See figure 5a for *S.bifidus* feeding rate data in relation to GSM density and figure 5b for feeding rate in relation to temperature. In these plots and in the estimate of control mortality data measured at 32.5°C was omitted. The number of mites dying in the absence of a predator at this temperature was extremely high and seen as an artifact of the experimental design. New Zealand's climate rarely has temperatures over 30°C for more than very short time periods. It is of interest however that no *Stethorus* deaths were recorded at 32.5°C. Humidity was not controlled in feeding rate experiments though recordings were taken, see table 5c.

Maximum feeding values in table 5b were taken from figure 5a as an estimate of maximum consumption at each temperature.

Table 5b: Maximum feeding rate of *S.bifidus* in relation to temperature

Temperature (°C)	Max no. of mites consumed/24hrs
6.5	4.52
11.5	11.30
15.5	12.18
20.5	25.94
24.5	40.38
27.5	52.80

Table 5c: Relative humidity measured at each temperature

Temperature (°C)	Relative humidity
5-8	75-85%
10-13	75-85%
14-17	45-60%
19-22	45-55%
23-26	40-60%
26-29	40-60%
31-34	40-55%

FIGURE 5A: Consumption by *Stethorus bifidus* in relation to GSM density at 6.5, 11.5, 15.5, 20.5, 24.5, and 27.5°C

Standard errors are plotted at 95% confidence intervals

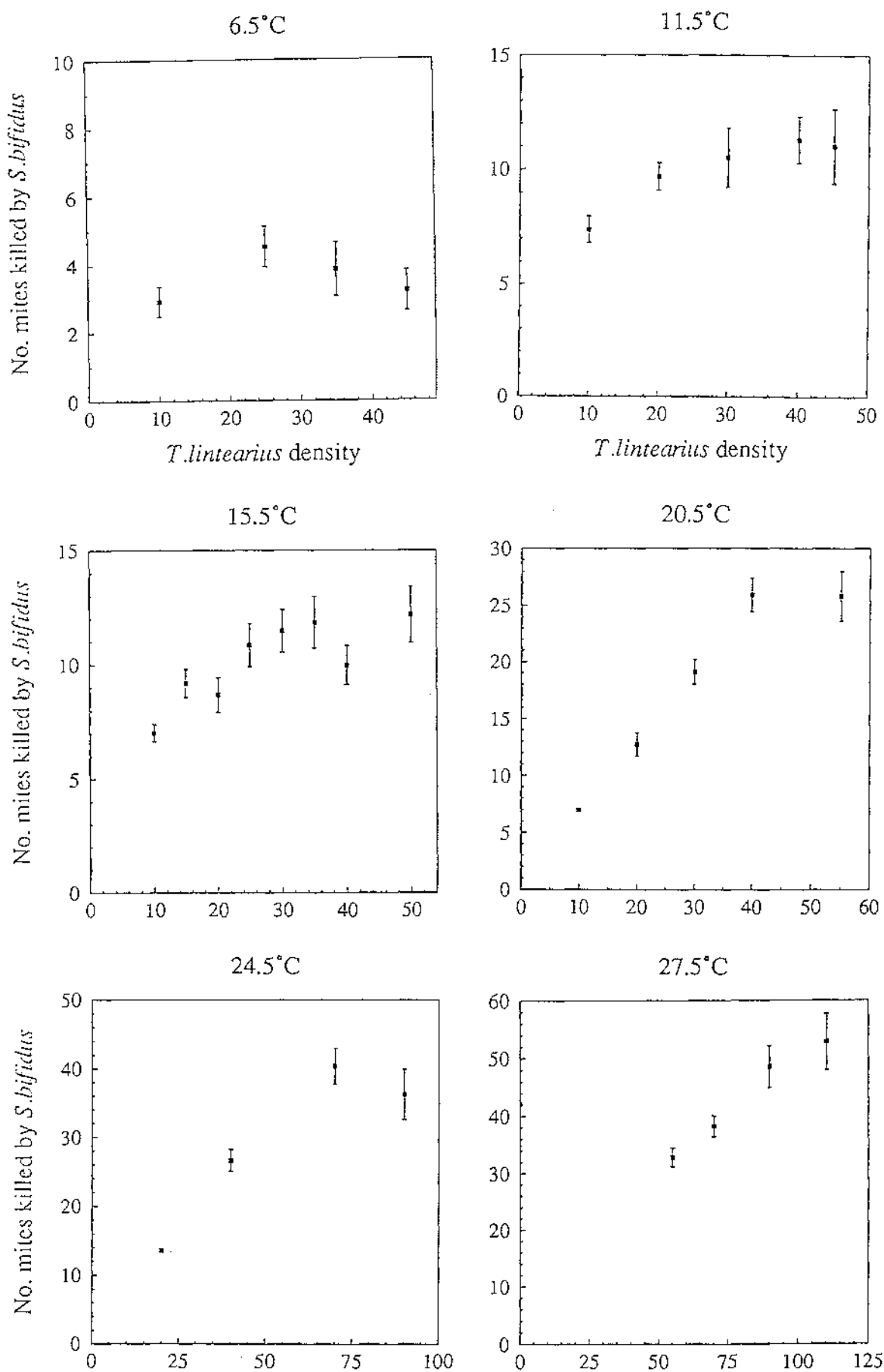
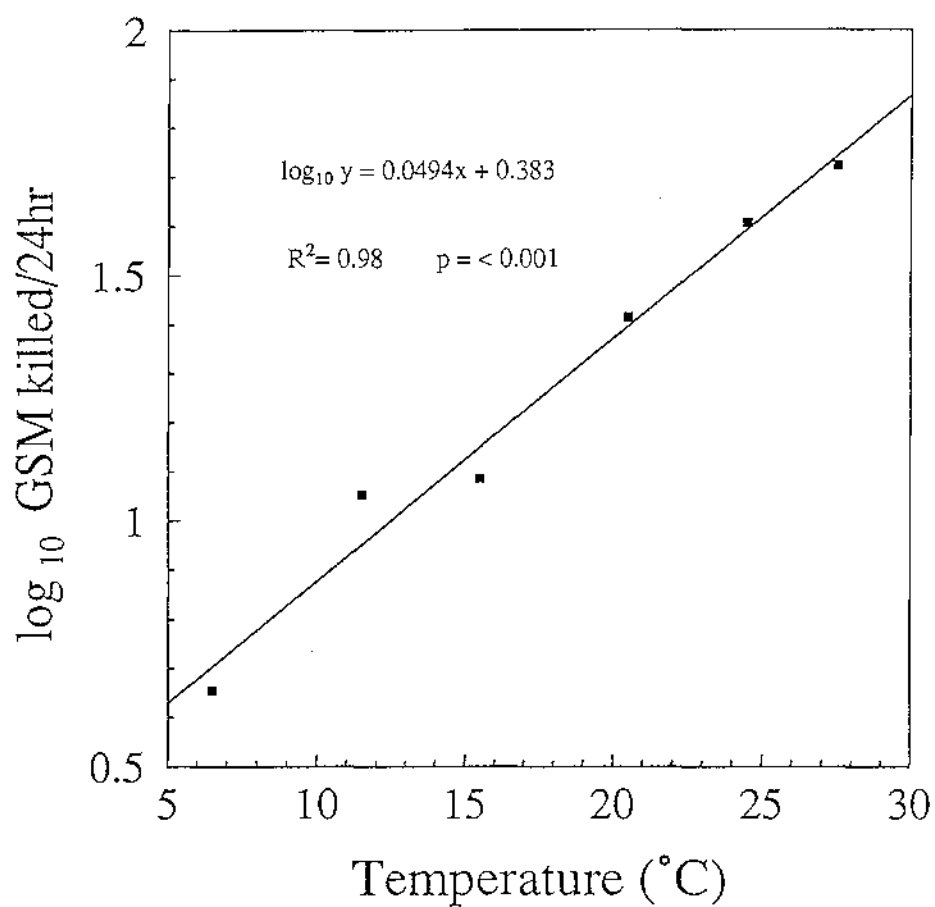


FIGURE 5B: Maximum consumption of GSM by *Stethorus bifidus* in relation to temperature

\log_{10} GSM killed by *S.bifidus* in relation to temperature



Discussion

Using *T.lin-tearius* as prey, the feeding rate of *S.bifidus* in relation to temperature was determined. Consumption rate in relation to temperature increased in an exponential fashion. In fact, even at high temperatures not characteristic of New Zealand, no reduction in the consumption rate of *S.bifidus* was recorded. Results suggest that the efficiency of *S.bifidus*, in terms of GSM consumption rate, will increase in warmer areas of the country. However in terms of *T.lin-tearius* survival the experimental parameters were unrealistic. This was demonstrated by a large increase in GSM 'control' mortality with increasing temperature. R.Hill (pers. comm.) also commented that gorse spider mites will not survive high temperatures for any length of time.

Summary

Consumption rates of *Stethorus bifidus* feeding on *Tetranychus lin-tearius* were measured under a 16L:8D photoperiod at 6.5, 11.5, 15.5, 20.5, 24.5, 27.5, and 32.5°C. Consumption at each temperature was measured at several mite densities. The number of mites eaten per unit time was a non-linear function of the number available; and maximum consumption rate was a non-linear function of temperature.

Conclusion

- Consumption by *S.bifidus* over a range of GSM densities was tested.
- GSM consumption by *S.bifidus* was plotted in relation to temperature using estimates of maximum consumption at each temperature independent of prey density.
- The ability of *S.bifidus* to consume *T.lin-tearius* in relation to temperature increases in a non-linear fashion approximated by: $\log(10)y = 0.0494x + 0.383$
- Although functional response analysis was not included in this work, prey consumption is definitely related to prey density. This will be investigated further in the following section.

SECTION TWO - Handling time

Introduction

Time and resource partitioning by *S.punctum* has been examined by Houck (1991) who recognized that starved coccinellids increased their handling time of each prey item.

Predator prey relationships are often discussed in relation to the Holling (1959b) disc equation. This model incorporates two non-concurrent variables of predation; attack rate and handling time. This section investigates handling time variation by *S.bifidus* feeding on *T.lintearius*.

Methods and Materials

Female *S.bifidus* were taken from a mixed population of adults collected from apple trees, gorse and laboratory reared stocks. Individuals had either recently been found in the field feeding on gorse spider mites or had been exposed exclusively to gorse spider mites over a period of six months in the laboratory. It was assumed that the predatory behaviour of *S.bifidus* would not be influenced by previous nutritive events.

Prior to each experiment, 15 females beetles were removed from the mixed population containing 29 males and 30 females of different ages. Modified McMurtry et al. (1974) cells (described earlier for feeding experiments) were filled with the appropriate number of adult gorse spider mites before beetles were added. The cell pad, accommodating predators and prey, was then placed into a constant temperature at $20.5 \pm 1.5^{\circ}\text{C}$. A relative humidity ranging from 65-75% was maintained using humidity chambers described earlier. The 15 replicates were accompanied by one control cell to check that the prey density supplied was the actual prey density available. Prey was replenished every 12 hours. This involved removing beetles from old cells and placing into new cells containing the same prey density.

Recording commenced after 72 hours of preconditioning. The importance of this conditioning period has been shown by Eveliegh & Chant (1981) working with *P.persimilis*.

After 72 hours the beetles were (as usual) moved into cells stocked with GSM at the appropriate density and the time for each beetle to 'consume' its first mite was recorded. Recording started only after the mite was secured by the beetle (**see plate 11a**). Long pursuits or grapplings were not included in the measure of handling time. In situations where mites released prey, to subsequently re-secure, timing was adjusted accordingly. The number of encounters preceding prey capture was not recorded but trends became apparent from observation at several densities. Each beetle was recorded twice, once after 72 hours and then again after 84 hours. The mean handling time was then calculated for each beetle and treated as a single data point. This procedure was repeated for each of the five prey densities.

A measure of body contents extracted from gorse spider mites by the beetles was taken at all prey densities. After captured mites were discarded, the remains were given a score of either 1,2 or 3, (the index of extraction), **see plate 11b**.

The scores used above equate to the following definitions.

- 1 = very slight feeding sometimes allowing prey to move off (later to die)
- 2 = approx 1/2 of the body contents removed leaving the mite dead
- 3 = extensive extraction of body contents leaving only the exuviae which in extreme cases had a chalky appearance.

These scores were added and a mean extraction/beetle was calculated providing a relative estimate of contents removed at each prey density **see Table 5**.

PLATE 11:

a- *S.bifidus* feeding having secured an adult GSM
(Magnification X 50)

**b- Three GSM corpses left by beetles that were (from left to right) starved
to satiated**
(Magnification X 70)



Results

Table 5 shows the relationship between GSM density and the index of extraction.

Table 5: Indices of extraction

GSM density	Index of Extraction
3	2.78
5	2.37
10	2.10
18	1.67
25	1.17

See **Figure 6** for *S.bifidus* handling time in relation to GSM density.

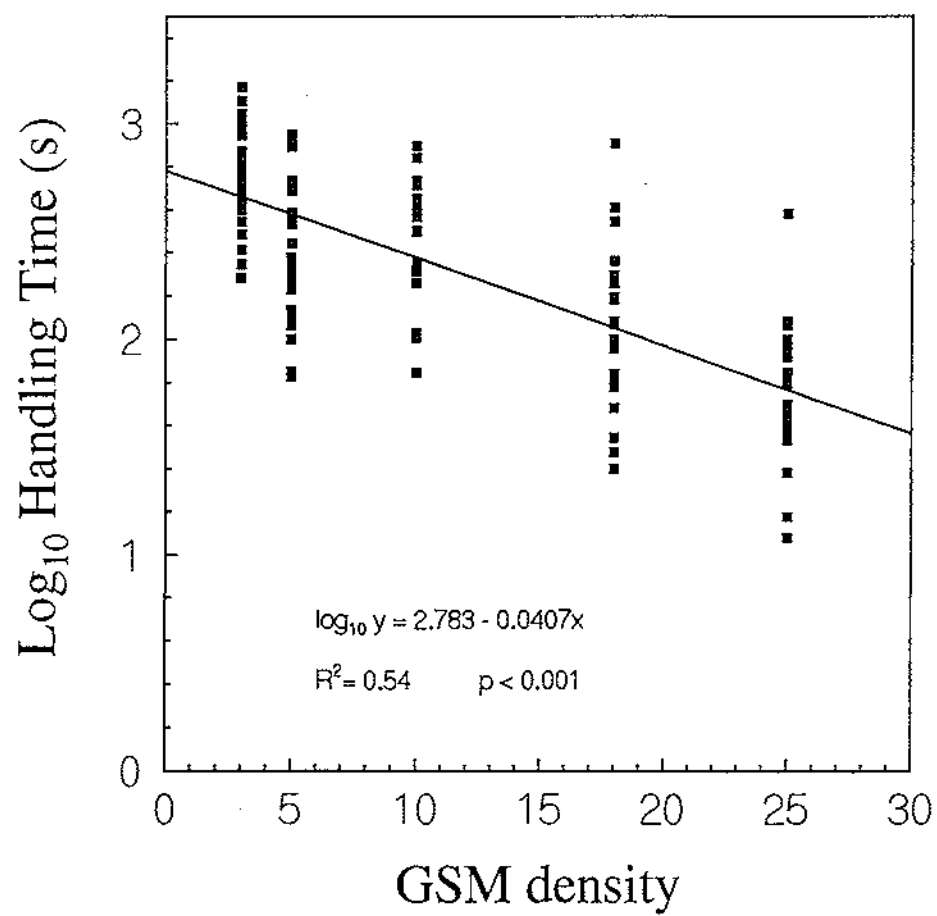
Supporting these empirical data were observations of beetle behaviour at the different densities of GSM. As starvation became more acute, beetles pursued and held prey with a greater degree of tenacity. An increase in tenacity was only apparent after prey detection, and the attack rate defined by Trexler et al. (1988), as the instantaneous searching rate (the area covered by a searching predator in a given amount of time), did not appear to be influenced. The time from the introduction of a predator to the first capture of prey declined noticeably as prey density was reduced. At low prey densities beetles were more tenacious and the first GSM detected was usually captured quickly.

Discussion

The measure of handling time is the time required to pursue, subdue, eat and digest the prey (Holling 1965, 1966; cited in Hassell 1976a). 'Active feeding' time, the time taken to consume and discard a mite after capture, was used as a proportional estimate of actual handling time for this work.

FIGURE 6: *Stethorus bifidus* prey handling time in relation to GSM density

Handling time in relation to prey density



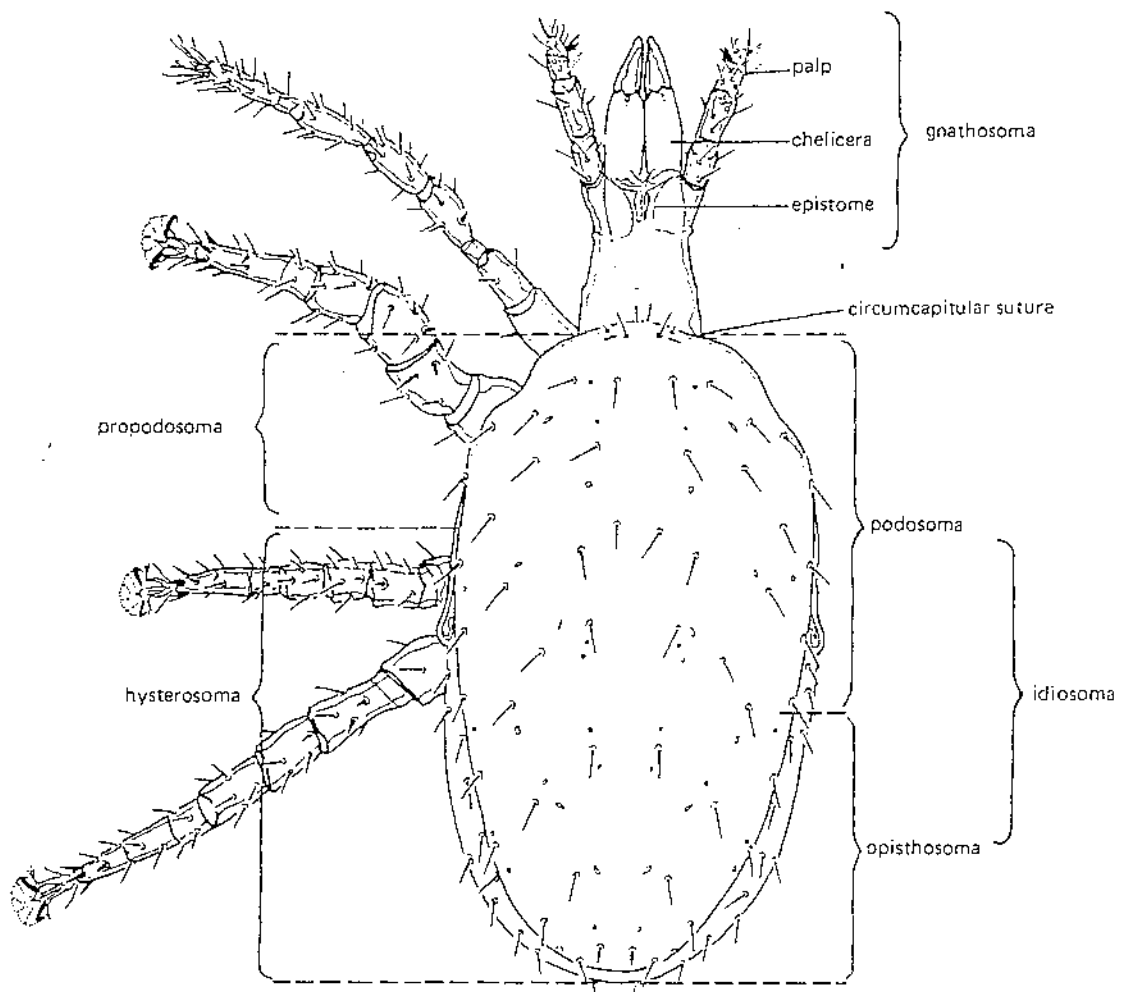
Data from this experiment clearly suggest a negative correlation between prey handling time and prey density. When prey density was low (ie. the adult beetles were hungry) mites were held for up to 10 times longer than when prey density was high, resulting in a more complete extraction of bodily fluids (see table 5). Prey were often manipulated twice, involving a momentary release and recapture, frequently resulting in a fresh grip and perhaps access to more food. This behaviour was not seen in satiated beetles where manipulation of the prey was invariably limited and extraction of body contents incomplete. Starved beetles were observed to re-attach themselves to the mite from a different position when releasing and resecuring. This behaviour was striking and consistent. Perhaps gripping a mite by either the gnathosoma or idiosoma only allows access to body fluids in either of these body segments. By releasing and re-securing a mite the predator may be moving across the circumcapitular suture giving access to still further bodily fluids (see figure 7). Krantz (1975) however notes that a colourless plasma (which the body organs bath in) moves freely throughout the body cavity, or haemocoel of mites. This suggests another explanation for this observed behaviour is required.

Evidence given here demonstrates density dependent feeding behaviour by *S.bifidus* adults. Mites are not discrete packages of food but rather of variable food quantity depending on the satiation level of the predator. At high mite densities the potential ability of *S.bifidus* to 'kill' gorse spider mites is increased as the 'food value' of each mite (to the predator) decreases. This subcomponent of the predation process indicates that there is at least one mechanism by which *S.bifidus* is responding functionally to densities of *T.lintearius*.

Summary

Handling time by the predator *Stethorus bifidus* was investigated over the range of prey densities; 3, 5, 10, 18 and 25 gorse spider mites/cell. Coccinellids were preconditioned to prey densities for 72 hours before measurements were taken. The results indicate that handling time by *S.bifidus* decreases in a non-linear fashion as the density of *T.lintearius* increases and is approximated by the equation: $\log(10)y = 2.783 - 0.0407x$. Experimentation suggests that *S.bifidus* has a higher potential to regulate *T.lintearius* populations than to regulate populations of less colonial mites like *T.urticae*.

FIGURE 7: Major body divisions of Acari (diagram from Krantz, G.W. (1975) In *A Manual of Acarology*, Oregon State University, Corvallis:pg.6.



Dorsum of *Macrocheles merdarius* Berlese (Subclass Acari) showing major body divisions.

Conclusion

- *Stethorus bifidus* is able to respond functionally to characteristics of *T.lintearius*.
- Variations in handling time is one mechanism by which the functional response of *S.bifidus* is expressed.
- As prey density increases handling time decreases and the proportion of body contents extracted from each prey item is reduced.

CHAPTER FIVE: DISCUSSION

Is *S.bifidus* regulating populations of *T.lin-tearius*?

The specific question here, is *S.bifidus* regulating populations of *T.lin-tearius*?, is ambiguous. It could either mean, is *S.bifidus* interacting with GSM in such a way as to have a 'role' in determining the abundance of GSM or has the predator an overriding importance in the regulation and therefore the distribution and abundance of GSM? The former situation in this case appears to be likely while the latter needs extremely careful consideration.

From field work measuring establishment success of GSM throughout the country, a consistent reduction in establishment success was observed above latitude 39°S (Hill et al. 1991). It could be argued, based on these observations, that *S.bifidus*, or any other predator of New Zealand wide distribution, is not exerting a fundamental or overriding regulatory role in the field. This comment however disregards the possibility that predation may be occurring in some regions of the country as a consequence of an abiotic (climatic) gradient from north to south down the country. That is, we may be dealing with a varying predatory potential/efficiency of *S.bifidus* as a consequence of variation in climatic (probably thermal) conditions (see note 7).

To determine the relative importance of two variables of suspected importance (temperature and predation pressure), exclusion or control of one is necessary. Due to the dependence of predation pressure on temperature this variable cannot be, and would be meaningless to separated out. Predation is the only variable that can be excluded.

Note 7 - The GSM strain failing to establish in northern regions of New Zealand originated in Cornwall, England. Two major climatic dissimilarities between Auckland, New Zealand and Cornwall, England are those of temperature and humidity. In general the literature suggests temperature as a more influential abiotic factor to tetranychid mites than humidity. Temperature, accordingly, was treated in this study as the major abiotic (climatic) factor influencing GSM establishment success.

Other workers have used exclusion or check methods. Exclusion of predators from an area of GSM establishment would be a highly desirable way to tackle this problem. Unfortunately this is impractical on a large scale and incorporates many complexities with a large mobile colony of mites. However three methods of predator exclusion that have been used previously include; insecticidal exclusion (Debach 1946), sleeve cage exclusion (Debach 1949), biological control of the predator usually by ants (Debach 1950). Huffaker et al. (1970b) points out however, that 'while the check method is the only means known of learning the degree of control a given enemy species can exert, it has limitations. It is designed only to test such action by an enemy. Its use may induce other changes in the environment important to the mite species under study.'

Alternatively, as has been done in this work, the regulatory potential of the predator can be investigated under artificial conditions where an important variable (temperature) can be manipulated. By comparing reactions of both *S.bifidus* and GSM to various temperatures information about their relative thermal requirements can be collected. The importance of this testing is therefore to determine if *S.bifidus* and GSM have similar thermal requirements.

Evidence suggests that there is a difference in thermal requirement between *S.bifidus* and GSM. The extent of GSM regulation by *S.bifidus* is likely to vary throughout New Zealand and be more extensive in Northern regions more suited to *S.bifidus*.

Points of theoretical importance in relation to population regulation:

To investigate regulatory potential of a predator a clear definition of the term regulation needs to be established. Secondly an account of the events leading up to and determining the extent of population regulation need to be discussed.

Huffaker (1971) describes population regulation as the maintenance of population numbers (or biomass) between certain upper and lower limits through a density induced mechanism. Price (1975) describes population regulation by stating that 'there are two concepts in population regulation: (1) that there are factors external to the population that influence population numbers and (2) that factors change within the population that affect numbers and produce regulation.' Only the first category is

considered here.

Events leading up to and determining the extent of population regulation include a multitude of biotic and abiotic variables. A review of past work is therefore invaluable, and allows a researcher to pin down factors that have been dubbed major contributors in similar interactions or situations previously studied. Work can then be directed into areas of, suspected or known, major importance.

With this information the importance of each factor can be estimated when occurring in a specific situation or variation. This is a ranking procedure whereby a specific question such as 'what is the most important factor regulating this organism under this set of environmental conditions?' can be answered with one word such as temperature, predation or disease. In this case such a question is being asked in relation to *T.lintearius*.

This 'obsession' to produce specific answers has lead to two main schools of thought addressing external factors instrumental in population regulation (Odum 1983; Huffaker 1971; Debach 1964; and Price 1975). The first school is based on population regulation by density independent mechanisms which are primarily seen as the abiotic variables of an organisms niche. The second is that of population regulation via density dependent mechanisms, largely recognized as the biotic variables. A third less prominent school follow an intermediate, between density-dependent and density-independent idea.

To clarify these factors a list of terms specific to each is given below from Price (1975).

Table 6 - Exogenous population processes responsible for population regulation

Density-dependent	Density-independent	Intermediate
Predation	Weather	Both density-dependent and or density-independent factors are important in specific cases
Food	Random changes	
Combination of predation and food		

Andrewartha and Birch (1954; cited in Price 1975) found little use for the terms density-dependent and density-independent and concluded that there is no component of the environment such that its influence is independent of population density. This view (perhaps prematurely) demonstrates the recent move away from using the terms density-dependent and density-independent as separate processes.

Debach and Rosen (1991) discuss the recent trend in biological control ecology with respect to regulatory processes. They acknowledge the controversy in opinion between population regulation by abiotic factors and that by biotic factors, the main distinction being, that physical factors are density-independent and biotic factors are density-dependent. 'Both density-independent and density-dependent processes are important factors in environmental resistance, (**see note 8**). However, their role in reducing population densities should not be confused with their potential role in the regulation, ie. in the maintenance of a dynamic equilibrium' (Debach and Rosen loc cit.). Debach and Rosen (loc cit.) highlight their comment 'role in reducing populations' by noting that the way in which weather acts to regulate insect population densities is by interacting with other physical and biotic aspects of a habitat. In line with the hypothesis for this work, Debach and Rosen (loc cit.) note that although weather in itself is not density-dependent, and thus cannot effect population regulation or natural control on its own, weather as a density-independent factor may combine with a density-dependent factor (like predation) to act in a regulatory manner.

For the remaining discussion the terms density-dependent and density-independent are not directly used. Instead the terms abiotic or climate will be used to describe density-independent processes and biotic will be used to describe density-dependent processes. This is an attempt to keep in line with the recent trend, ie. that density-dependent and density-independent processes differ only in their role in reducing populations and should be seen as operating as independent entities. Abiotic and biotic pressure combined must be important in most cases of population regulation whereby abiotic variables such as climate set the scene in which biotic processes such as predation operate.

Note 8 - Environmental resistance is defined as the opposing force to biotic potential of an organism, Debach and Rosen (1991).

Wallner (1987) states that 'on a global scale, seasonal temperatures and rainfall patterns constitute the major factors that determine the distribution of organisms in space.' Perhaps both abiotic and biotic variables could be seen as operating on a sliding scale of intensity (indicating continuous rather than discrete action) whereby the end product, the extent of population regulation, is dependent on both forces which will both alter according to spacial and temporal measures.

Determining the relative importance of abiotic and biotic regulatory factors is sometimes obscure and often extensive information about the establishment failure of an organism, (whether due to abiotic, biotic or a combination of the two), often can only be collected after the introduction has been made. Even then the significance of each factor may still be obscured to the extent that laboratory experimentation only leads to general predictions.

With the above consideration in mind this work to determine the relative effect of temperature on *S.bifidus* and *T.lintearius* attempts to combine field work carried out on GSM establishment success (Hill et al. 1991), with laboratory work on the relative performance of *S.bifidus* and GSM under a range of temperatures. Main criteria discussed above to check the predatory potential of *S.bifidus* are given in **figure 8**.

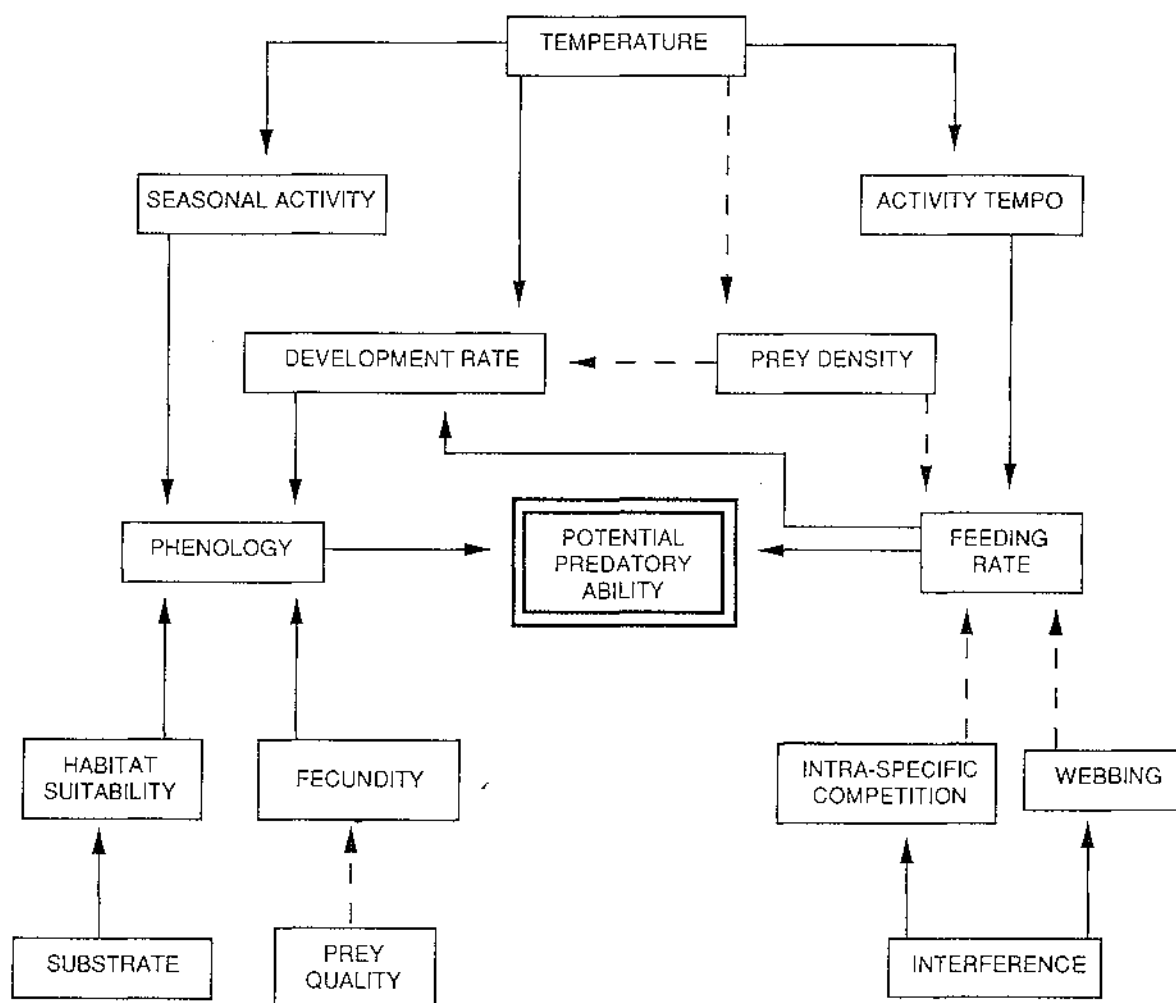
Indicators of the predatory potential of *S.bifidus*:

Two main features or 'intrinsic weapons' a predator exhibits which assist it when surviving on prey populations are the numerical and functional responses. **Chapter two** reviews literature on *Stethorus* predation in this light.

Numerical response:

The predators 'reproductive response', being a subcomponent of the numerical response, is considered in **chapter four: part one**. The development and oviposition characteristics of *S.bifidus* when exposed to *T.lintearius* at various temperatures were measured. This type of basic predator performance screening lays the foundation for sensible predictions on the probable outcome of a predator/prey interaction under known conditions. Where a 'novel' predator/prey relationship exists this type of

FIGURE 8: Factors determining the predatory potential of *S.bifidus*



Definitions of terms used in figure 8

Activity tempo - refers to the actual speed of searching or activity rate of *S.bifidus* in relation to temperature

Seasonal activity - refers to the annual activity cycle of the predator including periods of inactivity or dormancy in relation to temperature

Fecundity - the ability to produce offspring frequently and in large numbers; ie. the physiological ability to reproduce, as opposed to fertility.

screening is of increased relevance because at least one of the organisms has come from an outside location to live in 'unfamiliar' surroundings. Often new or extended surroundings mean dispersal into areas of poor suitability to the invading organism (in this case the gorse spider mite). When this is the case invariably the introduced organism will come up against abiotic (climatic and geographic), besides biotic, factors that will test and perhaps stress its powers of survival and persistence. A reduction in growth, reproduction and/or resilience may follow resulting in populations that are unable to successfully compete in the new food chain/web. It is postulated here that *S.bifidus* has the potential to regulate GSM populations, via a superior numerical response, in warmer regions of New Zealand.

Development:

T.lintearius / *S.bifidus* development rate comparison:

A comparison of the development performance of *S.bifidus* and *T.lintearius* is considered in relation to temperature. Stone (1986) looked at the development rate of *T.lintearius* in relation to temperature. **Table 7a** summarises these data, **Table 7b** is a repeat of data recorded from experimentation on the development of *S.bifidus*, see **chapter four: part one**.

Development rate data from *S.bifidus* and *T.lintearius* are compared in **figure 9**. It is important to note here that this comparison may not be entirely accurate because lower temperatures have not been tested with GSM. This may alter the curve of GSM development rate in relation to temperature. However from this comparison it is evident that the two species show different thermal preferences. **Figure 9** demonstrates that *S.bifidus* develop faster than GSM and that this is more marked at higher temperatures. The relative development rates of *S.bifidus* and GSM do not however indicate relative intrinsic rates of increase. Predicting the relative intrinsic rates of increase from development rate data is not valid because other variables like pre-oviposition period, oviposition rate in relation to temperature and longevity are all important constituents of the intrinsic rate of increase which are not included in this comparison. For example Stone (1986) found that the mean longevity of GSM reduced by ten days when temperature was increased from 15°C to 25°C.

Tanigoshi (1977a) provides another example where a prolonged oviposition period and greater longevity could explain the high potential increase of *Stethorus picipes* compared with its prey *Oligonychus punicae* despite the faster development rate of the mite. This may also have relevance to *S.bifidus* and GSM, implying that if intrinsic rates of increase in relation to temperature could be compared the different thermal requirements of each organism would be further demonstrated.

Table 7a: Development rate of *T.lin-tearius* in relation to temperature (Stone 1986).

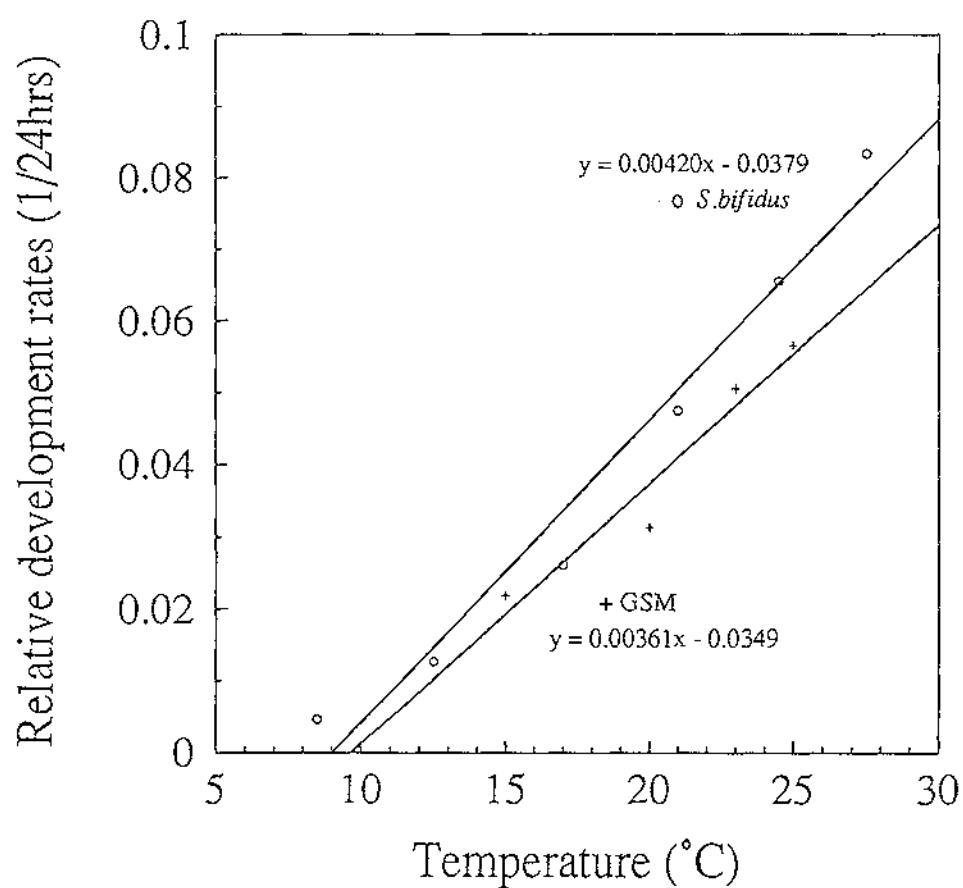
Temperature (°C)	Development time (days)	Rate (1/T)
15	45.8	.022
20	32.0	.031
23	19.8	.051
25	17.7	.056

Table 7b: Development rate of *S.bifidus* in relation to temperature.

Temperature (°C)	Development time (days)	Rate (1/T)
8.5	215	.005
12.5	79.0	.013
17.0	38.4	.026
21.0	21.1	.047
24.5	15.3	.065
27.5	12.0	.083

FIGURE 9: Comparison of development rates of *S.bifidus* and *T.lintearius* in relation to temperature.

S.bifidus/*T.lintearius* development rate comparison



Development thresholds:

The development thresholds of *S.bifidus* varied from 9.2 to 11.4°C. These values are only approximate. Actual values will be slightly lower because development rate in relation to temperature is not strictly linear (see figure 1). The lower threshold intercept for *S.bifidus* relative to GSM is probably deceptive and should not be taken literally, again, due to data not being available over a comparable range for both organisms particularly at cooler temperatures. Field observation has shown that GSM has a lower development threshold than *S.bifidus*, see pg.65 and appendix 1.

Mortality of *S.bifidus*:

The data suggest early larval instars are more vulnerable than later instars to death especially at low temperatures. High larval mortality at cool temperatures appeared to be a consequence of extending the duration of a vulnerable life stage. Observations of 1st instar larvae revealed that they were fatally vulnerable to becoming entangled in spider mite webbing. The problem faced by small or preimaginal predators appeared to be one primarily of scale. Early instars are extremely small ($\approx 0.6\text{mm}$) and capture of the first meal relatively soon after hatching appeared crucial to survival. Observation led to the impression that if a 1st instar secured its first meal quickly the chances of it surviving were increased dramatically. Both Dixon (1959) and Scriven (1960) comment on the relative vulnerability of early instars to starvation.

Oviposition of *S.bifidus*:

Oviposition by *S.bifidus* showed a direct relationship with temperature (see figure 2b) and is independent of prey density. Prey density is thus of minor importance when considering egg production. Very low densities of prey were not tested.

Functional response:

Two components of the functional response are investigated in **chapter four: part two**; how GSM consumption by *S.bifidus* varies with temperature; and how the handling time of *S.bifidus* varies in relation to GSM availability/density.

The colonial behaviour of GSM is unique amongst *Tetranychidae*. A comment made by Putman (1955), that the two spotted mite is more colonial than the European red mite and therefore more susceptible to attack by *S.punctillum*, suggests that *T.lin-tearius* may also be highly susceptible to attack by *Stethorus* species. Hence the functional response by the predator to prey density will be of importance when determining the ability of *S.bifidus* to regulate GSM. **Chapter four** provides a consideration of this point, and although actual functional response curves were not derived, a mechanism of the functional response, handling time, was determined. A variation in handling time as demonstrated here by definition suggests that a Holling type two curve may not describe this predator/prey interaction, **see chapter four: part two - pg.75.**

Feeding:

Feeding data indicate that prey consumption increased exponentially over the temperatures tested. This is surprising as *S.bifidus* is endemic to New Zealand but appears to feed (and reproduce) effectively at high temperatures rarely found in New Zealand. This raises questions as to the origin of *S.bifidus* and its time of dispersal to New Zealand. It is possible that *S.bifidus*, like *S.histrio*, has 'recently' dispersed from Australia. As noted by Houston (1990), *S.vagans* most closely related to *S.bifidus* is present in Australia and not New Zealand.

Handling time:

It has been demonstrated that prey handling time by *S.bifidus* is dependent on prey density. That is the number of mites in the immediate vicinity of the predator will determine the predation rate. If GSM density is high, *S.bifidus* handling time is short and the actual number of mites killed in a given time period increases in an exponential manner (within bounds). *S.bifidus* will accordingly have a high potential to regulate colonial prey such as GSM. This, coupled with an increased feeding rate at high temperatures, suggests that a high regulatory potential exists in warmer areas of the New Zealand (handling time data were only collected at 20.5°C and no information regarding variability in handling time in relation to temperature is available).

A compilation of data on development, feeding and handling time suggest that *S.bifidus* is unable to operate efficiently in the cooler climatic regimes of New Zealand. So although *S.bifidus* is present throughout New Zealand it is more likely that it is contributing significantly to the regulation of GSM in the warmer (Northern) regions of the country.

Extrapolation from theoretical prey population regulation to field prey population regulation:

When extrapolating experimental data (with field observations in mind) to the field it becomes apparent that other factors are likely to be instrumental in the establishment failure of GSM. For instance *S.bifidus* may be subjecting *T.lintearius* to high predation pressure in warmer regions of New Zealand relative to cooler regions coupled with abiotic conditions reducing the resistance of GSM (Cornwall strain) to predation pressure (in warmer regions of NZ relative to cooler regions) thus compounding/exaggerating the observed effect. This, as mentioned earlier, portrays an intermediate assessment of the population processes important in the regulation of GSM. That is, a possible combination of predation with climate.

In addition to the variation in *S.bifidus* predation potential (dependent on climate), the extent to which GSM presence has altered the predators 'feeding opportunity' needs to be discussed. To address the question of how GSM has changed the predatory niche (**see note 9**) of *S.bifidus* a consideration of the mite itself is necessary. How does the mite differ from the previous food supply of *S.bifidus*. Is the mite present in the field over a similar time period and what are the characteristics of its microspatial distribution?

Collyer (1964) notes that *S.bifidus*, feeding entirely on mites of several species, has two generations in summer on deciduous trees and was also active on citrus and other evergreens where it fed and reproduced during the winter. This raises questions concerning the suitability of gorse as an evergreen for winter feeding and reproduction

Note 9 - Niche here refers to the ecological niche as described by Odum (1983). This includes the physical space occupied by an organism, its functional role in the community (its trophic position) and its position in environmental gradients for example temperature and moisture.

of *S.bifidus*. Has an opportunity for *S.bifidus* to predate year round been presented by gorse with its built in food supply, GSM? It has been shown in New Zealand, at least from field work done during this study in Palmerston North, that GSM will feed and reproduce throughout the winter hence be available as prey. Despite winter association of *S.bifidus* with GSM, no reproduction of the former was witnessed during the winter season in Palmerston North. This is not true for areas in the upper half of the North Island where feeding and reproduction continue in *Stethorus* species throughout the winter (J.Charles pers comm.). Perhaps *S.bifidus* are feeding and reproducing on gorse year round in the favourable climate of the upper North Island. Development thresholds support this idea, **see appendix 1** (note these are annual averages). Year round predation is not found in Cornwall, England (the origin of the presently established GSM strain) where predators hibernate in winter (Collyer 1953b).

In short, feeding on abundant prey all year round on one plant (gorse) as opposed to feeding on *Tetranychus urticae* (two spotted mite) and *Panonychus ulmi* (european red mite) during spring and summer before relocation onto evergreen plants for winter, may confer some advantage to the predator.

Predator or Predation ?

Past work indicates the ability of *Stethorus* species to regulate prey under various prey-related conditions. The limitations of single predator species in relation to prey regulation have been well documented. *S.nigripes* is an important mite predator but its increase in numbers tends to lag behind those of the mites which is a consequence of it being an obligate mite eater (Bailey loc cit.). Oatman & McMurtry (1966) illustrates the point by showing that the predatory mite *P.persimilis* regulated populations of *T.urticae* if released before population densities of *T.urticae* reached a critical level, above which *P.persimilis* did not appear to exert effective population regulation. Huffaker et al. (1970b) summarizes by suggesting that 'the phytoseiid-type predator, on average, appears to be a better mite control agent at low density than does the insectan-type predator. Theoretical analyses indicate this, and empirical evidence suggests it. We do not claim, however, that phytoseiids in nature may necessarily be expected always to excel over the larger, more voracious, and often more general, insectan predators.' The predatory role of *Stethorus* species especially

when in association with other predators such as phytoseiids should not be underestimated. The concept of several predators exhibiting a higher degree of regulation when present together is addressed by Bailey & Caon (1986) who states that specialized predators may have limited regulatory effect individually, but that the combined effects of several species can give good prey population regulation.

In general the literature suggests that a prediction about the influence of predation, rather than that of a single predator, is necessary. Huffaker et al. (1970b) demonstrates the approach required to an understanding in this area when reporting on various 'attributes' of different predatory species in prey regulation. Phytoseiids may become active in early spring due to their relatively low food quantity requirements. *Stethorus* species, however, require large numbers of prey and do not become common until late in the season because their prey are too scarce to support large predator populations until then (Huffaker loc cit.). An exceptional situation reported by Putman and Herne (1966) supports this general view. These authors found that *Stethorus* may predate more effectively on *P.ulmi* early in the season when the mite is more aggregated, and locally more abundant, than later on when the population is more dispersed. Charles et al. (1985) also use a multi-predator approach when looking into the integrated control of *T.urticae* with *P.persimilis* and *S.bifidus* in commercial raspberry gardens. When consideration of this type, although labour intensive, is included the inadequacies of analysing the regulatory potential of one predator alone become apparent.

The notion of Coccinellids complementing phytoseiids as predators, however, is not without conflict. Evidence by Plaut (1965) looking at the phenology and control value of *S.punctillum* as a predator of *T.cinnabarinus* puts a greater emphasis on *Stethorus* alone as an effective predator finding no probable causes for the decline of spider mites other than *S.punctillum*.

In summary this 'complex' predator/prey interaction may provide an insight into the problem. As mentioned above *Stethorus* species are effective predators at high prey densities and do not persist at low prey densities. The knowledge that phytoseiid mites are effective predators at low densities suggests that the presence of predatory mites such as *Phytoseiulus persimilis* is consistent with elimination of whole GSM colonies. It would be worthwhile to determine the predatory activity of *P.persimilis* (as it is found in association with GSM and *S.bifidus*) to establish if feeding in colonies persists until complete annihilation occurs (as has been witnessed in glasshouse conditions). From previous work it appears unlikely that this will be the case with *S.bifidus*.

Although evidence suggests that *Stethorus* predation alone is not consistent with the complete elimination of prey (which is often seen in the field) the actual density of prey at which the predator abandons a diminishing food supply needs to be determined. A colonial organism is at a disadvantage if isolated from the main group, or if group numbers are reduced to a level whereby the advantages of being colonial, whatever they may be, are lost. If *S.bifidus* leave GSM colonies at a 'vulnerable' size/density (with respect to individual mite members), perhaps colony death subsequently occurs. So the failure of GSM colonies despite the 'incomplete feeding' of *S.bifidus* may still be occurring in the presence of *S.bifidus* alone. The important question is, at what density, if at all, do GSM colonies fail or break up and what are the consequences of this to individual colony members?

Additional possibilities for the establishment failure of GSM:

Additional factors of importance in mite establishment success need to be kept in mind. These include the pressure that novel predators may be placing on GSM colony structure, and GSM dispersal. Predators may be limiting GSM dispersal by regulating the density and/or size of the colonies in some regions. Evans (1961) referring to *P.ulmi* comments on how dispersal often takes place in dense mite populations.

Other organisms in New Zealand may also be limiting mite movement. Johnson (1979) working on the seasonal dispersal of the predacious mite *Amblyseius fallacis* found that the main mode of dispersal into nursery trees was via tree trunks, low

branches and grass connecting the foliage to the ground. This may have relevance to GSM dispersal where possible transportation media are destroyed. Situations in which stock ie. cattle, sheep and goats are left to graze/browse between gorse bushes or clumps is, however, unlikely to have an effect in many gorse infested areas where extremely dense stands pose no restriction to direct GSM movement from one plant to another.

Where to go from here?

During 1992 several Portuguese strains of the gorse spider mite were introduced into New Zealand in the hope that they may more readily colonize the upper North Island and West coast of the South Island. The Portuguese strains are adapted to a warmer wetter climate than the Cornish strain already established below latitude 39° S. Work is in progress to test the relative success of the 'old' and 'new' mite strains in identical field conditions. The outcome of these new introductions will help to predict the actual importance of predation on GSM populations. If the Portuguese strains establish successfully in northern regions of the country they may be demonstrating a superior fit to the prevailing climatic conditions, unlike the Cornish strain. Evidence for predation being the major process responsible for the original, Cornish strain, failure is lacking. However, this could either be interpreted differently as evidence for the recognition of climate as the major cause of GSM (Cornish strain) failure to establish, or perhaps it could be interpreted as evidence for superior resilience of the Portuguese strains in the face of predation that the Cornish strain may be failing to resist. However if the Portuguese GSM strains also fail to establish, this could be taken as evidence for predation rather than climate as being the most important regulatory process.

SUMMARY: Potential ability of *Stethorus bifidus* to regulate populations of *Tetranychus lintearius*:

1. The reproductive response of *S.bifidus* when feeding on *T.lintearius* was investigated.
2. Development rate is linearly related to temperature for all stages of *S.bifidus*.
($y = 0.0001753x - 0.00258$).
3. Development thresholds of *S.bifidus* varied slightly between instars and ranged between 9.2 (3rd instar) and 11.4°C (4th instar), **see tables 2a & 2b**.
4. Mortality of *S.bifidus* was high among early instars at cold temperatures, 1st instar larvae appeared to be especially vulnerable.
5. Oviposition by *S.bifidus* is independent of prey density between 11.5 and 32.5°C.
6. *S.bifidus* did not lay eggs at 6.5°C.
7. Oviposition by *S.bifidus* is linearly related to temperature between 11.5 and 32.5°C, ranging from 0.29 eggs at 11.5°C to 2.5 eggs at 32.5°C.
8. Investigation into the thermal microclimate under *T.lintearius* webbing revealed that an elevation of up to 11°C above ambient may occur during periods of direct sunlight with a daily average elevation between 1-2°C.
9. Comparison of GSM establishment success by Hill et al. (1991) with average annual temperatures throughout the North Island, suggest that at 13.5°C (ambient), ≈15.0 (actual), the chance of GSM colonies establishing successfully is 50%.
10. Development of *S.bifidus* is more suited to the thermal regime of the upper North Island than that of GSM.

11. Feeding by *S.bifidus* was tested between 6.5 and 32.5°C and the consumption of GSM by ovipositing *S.bifidus* doubled every 6°C between 6.5 and 27.5°C.
12. Feeding experiments suggest that *S.bifidus* will be a more efficient predator in warmer regions of the country because of a non-linear increase in feeding rate in relation temperature.
13. Handling time of *T.lin-tearius* by *S.bifidus* was measured and *S.bifidus* females spent up to 10 times longer feeding on individual mites when starved than when well fed.
14. Handling time data indicate *S.bifidus* has a high predatory potential in dense mite populations.
15. The increased handling time at low mite densities was the result of a more complex extraction of mite contents.
16. Development and feeding rates of *S.bifidus* were examined in relation to temperature and the effect of prey density was tested by measuring prey handling time.
17. Temperature is a major factor determining the numerical response, feeding response and, ultimately, the predatory potential of *S.bifidus*.
18. Although *S.bifidus* is a warmer adapted species relative to *T.lin-tearius*, the extent to which this is determining the regulatory potential of *S.bifidus* feeding on *T.lin-tearius* is unclear.

APPENDIX:

Appendix 1:

Air temperature measurements from meterological service climate map series.

Location	≈ latitude (°S)	Average annual temperature (°C)
Kaitia	35.0	16
Whangarei	35.5	15
Auckland	37.0	15
Hamilton	38.0	14
Rotorua	38.0	12
Gisborne	38.5	14
Taupo	38.5	12
Napier	39.5	14
New Plymouth	39.0	14
Palmerston North	40.5	13
Wellington	41.5	13
Nelson	41.5	13
Blenheim	41.5	12
Westport	42.0	12
Christchurch	43.5	12
Westland	-	11
Queensland	45.0	10
Dunedin	46.0	11
Invercargill	46.5	10

Appendix 2:

Field observation and collection

Date	Site	Specimens and substrate collected (adults unless otherwise stated)
-12/92	Batty Rd.	<i>S.histrion</i> swept off Casuarina in kiwifruit orchard.
9/3/92	Cloverly Rd.	Swept near 'tae berry' (bramble) and collected <i>S.histrion</i> off <i>Cryptomeria</i> .
10/3/92	Old West Rd.	Took gorse shoots holding <i>S.bifidus</i> .
18/3/92	Levin Hort.	Swept <i>S.bifidus</i> off granny smith apple trees with ERM. Research Cntr. (25 males & females), one specimen of <i>S.histrion</i> .
8/4/92	Old West Rd.	Took gorse shoots (found all stages of GSM) <i>S.bifidus</i> specimens contained (9 males, 2 females, two unhatched pupa and one pupal case). <i>Phytoseiulus persimilis</i> , (whirling mite) <i>Anystis baccarium</i> and the snout mite, <i>Bellodes viveti</i> were also collected.
1/5/92	Old West Rd.	Took gorse shoots (found with all stages of GSM). <i>S.bifidus</i> found included 6 females, 2 males, 1 pupal case and 2 2nd or 3rd instar. Larvae found were feeding on deutonymph and adult GSM. Adults Coccinellids were found feeding relatively high up in the colony; ie. 5-10 cm. below the advancing GSM colony. <i>P.persimilis</i> and <i>Eupodidae</i> were collected.
24/5/92	Old West Rd.	Took shoots, found all GSM stages, with <i>S.bifidus</i> (8 females; one just emerged from a pupal case), 2 males and 1 pupa which later degenerated). <i>P.persimilis</i> was collected.
5/6/92	Old West Rd.	Took shoots, found with all GSM stages. <i>S.bifidus</i> (2 females and 1 male) and <i>Eupodidae</i> were collected.
19/6/92	Albany	Albany observation - <i>Stethorus</i> (unsure of species) were found by C.Winks approximately six weeks previously to the visit I made with him. They were found on the earlier occasion within a large GSM colony. On return we found only a remnant of the original GSM colony (ie one group of approximately 500 individuals) and failed to find any <i>Stethorus</i> specimens. Took

- gorse shoots, beat gorse & took litter samples. No *Stethorus* were found. *P.persimilis* were collected.
- 21/6/92 Kopuriki (Murapara) GSM damage found though no colonies could be located. Penetration into gorse was limited though due to the height and density of gorse and bramble.
- 26/6/92 Old West Rd. Took shoots, GSM eggs not found though all other stages were. *S.bifidus*, (3 females and 4 males). *P.persimilis* and *Eupodidae* were collected.
- 20/7/92 Old West Rd. Took shoots, all stages of GSM found. *S.bifidus* (1 Female and 1 male) and *Eupodidae* were collected.
- 15/8/92 Old West Rd. Took shoots, very few GSM found. Mite colonies were broken and webbing very scarce. It has rained almost every day for the last two weeks. GSM eggs appeared to be the only remaining stages surviving in many rain damaged colonies. (Note - many mites were plastered together supposedly unable to escape.) One *S.bifidus* male was found.
- 7/9/92 Old West Rd. Took shoots, very few GSM found however eggs were found. *S.bifidus* was found (2 females). These females were tested for egg-laying by keeping in cells with GSM for one week in the laboratory. No eggs were laid so they were put into cells at 20-22°C, one female laid immediately (the next day) and the other did not lay and was followed until the 28/9.
- 25/9/92 Old West Rd. Took shoots, very few GSM found. Huge amounts of fungus on old webbing and dead mites. The last two months have had unusually large amounts of rain causing extensive flooding in the Manawatu. No *S.bifidus* were found despite an extensive search.
- 1/10/92 Old West Rd. Very few GSM found alive, many were found dead in webbing 'gummed' together supposedly by water. 63 of the last 66 days have had some rain. GSM eggs appear to have survived the rain while other stages have not (this observation is not backed up by testing for egg hatching). One small live GSM colony found was teeming with *Eupodidae*? No *S.bifidus* were found despite an extensive search.

Appendix 3:

Data logger recordings from temperature probe.

- Measurements were made on 20/10/92 in Palmerston North.
- Probe 8 (above gorse plants) was not standardized and data from night-time recording suggests that this probe was reading high. Measurements from probe 8 closely followed those of probe 4 with a consistent thermal displacement of $\approx 1^{\circ}\text{C}$. Probe 4, only, is discussed here as a representative of ambient temperature relative to the temperature under GSM web.
- The data logger was not set for daylight savings. Accordingly one hour needs to be subtracted from each time record.
- Data in in reverse order (as stored by the data logger)

921020	1410	3P	.2085E+02T3	4P	.1966E+02T4	8P	.2058E+02T8
921020	1400	3P	.2388E+02T3	4P	.2083E+02T4	8P	.2172E+02T8
921020	1350	3P	.2269E+02T3	4P	.2196E+02T4	8P	.2230E+02T8
921020	1340	3P	.2090E+02T3	4P	.1994E+02T4	8P	.2046E+02T8
921020	1330	3P	.2432E+02T3	4P	.2036E+02T4	8P	.2143E+02T8
921020	1320	3P	.2938E+02T3	4P	.2580E+02T4	8P	.2370E+02T8
921020	1310	3P	.2189E+02T3	4P	.2048E+02T4	8P	.2070E+02T8
921020	1300	3P	.2578E+02T3	4P	.2226E+02T4	8P	.2369E+02T8
921020	1250	3P	.2832E+02T3	4P	.2480E+02T4	8P	.2703E+02T8
921020	1240	3P	.3147E+02T3	4P	.1944E+02T4	8P	.2629E+02T8
921020	1230	3P	.2653E+02T3	4P	.2025E+02T4	8P	.2341E+02T8
921020	1220	3P	.3041E+02T3	4P	.2137E+02T4	8P	.2634E+02T8
921020	1210	3P	.2269E+02T3	4P	.2001E+02T4	8P	.2201E+02T8
921020	1200	3P	.2471E+02T3	4P	.2234E+02T4	8P	.2496E+02T8
921020	1150	3P	.2420E+02T3	4P	.2043E+02T4	8P	.2371E+02T8

Appendix 3 continued:

921020	2350	3P	.9985E+01T3	4P	.9521E+01T4	8P	.1113E+02T8
921020	2340	3P	.1024E+02T3	4P	.1010E+02T4	8P	.1152E+02T8
921020	2330	3P	.1024E+02T3	4P	.1005E+02T4	8P	.1138E+02T8
921020	2320	3P	.1024E+02T3	4P	.1000E+02T4	8P	.1128E+02T8
921020	2310	3P	.1023E+02T3	4P	.9710E+01T4	8P	.1127E+02T8
921020	2300	3P	.1023E+02T3	4P	.9899E+01T4	8P	.1122E+02T8
921020	2250	3P	.1018E+02T3	4P	.9662E+01T4	8P	.1127E+02T8
921020	2240	3P	.1033E+02T3	4P	.9899E+01T4	8P	.1146E+02T8
921020	2230	3P	.1028E+02T3	4P	.1023E+02T4	8P	.1146E+02T8
921020	2220	3P	.1017E+02T3	4P	.9798E+01T4	8P	.1131E+02T8
921020	2210	3P	.1013E+02T3	4P	.9286E+01T4	8P	.1122E+02T8
921020	2200	3P	.1032E+02T3	4P	.9750E+01T4	8P	.1146E+02T8
921020	2150	3P	.1061E+02T3	4P	.1013E+02T4	8P	.1198E+02T8
921020	2140	3P	.1088E+02T3	4P	.1053E+02T4	8P	.1229E+02T8
921020	2130	3P	.1097E+02T3	4P	.1087E+02T4	8P	.1249E+02T8
921020	2120	3P	.1112E+02T3	4P	.1116E+02T4	8P	.1267E+02T8
921020	2110	3P	.1117E+02T3	4P	.1111E+02T4	8P	.1273E+02T8
921020	2100	3P	.1142E+02T3	4P	.1116E+02T4	8P	.1292E+02T8
921020	2050	3P	.1177E+02T3	4P	.1165E+02T4	8P	.1327E+02T8
921020	2040	3P	.1202E+02T3	4P	.1210E+02T4	8P	.1362E+02T8
921020	2030	3P	.1212E+02T3	4P	.1230E+02T4	8P	.1372E+02T8
921020	2020	3P	.1227E+02T3	4P	.1254E+02T4	8P	.1391E+02T8
921020	2010	3P	.1237E+02T3	4P	.1254E+02T4	8P	.1401E+02T8
921020	2000	3P	.1258E+02T3	4P	.1280E+02T4	8P	.1421E+02T8
921020	1950	3P	.1273E+02T3	4P	.1305E+02T4	8P	.1441E+02T8
921020	1940	3P	.1290E+02T3	4P	.1326E+02T4	8P	.1462E+02T8
921020	1930	3P	.1321E+02T3	4P	.1357E+02T4	8P	.1493E+02T8
921020	1920	3P	.1362E+02T3	4P	.1398E+02T4	8P	.1528E+02T8
921020	1910	3P	.1394E+02T3	4P	.1436E+02T4	8P	.1571E+02T8
921020	1900	3P	.1426E+02T3	4P	.1472E+02T4	8P	.1596E+02T8
921020	1850	3P	.1534E+02T3	4P	.1542E+02T4	8P	.1654E+02T8
921020	1840	3P	.1572E+02T3	4P	.1573E+02T4	8P	.1701E+02T8
921020	1830	3P	.1673E+02T3	4P	.1607E+02T4	8P	.1729E+02T8
921020	1820	3P	.1792E+02T3	4P	.1778E+02T4	8P	.1908E+02T8
921020	1810	3P	.1825E+02T3	4P	.1732E+02T4	8P	.1863E+02T8
921020	1800	3P	.1690E+02T3	4P	.1722E+02T4	8P	.1842E+02T8
921020	1750	3P	.1700E+02T3	4P	.1699E+02T4	8P	.1808E+02T8
921020	1740	3P	.1673E+02T3	4P	.1683E+02T4	8P	.1793E+02T8
921020	1730	3P	.1717E+02T3	4P	.1710E+02T4	8P	.1819E+02T8
921020	1720	3P	.1820E+02T3	4P	.1795E+02T4	8P	.1897E+02T8
921020	1710	3P	.1965E+02T3	4P	.1890E+02T4	8P	.1979E+02T8
921020	1700	3P	.1989E+02T3	4P	.1942E+02T4	8P	.2035E+02T8
921020	1650	3P	.1966E+02T3	4P	.1874E+02T4	8P	.1980E+02T8
921020	1640	3P	.2037E+02T3	4P	.1978E+02T4	8P	.2070E+02T8
921020	1630	3P	.2030E+02T3	4P	.1942E+02T4	8P	.2023E+02T8
921020	1620	3P	.1989E+02T3	4P	.1902E+02T4	8P	.1984E+02T8
921020	1610	3P	.1936E+02T3	4P	.1885E+02T4	8P	.1962E+02T8
921020	1600	3P	.1808E+02T3	4P	.1738E+02T4	8P	.1847E+02T8
921020	1550	3P	.1785E+02T3	4P	.1743E+02T4	8P	.1841E+02T8
921020	1540	3P	.1844E+02T3	4P	.1772E+02T4	8P	.1864E+02T8
921020	1530	3P	.2024E+02T3	4P	.1925E+02T4	8P	.2001E+02T8
921020	1520	3P	.2114E+02T3	4P	.2006E+02T4	8P	.2063E+02T8
921020	1510	3P	.2194E+02T3	4P	.2000E+02T4	8P	.2080E+02T8
921020	1500	3P	.2128E+02T3	4P	.1995E+02T4	8P	.2081E+02T8
921020	1450	3P	.1994E+02T3	4P	.1912E+02T4	8P	.1978E+02T8
921020	1440	3P	.1952E+02T3	4P	.1855E+02T4	8P	.1939E+02T8
921020	1430	3P	.2043E+02T3	4P	.1886E+02T4	8P	.1969E+02T8
921020	1420	3P	.2072E+02T3	4P	.1994E+02T4	8P	.2063E+02T8

Appendix 3 continued: Weather recordings made in conjunction with temperature probe readings, (20/10/92).

Time (24hr)	Prevailing conditions
10:50	gusty, direct sunlight
11:00	gusty, direct sunlight
11:10	breezy, direct sunlight
11:20	breezy, direct sunlight
11:30	breezy, overcast
11:40	breezy, direct sunlight
11:50	breezy, overcast
12:00	breezy, overcast
12:10	breezy, overcast
12:20	breezy, direct sunlight
12:30	breezy, direct sunlight
12:40	breezy, direct sunlight
12:50	breezy, direct sunlight
13:00	breezy, direct sunlight
13:10	breezy, overcast
13:20	breezy, shaded
13:30	breezy, shaded
13:40	breezy, shaded

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