A LABORATORY BEHAVIORAL ASSESSMENT ON PREDATORY POTENTIAL OF THE GREEN LACEWING *MALLADA BASALIS* WALKER (NEUROPTERA: CHRYSOPIDAE) ON TWO SPECIES OF PAPAYA PEST MITES, *TETRANYCHUS KANZAWAI* KISHIDA AND *PANONYCHUS CITRI* (MCGREGOR) (ACARI: TETRANYCHIDAE)

by

LING-LAN CHENG

M.S., Kansas State University, 2002

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Entomology
College of Agriculture

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Abstract

Tetranychus kanzawai Kishida and *Panonychus citri* **(**McGregor) are the two major arachnid pests of screenhouse-cultivated papayas in Taiwan. Control of these mites has become more difficult because both pests have become resistant to most registered miticides. This laboratory study investigated the feeding behaviors, predatory potential, and prey preference of a domesticated line of *Mallada basalis* Walker, a commonly-occurring chrysopid in Taiwan, to both of these pest mites. A laboratory assessment on control efficacies of different predator:prey release ratios to single and mixed-pest species was also conducted. Behavioral study showed that all larval stages of *M. basalis* exhibited a high rate of acceptance of all life stages of both *T. kanzawai* and *P. citri*. Second and third instar predators foraged actively during most of the 2-h tests. Numbers and rates of prey consumption were measured for each instar of predator and prey. Results showed that consumption increased and prey handling time decreased as predator life stage advanced, and prey stage decreased. *Mallada basalis* exhibited both a shorter handling time and corresponding higher consumption rate on *P. citri* compared with *T. kanzawai*. Handling time and consumption rate also were positively affected by increasing prey density. *Mallada basalis* did not exhibit notable species or life stage preferences, and prior feeding experience on one mite species did not affect subsequent prey choice between the two mites. Lacewings significantly reduced *T. kanzawai* and *P. citri* populations at a predator:prey ratio of 1:30 and this improved at ratios of 1:15 and 1:10. Control of *T. kanzawai* was slightly better than *P. citri* when the mites occurred singly and together. Consumption by *M. basalis* increased with temperature up to 30°C. I conclude that *M. basalis* has high potential for augmentative biological control of papaya mites. Further field investigations are needed for making final recommendations.

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Major Professor
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CHAPTER 1 - Introduction and Literature Review

General information about papayas

The papaya, *Carica papaya* L., belongs to the small family Caricaceae allied to the Passifloraceae. It is believed to be native to southern Mexico and neighboring Central America, and is now present in many tropical and subtropical countries (Morton, 1987; Nakasone and Paul, 1998). The papaya is a short-lived, fast-growing, woody, large perennial herb, that can reach 6-9 m in height. The hollow green or deep purple trunk is straight and cylindrical with prominent leaf scars. Its stem is usually hollow, herbaceous, and unbranched. The leaves emerge directly from the upper part of the stem in a spiral on nearly horizontal petioles 0.3-1.05 m long, and the blade is deeply divided into 5 to 9 main segments. Both the stem and leaves contain copious white milky latex (Morton, 1987).

The papaya bears 5-petalled flowers that are fleshy, waxy and slightly fragrant. Some plants bear only pistillate (female) flowers, some bear hermaphrodite (perfect) flowers having both female and male organs, while others bear only staminate (male) flowers. Pollination mechanisms in papaya are not well-known. Wind, bees, and moths can be important agents (Prest, 1957; Stambaugh, 1960; Garrett, 1995; Nakasone and Paull, 1998); however, hand pollination is sometimes necessary for a proper fruit set. The fruit is pear-shaped with golden-yellow skin. The flesh, also golden-yellow, is juicy and silky smooth, with a sweet-tart flavor (Morton, 1987).

Ripe papaya is usually consumed fresh as a breakfast or dessert fruit. It can also be processed and used in a variety of products such as jams, fruit juices, and ice cream. Unripe fruits and leaves are consumed as vegetables (Morton, 1987; Tipton *et al.*, 1990; Villegas, 1997; Watson, 1997). Several enzymes have been found in papayas, of which papain is of commercial importance. Papain is a milky latex collected by making incisions in unripe papayas (Nakasone and Paull, 1998). It resembles the animal enzyme, pepsin, in its digestive action. Papaya latex is either sun-dried or oven-dried and sold in powdered form to be used in beer clarifiers, meat tenderizers, digestion aids, wound debridement aids, tooth-cleaning powders, and other products (Villegas, 1997; Nakasone and Paull, 1998; El Moussaoui *et al*., 2001).

A number of insect and mite pests attack papayas (Morton, 1987; Pena and Johnson, 1998; Mossler and Nesheim, 2002). These include tobacco thrips (*Thrips tabaci* Lindeman), the papaya whitefly (*Trialeurodes variabilis* (Quaintance)), papaya scale (*Philephedra tuberculosa* Nakahara and Gill), mealybugs (*Pseudococcus longispinus* (Targioni-Tozzetti)), papaya fruit fly (*Toxotrypana curvicauda* Gerstaecker), and spider mites (*Tetranychus* spp. and *Panonychus citri* (McGregor)). In addition, plant parasitic nematodes may cause problems on papayas in some areas. Species of plant parasitic nematodes reported to be associated with papaya plants include *Rotylenchulus reniformis* Linford & Oliveira, *Meloidogyne* spp., *Helicotylenchus dihysteria* (Cobb) Sher, *Quinisulcius acutus* (Allen) Siddiqi, and *Criconemella* spp. (Mossler and Nesheim, 2002).

The principle diseases affecting papaya include papaya ringspot virus, anthracnose (*Colletotrichum gloeosporioides*), powdery mildew (*Oidium caricae*), leaf spot (*Asperiosporium caricae*), blight (*Phytophthora palmivora*) and papaya droopy necrosis virus (Sun, 1978). These diseases attack papaya plants and/or fruits and can be great threats to papaya growth and production.

Papayas in Taiwan

The papaya is an important fruit crop in Taiwan. The growing area of papayas in Taiwan is about 3800 hectares, with annual production of 126,500 tons (Anonymous, 2006). Most of the papayas are grown in the middle, southern, and eastern parts of Taiwan, but some are produced in northern Taiwan (Wang, 1991). Papaya cultivation in Taiwan has two seasons: spring and fall. The spring crop begins in December and harvest occurs from November to the following May, whereas fall papayas are planted in August and harvested from July to the following January.

‘Tainung No. 2’ is the principle papaya variety cultivated in Taiwan (Wang, 1991). This cultivar grows vigorously, matures early, and sets fruit at low stem sites. The long, oval fruit is medium-sized, weighs about 1 kg, has deep green skin, juicy red flesh, and a rich sweet flavor.

Papaya pest and disease problems in Taiwan

A number of common pests and diseases affect papayas in Taiwan (Hao *et al*., 1996). Papaya ringspot virus (PRSV) is one of the most destructive diseases of papaya (Purcifull *et al*., 1984). It was discovered in Taiwan in 1975 and has spread throughout the country, destroying the most commercial papaya plantations within 2 to 3 years of infection (Wang *et al*., 1978; Wey *et al*., 1978). The most popular papaya cultivar in Taiwan, 'Tainung No. 2', is particularly susceptible to PRSV (Lin *et al*., 1989). This disease is nonpersistently transmitted by a number of aphid species, including *Myzus persicae* Sulzer, *Aphis gossypii* Glover, *Aphis medicaginis* Koch, *Aphis rumicis* Linn., and *Micromyzus formosanus* Tak. (Jensen, 1949; Zetter, *et al*., 1968; Wang, 1981; Purcifull *et al*., 1984). The virus does not multiply within the aphid vectors. Instead, it is carried on their mouthparts and is transmitted from plant to plant during feeding (Namba and Higa, 1975; 1977; Wang, 1981). The disease can also be spread by planting infected papaya seedlings in uninfected areas. The first symptoms are irregular mottling of young leaves, followed by leaf yellowing with transparent areas, leaf distortion, growth retardation, and dark green concentric rings or green spots on the fruit. Fruit set is sharply deformed and smaller when the disease progresses; and fruits borne 2 or 3 months after the first symptoms will have a disagreeable bitter flavor (Cook, 1972; Purcifull *et al*., 1984). There is no cure for infected plants. If affected plants are not removed, the condition spreads throughout the plantation.

Techniques involving cross-protection (i.e., infecting papayas with mild PRSV strains), disease-resistant breeding, and genetic modification have been developed (Wang, 1982; Wang, 1987; Wang, *et. al*., 1987; Yeh *et al*., 1988; Bau *et al*., 2003a; 2003b; 2004). However, cross-protection cannot completely protect papayas from papaya ringspot virus (Lin *et al*., 1989) while disease-resistant varieties are less popular in the market than 'Tainung No. 2' (Wang, 1991). Genetically modified papayas have not yet been released to farmers by the Taiwanese government yet. Cultivation of papayas in screenhouses has also been developed to protect papayas from aphids that vector papaya ringspot virus, and the protection as high as 97% has been demonstrated (Shi *et al*., 1990). Therefore, most papayas in Taiwan are now cultivated in screenhouses. However, the unventilated, warm screenhouse conditions favor the outbreaks of mite pests (Hao *et al.*, 1996).

Mite pests

The Kanzawa spider mite, *Tetranychus kanzawai* Kishida, and the citrus red mite, *Panonychus citri* (McGregor), are major pests of papayas in Taiwanese screenhouses (Ho *et al*. 1997) where they occur year-round (Anonymous 2002). Both *T. kanzawai* and *P. citri* belong to the family Tetranychidae of the order Prostigmata. Tetranychid mites develop through four life stages: egg, larva, protonymph, deutonymph, and adult (Jeppson *et al*., 1975). The nymphal and adult stages are initiated during intervening periods of inactivity called the protochrysalis, deutocrysalis, and teliochrysalis. During these periods the mite anchors itself to a leaf or to its webbing. The legs are bent upon themselves and a new cuticle is prepared before the exuvium is cast off (Jeppson *et al*., 1975). There are two sexes in *Panonychus* and *Tetranychus*, and their reproduction is based on arrhenotokous parthenogenesis. That is, unfertilized females produce only male offspring and fertilized females produce both females and males (Taylor and Smith, 1956; Boudreaux, 1963; Helle and van Zon, 1966). The chromosome number in males is haploid. Males develop slightly faster than females, which allows them to find, guard and fight with other males for quiescent deutonymph females (Cone, 1985). Sex pheromones released by the female may be involved in mate-finding (Cone *et al*., 1971; Oku *et al*., 2005). The mating process is usually accomplished immediately after the last molt of the female. The male crawls head first under the posterior end of the teneral female and arches the end of the abdomen upward to accomplish coupling. The female is held by the 2 pairs of fore limbs of the male in the process (Gasser, 1951; Evans, *et al*., 1961; Boudreaux, 1963).

Tetranychid mites feed by penetrating the plant tissue with sharp stylets to remove the cell contents. The chloroplasts disappear and the small amount of remaining cellular material coagulates to form an amber mass (Jeppson *et al*., 1975). In the palisade layers, only the penetrated cells are damaged; adjacent cells show no evidence of injury. High citrus red mite populations on citrus cause substantial changes in photosynthesis and transpiration rates (Wedding *et al*., 1958). It has been shown that transpiration increases during heavy feeding, but then decreases below normal levels after mites have been removed. The amount of chlorophyll in the leaf may be decreased as much as 60 percent (Wedding *et al*., 1958). Certain substances may be secreted into the plant tissue during feeding by tetranychids (Liesering, 1960). The puncture of new cells proceeds from one spot to another in the form of a circle which results in the formation of small rounded chlorotic spots. Continued feeding leads to irregular spots formed by the integration of primary suction spots; finally the typical picture of tetranychid injury appears. Transpiration is highly accelerated, which eventually leads to the drying out and dropping of leaves. Strongly injured leaves may exhibit no photosynthesis at all (Liesering, 1960).

Tetranychids may be spread from plant to plant by air currents. They may also be spread by the movement of infested plants or contaminated tools or clothing. They also can crawl to nearby plants, especially when the infestation is severe and leaves become dry (Jeppson, *et al*., 1975).

Tetranychus kanzawai

Tetranychus kanzawai is an important pest mite throughout East and Southeast Asia, attacking over a hundred species of plants, including many crops and ornamental plants (Bolland *et al*., 1998; Zhang, 2003). It is normally an outdoor species, but can attack greenhouse plants as well. The eggs are often laid on the undersides of leaves. They are spherical in shape and are clear when freshly laid. The larvae and nymphs are yellowish green, and the adults are red or yellowish red depending on host plants. They often feed on chloroplasts on the under surface of the leaf, which causes the upper leaf surface to develop characteristic whitish or yellowish stippling. As mite feeding continues, the stippling coalesces to form brownish lesions (Helle and Sabelis, 1985; Yamada and Tsutsumi, 1990; Zang, 2003). Heavy damage eventually leads to wilting and defoliation, which further reduces plant growth.

Development of *T. Kanzawai* occurs above 10.3°C. Development time from egg to adult is 19 to12 days at 20 to 25°C, respectively. Adult sex ratio is usually female biased to about 67%. Adult life span is 20-33 days in females and 19-35 days in males at 15-30°C. Fecundity ranges from 28 eggs/female at 15°C to 76 eggs/female at 30°C (Zhang, 2003). Reproductive diapause is facultative and a higher proportion of females enter diapause at lower temperatures. At 16°C, 100% of females enter diapause (Fujibayashi and Sekita, 1993).

Panonychus citri

Panonychus citri has a worldwide distribution and is known to occur on over 80 species of plants, including citrus, rose, almond, pear, castor bean, and several broadleaf evergreen ornamentals (Bolland *et al*., 1998; Zhang, 2003). The eggs are pale to red, nearly spherical, somewhat flattened on the bottom, and stalked on the top with guy fibrils radiating from the tip of the stalk to the leaf surface. The larvae, nymphs and adults are dark red to purplish in color. This species can feed on both sides of leaves and produces a stippled appearance initially, which develops into pale patches later. With continuous feeding and damage, the leaves become grey, silver or yellow. Development occurs above 10°C and all stages die at 40°C. Developmental time is shorter at higher temperatures and is about ten days near 25°C, which is the optimal temperature. At this temperature, adult females live for about nine days and lay an average of 25 eggs (Zhang, 2003). Sex ratio is biased, with about 70% females. A relative humidity of 65% is optimal for development and reproduction (Beitia and Garrido, 1991b; Tian and Pang, 1997). This species prefers moderate climatic conditions. Low humidity and very high temperature are detrimental to population development of this mite.

Management of *T. kanzawai* and *P. citri*

Chemical control

Petroleum oils, chlorinated hydrocarbons, and synthetic dinitrophenyl, organophosphorus and carbamate acaricides, as well as seed oil of chinaberry (*Melia azedarach*) and certain new types of pesticides, such as abamectin, have been used to control *T. kanzawai*, *P. citri* and other tetranychid mites (Jeppson, *et al*., 1975; Zhang, 2003). However, spider mites in the genera *Panonychus* and *Tetranychus* are capable of rapidly developing resistance to a wide variety of toxicants (Jeppson, *et al*., 1975; Kuwahara, 1977; Cranham and Helle, 1985; Hoy and Conley, 1987; Richter and Schulze, 1990; Herron, *et al*., 1993). Mite populations resistant to a toxicant are often cross-resistant to chemically-related, and to some unrelated, compounds (Hansen *et al*., 1963;

Jeppson, 1963). Thus, the control of the spider mites has been difficult by chemical means. Moreover, chemical applications suppress natural enemies of the spider mites, which often leads to mite outbreaks (Furuhashi, 1990). To improve efficacy and reduce adverse impacts on the environment, newer approaches to mite control have been developed recently, which incorporate the principles of integrated pest management, and offer alternatives that reduce dependency on chemical pesticides.

Biological control

One such alternative is biological control, which utilizes the natural enemies of a pest to suppress the pest's population, making it less abundant and thus less damaging than it would otherwise be. Biological control contributes to pest suppression, either by replacing pesticides or by reducing the amount and frequency needed. In this way, there is less environmental contamination and less disruption to beneficial and other non-harmful species. Among the natural enemies that feed on mites in the genus *Tetranychus* are predatory mites, especially phytoseiids; coccinellid beetles in the genus *Stethorus*; staphylinid beetles in the genus *Oligota*; chrysopids; some species of coniopterygids; predacious Hemiptera belonging to the families Anthocridae and Miridae; predacious thrips; and Cecidomyiid flies (Jeppson, *et al*., 1975; Helle and Sabelis, 1985; Zhang, 2003).

Of these, phytoseiid mites have received the most intensive study, and are now widely-used in many parts of the world for the control of phytophagous mites (McMurtry and Croft, 1997; Gerson *et al*., 2003). Many phytoseiids have a shorter life cycle than their prey, equivalent reproductive potential, good searching capacity, and ability to survive on relatively few prey. But most phytoseiids are limited by the amount of prey they can consume. On the other hand, green lacewings (Neuroptera: Chrysopidae) with their excellent searching ability, voracious prey consumption, and wide host range have the potential to prevent the development of high mite populations.

Biological control using green lacewings

The family Chrysopidae includes over 1,200 currently recognized species and subspecies (Gepp 1984, Brooks and Barnard 1990). The adults have long filiform antennae, strong mandibles and cursorial legs. The wings are large and subequal. Much of the venation is green, but some veins in a few species are dark (Stelzl and Devetak, 1999). Eggs are normally stalked, up to 3mm in length, and elongate-oval in shape. The length of the stalk compared to the length of the egg differs widely and is characteristic for the species. Eggs can be deposited singly, in loose groups, or in clusters, which is also a species specific characteristic (Stelzl and Devetak, 1999). The elongate larvae are campodeiform and may be either active or cryptic predators. Mandibles and maxillae are curved and are closely associated on each side to form a channel for passage of food (Gepp 1984). The larval stages of many chrysopids cover their dorsum with debris, including their own cast cuticles, remains of prey, and fragments of vegetable or other matter. Such larvae are commonly referred to as "trash-carriers" or "debris-carriers" (Canard and Principi, 1984). It has been suggested that the debris may protect the larvae against natural enemies (Principi 1946, New 1969, Eisner *et al*. 1978). Certain non-debris-carrying or naked larvae, in the presence of a potential enemy, can curve the abdomen upwards and project from the anus a droplet of liquid towards the potential attacker. This acts as a repellent and has been noted to paralyze antagonists (Kennett, 1948) or even congenerics at the start of a cannibalistic encounter.

There are three larval instars - all predaceous. The third instar spins a cocoon of Malpighian tubule silk in which it becomes enclosed. The larval-pupal molt occurs within the cocoon, and the dectious pupa leaves the cocoon a few hours before the imaginal ecdysis (Canard and Principi, 1984). All chrysopid larvae naturally feed on small, comparatively soft-bodied arthropods. They are characteristically highly voracious and often have a broad prey range. Prey that have been recorded include aphids of nearly all families; a wide range of Coccoidea, including Monophlebidae, Pseudococcidae, Eriococcidae, Coccidae, Diaspididae and others; various leafhoppers and related families including Cercopidae, Cicadellidae, Membracidae and Fulgoridae; whiteflies; psyllids; thrips; psocids; Lepidoptera, including eggs and larvae of Tortricidae, Pyralidae, Noctuidae and Pieridae; tetranychid and eriophyid mites; and, less commonly, larvae and eggs of beetles, the flies, sawflies and of other Neuroptera (Pariser, 1919, Killington, 1936).

Because of their polyphagous nature and high search rates for prey, green lacewings have drawn much interest as biological control agents. Investigators have suggested their potential against several species of major agricultural pests, such as various aphids, Colorado potato beetle, European red mite, grape mealybug, bollworm, and tobacco budworm (Ridgway and Murphy, 1984). In addition, some green lacewings are known to have tolerance to commonly-used pesticides (Bigler, 1984), and they are relatively easy to rear in captivity (Tulisalo, 1984). These traits enhance their value for integrated pest management. Currently, some green lacewings are commercially produced for use in biological control programs (Tulisalo, 1984).

Mallada basalis

Mallada basalis Walker is the common chrysopid in agricultural fields in Taiwan. Eggs are green in color, and are laid singly on stalks. Larvae are trash-carriers and are predacious. Adults feed only on honey and pollen and they are attracted to light. The yearly average developmental time from egg to adult is 28.1 days with 4.4 days for egg, 11.8 days for larva, and 11.9 days for pupa (temperature ranged 14 - 30°C). Adults can live for 2 to 3 months. Females live for a shorter time than males and can lay about 800 eggs during their life (Chang, 2000). Previous investigations have suggested the potential of *M. basalis* as a biological control agent against several species of arthropods, such as *Phyllocnistis citrella* Stainton, *Aphis* spp, *Nipaecoccus filamentosus* (Cockerell), *Diaphorina citri* Kuwayama, and *P. citri* on citrus; *T. kanzawai* on papaya; *P. citri* on Indian jujube; *T. urticae* and *T. kanzawai* on strawberry (Lo 1997). *Mallada basalis* can be successively mass-produced using a microcapsulated artificial diet in a cost-effective manner. For example, it costs about $0.028 (U.S.) to produce one adult (includes diets, labor, utilities and facility) and each female can produce an average of 736.3 eggs (Chang, 2000; Lee, 2003). Besides, cold-storage techniques have been developed for eggs, larvae, and pupae, which improves shipping and making scheduled releases (Wu 1992). As with other green lacewings, *M. basalis* has been shown to have some tolerance to certain insecticides, fungicides, and acaricides (Tzeng and Kao 1996, Lo 2002). All of this information suggests that *M. basalis* may be very compatible for use in integrated pest management. Although field evaluations of *M. basalis* have been done (Hao, *et al.*, 1996; Lo, 1997; Hao, 2002), little is known about its feeding and other predatory behaviors. Moreover, precise predator:prey ratios for effective biological control have not yet been investigated.

Therefore, my dissertation has focused on a series of laboratory studies – many involving direct observations under the microscope – to investigate the feeding behaviors, predatory potential, and prey preference of *M. basalis* to the two major papaya acarine pests, *T. Kanzawai* and *P. citri*. A laboratory assessment on control efficacies of different predator:prey release ratios of *M. basalis* to a single mite species, *T. kanzawai* or *P. citri*, and a mixture of these two mite species was also conducted. Results from these studies will help in making recommendations for effective application of green lacewings in the papaya integrated pest management program.

Specific objectives and hypotheses of this study

(1) To determine the prey acceptability, handling times, and relative consumption rates of larval stages of *M. basalis* to different life stages of the Kanzawa spider mite, *T. kanzawai*, and the citrus red mite, *P. citri* (the latter were evaluated at two densities).

Hypothesis:

Feeding behaviors (e.g., prey acceptability, handling times, and relative consumption rates) of the predator will be affected by the predator's age as well as the prey species, prey age, and prey density.

(2) To evaluate prey preference of each larval instar of *M. basalis* when exposed to mixture of life stages of *T. kanzawai* and *P. citri* (each mite species tested separately).

Hypothesis:

M. basalis will exhibit prey preference among different life stages of the mite species, and the preference will change over the lacewing's age.

(3) To determine if *M. basalis* exhibits a preference between *T. kanzawai* and *P. citri*, and if the effect of prior feeding experience on one prey species will affect foraging behavior on the second prey species.

Hypotheses:

1. *M. basalis* will exhibit a preference for one mite species over the other.

2. *M. basalis* will change prey preference based on its previous feeding experience.

(4) To compare the control efficacies of different predator:prey release ratios of *M. basalis* for a single mite species, the Kanzawa spider mite or the citrus red mite, and for a mixture of these two mite species.

Hypotheses:

1. Control efficacy of *M. basalis* to the pest mites would increase as the predator-to-prey ratio decreases.
2. The response (predation rate) to predator-prey ratios would differ depending on which prey species (or mixture of species) is presented to *M. basalis*.

(5) To determine the effect of temperature on prey consumption rate of *M. basalis*.

Hypotheses:

1. Within the temperature range of temperature favorable for growth and development, prey consumption by *M. basalis* will increase directly with temperature.
2. The relationship between temperature and prey consumption would differ for *T. kanzawai* and *P. citri*.

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CHAPTER 2 - Foraging, prey acceptability, handling times, and consumption rates by the green lacewing *Mallada basalis* Walker (Neuroptera: Chrysopidae) on two species of papaya pest mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor) (Acari: Tetranychidae)

ABSTRACT

We measured prey acceptability, foraging schedule, short term consumption rate, and handling time of larvae of a domesticated line of the green lacewing, *Mallada basalis*, in no-choice tests with different life stages of two mite pest species of papaya, *Tetranychus kanzawai* and *Panonychus citri*. Following a specific period without prey, all three larval instars of *M. basalis* generally exhibited considerably high rate of acceptance of all life stages of both *T. kanzawai* (59-94%) and *P. citri* (62-100%). In 2-h trials, second and third instar lacewings spent an average of 112.3 min actively foraging compared to only 48.5 min for 1st instars, which spent proportionately more time at rest. Prey consumption increased with life stage of *M. basalis*, but decreased with prey life stage. Third instar lacewings consumed an average of 311.4 *T. kanzawai* eggs or 68.2 adults in 2 hours. These prey consumption rates were 2.3-2.6 times greater than those observed for second instar lacewings, and were 15.9-17.x times greater than those observed for first instar lacewings. In general, *M. basalis* consumed more *P. citri* than *T. kanzawai* in the tests. Third instar lacewings consumed an average of 303.0 *P. citri* eggs to 114.0 adults in 2 hours. These prey consumption rates were 2.0-2.6 times greater than those observed for second instar lacewings, and were 3.6-9.3 times greater than those observed for first instar lacewings. The prey handling time for *M. basalis* decreased with advancing larval age of the predator, but increased with advancing life stage of prey. Third instar *M. basalis* consumed a *T. kanzawai* egg in only 7 sec and consumed an adult within 1 min, while first instar used an average of 23 sec to consume a *T. kanzawai* egg, and an average of 8 min and 46 sec to consume an adult. With exception of prey eggs, handling times of *T. kanzawai* were generally longer than *P. citri* by all *M. basalis* instars. Handling times were shorter, and numbers of *P. citri* consumed were greater at the higher mite density than at the lower density, while there were generally no significant differences in prey acceptability and foraging time between these two densities. Collectively, this study demonstrated that larvae of a domesticated line of *M. basalis* are active foragers, exhibit consistently high levels of prey acceptability, have short handling times relative to other predators, and possess a high capacity for prey consumption for both mite pests. These findings suggest that *M. basalis* larvae may have high potential for augmentative biological control of mites on papayas.

Key Words: phytophagous mites; predator-prey interaction; feeding behavior; predatory potential; biological control

INTRODUCTION

Papaya is an important fruit crop in Taiwan with annual production estimated at about 126,500 tons (Anonymous, 2006). The principle papaya variety in Taiwan is 'Tainung No. 2' (Wang, 1991). However, this cultivar is susceptible to the papaya ringspot potyvirus (Lin *et al*., 1989), which is one of the most destructive diseases affecting papaya (Purcifull *et al*., 1984). Cultivation of papayas in screenhouses has been developed to help protect this crop from aphids which serve as vectors for papaya ringspot virus. Demonstrated levels of protection have reached 97% (Shi *et al*., 1990). Therefore, most papayas in Taiwan are now grown in screenhouses. However, the unventilated, warm conditions in screenhouses favor outbreaks of acarine pests (Hao *et al*., 1996).

The Kanzawa spider mite, *Tetranychus kanzawai* Kishida, and the citrus red mite, *Panonychus citri* (McGregor), are two major acarine pests of papayas in screenhouses (Ho *et al*. 1997). Both occur throughout the year in Taiwan with populations peaking in dry months of October through May (Cheng, 1966; Huang, *et al*., 1997; Anonymous 2002). *T. kanzawai* feed on cell chloroplasts on the under surface of the leaf, causing the upper surface of the leaf to develop a characteristic whitish or yellowish stippling, which joins and becomes brownish as mite feeding continues (Helle and Sabelis, 1985; Yamada and Tsutsumi, 1990; Zang, 2003). Heavy damage causes wilting and defoliation. *P. citri* feeds on both sides of leaves and produces a stippled appearance initially, which develops into pale patches later. With continuous feeding and damage, the leaves become grey, silver or yellow (Zhang, 2003).

Control of mite pests on papayas depends mainly on chemical applications. However, the intensive application of miticides, and the short life cycle and high reproductive rates of mites have led to the development of resistance in both the Kanzawa and citrus red mite to many registered miticides (Cranham and Helle, 1985; Furuhashi, 1994; Masui *et al*., 1995; Yamamoto, *et al*., 1996; Goka, 1998; Aiki *et al*., 2005). The number of miticides that can be used is further limited because many miticides produce unacceptable phytotoxicity to papayas (Lo, 2002). It is therefore necessary to search for alternative approaches for controlling papaya mite pests.

The green lacewing, *Mallada basalis* (Walker) (Neuroptera: Chrysopidae) is common in agricultural fields in Taiwan. The adults feed on nectar and honeydew, but larvae are generalist predators (Wu, 1995). Previous investigations have suggested the potential of this lacewing species as a biological control agent of several species of arthropod pests, including *Phyllocnistis citrella* Stainton, *Aphis* spp, *Nipaecoccus filamentosus* (Cockerell), *Diaphorina citri* Kuwayama, and *P. citri* on citrus; *T. urticae* Koch and *T. kanzawa* on strawberry; and *P. citri* on Indian jujube (Lo, 1997). *M. basalis* can be successfully mass-produced using a microencapsulated artificial diet in a cost-effective manner (Lee, 1994; 1995; 2003). Cold storage techniques have also been established for maintaining various stages for shipping and scheduled releases (Wu, 1992). In addition, tolerance of *M. basalis* to some insecticides, fungicides, and acaricides has been demonstrated (Tzeng and Kao, 1996, Lo, 2002). For all of these reasons, *M. basalis* may be a compatible, viable candidate species for use in integrated pest management programs.

Although there have been many field evaluations of *M. basalis* (Lo, 1997), little is known about its prey selection and feeding behaviors. Knowledge of predator feeding behavior is crucial for evaluating *M. basalis* as a biological control agent of papaya mites. Therefore, this study investigated aspects of the feeding behavior and predatory potential, i.e., foraging schedule, prey acceptance, handling times and consumption rates, of *M. basalis* on *T. kanzawa* and *P. citri* in the laboratory.

MATERIALS AND METHODS

Insect and plant cultures

Papayas:

Papaya seedlings (*Carica papaya* L., ‘Tainung No. 2’) were purchased from a commercial nursery 3-4 weeks after germination. The seedlings were then transferred individually to 9-cm diameter pots, and maintained in a room at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D) until they were approximately 25 cm tall and suitable for rearing mites. The seedlings were watered twice a week, but without any fertilization.

Mites:

Tetranychus kanzawai and *Panonychus citri* were collected from papaya plantations in the Nantou area of Taiwan in 2003 and maintained in separate rooms on papaya seedlings at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D).

Green lacewings:

The *Mallada basalis* used in this study were from a colony that had been maintained in the laboratory continually since 1999 when field collections were made, and thereafter, no wild individuals have been introduced into the colony. For rearing and experiments, lacewings were kept in a room at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D). Larvae were reared on a microencapsulated artificial diet consisting of honey, sugar, Brewer's yeast, yeast autolysate, casein hydrolysate, egg yolk, honeybee larvae and distilled water (Lee, 1994; 1995). The microcapsules had a diameter of 465 µm and a thickness of 10µm. Larvae were reared in plastic pans (40 x 30 x 10.5 cm (L x W x H)). Corrugated paper rolls (10 cm diameter and 1.5 cm thick) were first placed in each pan, and each pan then received two tablespoons of sawdust, 25 ml of microencapsulated diet, and approximately 1,000 green lacewing eggs. Subsequently, diet was added three more times at 3-day intervals in the following amounts: 75, 100 and 25 ml. These amounts corresponded to relative feeding rates of larvae during growth and development. To prevent lacewing larvae from escaping, and to avoid invasion by predators such as ants and spiders, a piece of 200 mesh white screen was taped over the top of each rearing pan.

Most larvae pupated on or inside the corrugated paper rolls after which they were moved to a black acrylic box (45 x 45x 45 cm) for collection of emerging adults. The lid of the box was fitted with a clear acrylic cylinder (15 cm diameter and 20 cm height). Upon emergence, lacewing adults were attracted to light and would fly up into the cylinder. The adults were then placed in another acrylic cylinder with a piece of white paper attached to the inside wall for oviposition. The white paper was changed once every day. Adult lacewings were maintained on a diet of Brewer's yeast and honey (1:1).

To feed adults, diet was applied to a section of plastic slide which was then hung inside the cylinder. Water was provided by wetting a cotton ball.

General experimental procedures

Tests with predators and prey were done on individual pieces of papaya leaf (size range: 225 mm^2 to 3160 mm^2 depending on size of mite life stage to maintain equal densities) which were floated in water with the lower leaf surface facing up in a 9-cm diameter plastic petri dish. Specified numbers of *T. kanzawai* or *P. citri* and one *M. basalis* larva were placed on the leaf with a fine-hair paint brush. The experimental setting kept the lacewing and the mites on the leaf throughout the observational period. The feeding activities of the lacewing larva were continuously observed under a microscope for two hours. Light was provided by a fluorescent illuminator (KL 1500 electronic, SCHOTT) (~95 lux) and room temperature was 26±2°C. Tests were done with all combinations of the three lacewing instars and the four mite instars (egg, larva, nymph, adult female) for a total of 12 treatment combinations for each mite species. Lacewing larvae were in the first day of each instar and prior to testing had been held in individual vials without food for 2, 4 or 8 h for 1st, 2nd and 3rd instars, respectively, as it was thought that different predator instars may withstand different durations of food deprivation to reach the same hunger status. Preliminary tests indicated that these periods of food deprivation would trigger the lacewing foraging immediately after release, but without causing a weakened foraging ability.

The mite densities used in various tests were as follows based on mite's life stage: 33 eggs, 27 larvae, 19 nymphs, and 13 adult females per 100 mm^2 leaf area. These densities correspond to the volumetric ratios of various life stages of the two mites (egg : larva : nymph : adult female = 1: 3 : 5: 7), and were used to make the distances that the lacewings needed to travel to encounter (physically contact) a prey more similar in various tests. The total amount of mites provided in each test was 1.5-fold the amount that a lacewing usually could take during a 2-hour period. Five observations were carried out for each predator-prey combination.

Data collected included a sequential record of prey handling times (measured as the time from a prey encounter to consumption; handling times were then averaged for each individual predator), periods of active foraging (searching plus handling prey) and rest, and the number of prey consumed (including both fully and partially consumed). Prey acceptability was computed as the proportion of encountered prey that were attacked and consumed.

The spatial distributions of *T. kanzawai* and *P. citri* on papaya differ in the field. *T. kanzawai* has a clumped distribution, whereas *P. citri* are more evenly spaced over the leaves. Relative abundance also differs between the two species, with *P. citri* occurring at lower densities in nature than *T. kanzawai*. The mite densities we used in comparisons between species were similar but represent a moderately high field density for *T. kanzawai* but an extremely high density for *P. citri*. To examine response of lacewing larvae to more representative densities of the latter mite, tests with *P. citri* at what we termed "low" density (i.e., 1.7 eggs, 1.4 larvae, 0.9 nymphs, and 0.6 adult females per 100 mm^2 leaf area, and papaya leaves of 14,200 – 17,400 mm^2) were also carried out; these were about 1/20 of the high densities, and represent moderate densities of *P. citri* occurring in the field. Observations for the various predator-prey combinations (3 predator instars x 4 mite instars x 2 mite species x 2 mite densities [for *P. citri*]) were blocked over time and the order of observations was randomized for each block.

Data analyses

Data for various comparisons were subjected to a variance check first to determine if the data meet the assumption underlying analysis of variance that the standard deviations of all categories subjected to the same comparisons are equal. In cases where the data were shown to have unequal variance (e.g., handling times comparisons), square root transformations were performed prior to analysis. Subsequently, normally distributed (or normalized) data were analyzed using analysis of variance (ANOVA), and non-normally distributed data were analyzed with the Kruskal-Wallis test. Means were separated for significance using Fisher's protected LSD procedure. For pair-wise comparisons, a *t*-test assuming equal variance was used to analyze normally distributed data, and a Mann-Whitney W test was used to analyze non-normally distributed data for the comparisons between different mite species, and a *t*-test assuming unequal variance was used for comparisons between the two mite densities. The significance level was set at $P < 0.05$. All analyses were conducted using STATGRAPHICS Centurion XV, software, 2005 (Statpoint, Inc, Herndon, VA. USA).

RESULTS

Prey acceptability

All larval stages of *Mallada basalis* exhibited moderate to high rates of prey acceptability for various life stages of *T. kanzawai* (59-94%) and *P. citri* (62-100%), and in general there were no significant differences in prey acceptability of the lacewing among various life stages of each mite species (Tables 1-3). However, prey acceptability of adult *T. kanzawai* was significantly higher for 3rd instar *M. basalis* than for 1st or 2nd instars ($F = 6.53$; df = 14; $P = 0.01$) (Fig. 1). Otherwise, prey acceptability did not differ among *M. basalis* instars (Figs. 1-3).

Acceptance of *T. kanzawai* and *P. citri* generally did not differ for the various *M. basalis* instars except that 1st instar ($t = 2.83$; df = 4; $P = 0.02$) and 3rd instar ($W = -11.5$; df = 4; $P = 0.02$) predators accepted a greater proportion of *P. citri* larvae than *T. kanzawai* larvae (Figs. 4-6). When *P. citri* were present at the lower density (1.7 eggs, 1.4 larvae, 0.9 nymphs, or 0.6 adult females per 100 mm^2 leaf area), which represents a moderate density in the field, *M. basalis* exhibited prey acceptability rates that were mostly similar to those exhibited when *P. citri* were present at the higher density (33 eggs, 27 larvae, 19 nymphs, or 13 adult females per 100 mm^2 leaf area) (Fig. 7-9).

Foraging time

In 2-h trials, second and third instar lacewings spent most of their time actively foraging (mean = 112.3 min) while 1st instars spent less time actively foraging (mean = 48.5 min) and relatively more time at rest ($P < 0.05$) (Tables 1-3 and Figs. 1-3). The time spent by *M. basalis* foraging for the two mites generally did not differ among various mite life stages (Tables 1-3) except that first instars foraged longer for later-instar *T. kanzawai* than for earlier stages ($F = 8.73$; df = 19; $P = 0.001$) (Table 1).

A comparison of lacewing foraging times between the two mite species showed that there were generally no differences between the two mites, except that 1st (t = 9.83; df = 4; $P < 0.001$) and 2nd (W = -10.5; df = 4; P = 0.03) instar predators actively foraged for a significantly longer time on *P. citri* eggs than on *T. kanzawai* eggs (Figs. 4-6). There were generally no *P. citri* density-related differences in foraging time among *M. basalis* instars. However, first and second instar *M. basalis* took significantly longer to forage on *P. citri* adults at high density than at low density (*t* = 2.43 and 2.89; *P* = 0.04 and 0.02; df = 4, for 1st and 2nd instar, respectively) (Figs. 7-8).

Handling time

In all three *M. basalis* instars, handling times of both *T. kanzawai* and *P. citri* increased with advancing age/stage of prey (Tables 1-3). For example, third instar *M. basalis* consumed a *T. kanzawai* egg in about 7 sec and an adult in about 60 sec, compared to an average of 9 and 30 sec, respectively, for *P. citri*. On both mite species the handling times for *M. basalis* generally decreased with lacewing age (Figs. 1-3). Handling times were shortest for 3rd instars *M. basalis* and longest for 1st instars (Figs. 1-3). Treating the average handling time of each predator as a response and using the analysis of variance to compare means across stages is a robust way to analyze these data. However, comparisons of within and among predator variances indicate that treating these responses as random samples from normal distributions that may only differ in stage means is difficult to justify. This problem cannot be fixed by transforming the data or using nonparametric analyses. Therefore, assessing statistical significance from the available data should be considered as tentative until future studies which record covariates, such as prey size, are carried out.

M. basalis mostly took a shorter time to handle *P. citri* than to handle *T. kanzawai* except for prey eggs where the mean handling time was significantly longer for *P. citri* than for *T. kanzawai* (1st instar: *t* = -4.11; df = 4; *P* = 0.0147; 2nd instar: *t* = -4.93; df = 4; *P* = 0.0079; 3rd instar: *t* = 3.96; df = 4; *P* = 0.0167) (Figs. 4-6). With respect to *P. citri* density, handling times in most cases were consistently shorter for *M. basalis* at the higher *P. citri* density than at the lower one (Figs. 7-9). Greatest statistical differences were observed for 3rd instar predators.

Short-term consumption rate

In 2-h no-choice tests, consumption of *T. kanzawai* by *M. basalis* increased significantly with predator life stage ($P < 0.0001$) (Fig. 1). Third instars consumed ~ 68 *T. kanzawai* adults and ~ 311 eggs, 2nd instars consumed ~ 26 adults and ~ 136 eggs, and 1st instars consumed ~ 4 adults and ~ 20 eggs (Table 1). There was a trend for decreased consumption by *M. basalis* as prey life stage increased. Results were significant between mite immature and adult stages ($P < 0.05$) (Table 1).

A similar trend for increased prey consumption with advancing predator larval instar was observed when *M. basalis* fed on *P. citri* (Table 2 and Fig. 2). In 2-h no-choice trials, 3rd instar lacewing consumed ~ 114 *P. citri* adults, and ~ 303 eggs, while 1st instar consumed ~ 12 adults and ~ 83 eggs, respectively. As with *T. kanzawai*, consumption of *P. citri* by *M. basalis* decreased with advancing prey life stage (Table 2). However, there was a different trend between the two mite species: *M. basalis* consumed statistically similar amounts of *T. kanzawai* eggs, larvae and nymphs, and significantly fewer adults (Table 1); whereas, statistical differences in prey consumption were found for all immature stages of *P. citri*, but not between nymphs and adults (Table 2). In general, all larval instars of *M. basalis* consumed more *P. citri* than *T. kanzawai*. However, differences in consumption between mite species were consistently statistically significant only for adult prey (1st instar: $t = 3.55$, df = 4, $P = 0.008$; 2nd instar: $t = 3.55$, df = 4, $P = 0.007$; 3rd instar: $t = 2.93$, df = 4, $P = 0.02$, respectively) (Figs. 4-6).

Consumption was also influenced by prey density. All instars of *M. basalis* consumed fewer prey when *P. citri* was offered at low density than at high density ($P < 0.05$) (Figs. 7-9). Furthermore, whereas numbers of *P. citri* consumed differed among life stages at the higher prey density (Table 2), at the low density, the only significant differences in prey consumption among mite life stages were found in 2nd instar predators (Table 3). Among *M. basalis* larval stages, 1st instars consumed significantly fewer of each prey life stage at low density than did 2nd or 3rd instars (H = 9.12, F = 14.82, 16.05, 15.32 ; df = 14; P = 0.01, 0.001, 0.0004, 0.0005, respectively, for mite egg, larva, nymph and adult), while there were no significant differences in prey consumption between the second and the third instars (Fig. 3).

DISCUSSION

Green lacewings are generalist predators, preying on many small, comparatively soft-bodied arthropods including aphids, scales, leaf hoppers, whiteflies, thrips, certain lepidopteran insects, and tetranychid and eriophyid mites. Despite their broad prey range, not all species of insects in these categories are accepted as prey, or at least not equally so. For example, Brettell (1979) found that eggs of *Spodoptera littoralis* and *Diparopsis castanea* are too hard for first instars of *Anisochrysa boninensis* to pierce, and Toschi (1965) reported *Meleoma emuncta* likewise fail to penetrate the cuticle of adult aphids *Euthoracaphis umbellariae*. Ru *et al*. (1975) demonstrated that adult *Chrysoperla lanata* refuse to prey on the waxy cabbage aphid, *Brevicoryne brassicae*, but do accept eggs of the noctuid moth, *Trichoplusia ni*. Chen and Liu (2004) found that *Lipaphis erysimi* (Kaltenbach) is not suitable prey for *C. rufilabris* and results in a lower prey consumption. Our results indicated that both *T. kanzawai* and *P. citri* had considerably high acceptability to all three larval instars of *M. basalis*, and that the high acceptability covered all life stages of these mite species.

Additionally, *M. basalis* had a statistically similar degree of prey acceptability to both mites at comparable field densities. *T. kanzawai* and *P. citri* can occur simultaneously on papaya, including co-infestation of the same leaves. Therefore, my results suggest that predation rates may be similar regardless of the species or life stage of mite prey encountered. In general, effective biological control agents should be able to control the early pest life stages (Royama, 1981; Bellows *et al*., 1992). The fact that *M. basalis* shows high prey acceptability to all life stages of both papaya mites is a positive indicator when evaluating this predator for augmentative biological control.

A comparison among *M. basalis* life stages showed that third instars accepted *T. kanzawai* adults to a greater extent than did first and the second instars. In some predators, having a sufficiently large body size relative to the size of the prey is important for successful predation and, hence, may affect relative acceptability (Manly *et al*., 1972; Mollers and Pietruszka, 1987; Sabelis, 1992; Dean and Schuster, 1995). In part, size differences between prey and predator may contribute to prey defense (Pastorok, 1981). In this study, behavioral observations suggest that the lower acceptability of *T. kanzawai* adults by first and second instar *M. basalis* may be attributed to the greater mobility of adult mites, which could make it easier to evade capture.

Most insects spend only a small part of their time feeding as compared to resting and other activities (Matthews and Matthews, 1978; Cohen, 1985; Wiedenmann and O'Neil, 1991). The duration of feeding also depends on the nutritional value of food (Hassell and Southwood, 1978; Lance *et al*., 1986; Slansky and Wheeler, 1989). My study indicated that during a 2-h period following an absence of prey, 2nd and 3rd instar *M. basalis* can continue foraging for most of the time on all life stages of *T. kanzawai* and *P. citri*, whereas first instars spent only half of the time actively foraging. One possible explanation for reduced foraging in first instars is that they require less food to become satiated than later instars.

Foraging generally did not differ between the two mite species or between high and low population densities of *P. citri.* The long period of foraging on both pest mites increases the potential effectiveness of *M. basalis* as a biological control agent. However, first instar lacewings spent a significantly greater proportion of time foraging for *T. kanzawai* nymphs and adults compared to eggs or larvae. The longer activity periods on mite nymphs and adults may be linked to longer handling times needed or lower foraging efficiency for these later life stages. In fact, handling times were longer on mite nymphs and adults than on eggs and larvae despite the fact that the latter were fully consumed by first instar *M. basalis* while nymphs and adults were often partially eaten. Interestingly, there were no significant differences in predator foraging time among life stages of *P. citri* although adult prey were still often partially consumed. In addition, first and second instar *M. basalis* had significantly longer foraging times on *P. citri* eggs compared to *T. kanzawai* eggs regardless of the fact that eggs of both mite species are similar in size. Although untested, these results may reflect differences in nutritional quality among various life stages of different mite species which, indirectly, may have affected foraging time.

Recently, phytoseiid mites have gained the most attention for biological control of teteranychid mites. Zhang (2003) indicated that during the nymphal stages, a

Phytoseiulus persimilis Athias-Herriot attacks 15 eggs of *Tetranychus urticae* and 13 eggs of *T. cinnabarinus*, and a *Neoseiulus californicus* (McGregor) attacks 13 eggs of *T. urticae* and 11 eggs of *T. cinnabarinus*. Whereas an adult female *P. persimilis* consumes 10 to 20 *Tetranychus* spider mites eggs per day, a *N. wormersleyi* female consumes 32 *T. kanzawai* eggs per day; and a *N. longispinosus* female consumes 26 eggs per day. My investigations showed that even as first instars, *M. basalis* possess a much greater predatory capability than phytoseiid mites, and the predatory capability of *M. basalis* increases with mite density. This may enable *M. basalis* to control the mites at high population densities. Although first instar lacewings exhibited a much lower predatory capability than second and third instars, the duration of this stage lasts only about 2–3 days in the field. Thus the longest period of predation occurs when larvae are in the voracious second and third instars. We also found that total consumption was higher on *P. citri* than on *T. kanzawai*, and the difference was especially significant for adult mites. Additionally, relative consumption rates of mite life stages by different instars of *M. basalis* were not the same for the two prey species. These differences may be due to differences in biomass or in the nutritional contents, and it could affect control efficacy of *M. basalis* on these pest mites.

Handling time is an important factor influencing the amount of prey consumed (Rogers, 1972). My results showed that the handling time of *M. basalis* on both mite species increased with prey age and decreased with predator age. This corresponds to most of the findings that handling time is relative to predator-prey size (Cook and Cockrell, 1978; Mills, 1982; Cohen and Tang, 1997). I found that 3rd instar *M. basalis* consume a Kanzawa mite adult within a minute. This handling time is much shorter than those recorded (~4-200 min) for predatory mites feeding on phytophagous mites (Zhang *et al*., 2000; Cote, 2001). The short handling time permits great predatory capability in *M. basalis* to these two pest mites.

With the exception of prey eggs, *M. basalis* spent less time handling *P. citri* than *T. kanzawai*. This may account for the higher consumption of *P. citri*. However, for prey eggs, consumption of *P. citri* was higher than for *T. kanzawai* despite the fact that handling time for the former was longer than for the latter. In fact, I found that the foraging time for eggs of *P. citri* was longer than for eggs of *T. kanzawai*, which likely explains higher consumption of *P. citri* eggs. We do not understand why *M. basalis* spent more time foraging for *P. citri*. One possible explanation is that *P. citri* eggs are less nutritious than those of *T. kanzawai*. However, this needs to be examined.

My study also showed that lacewing handling times were shorter when *P. citri* were offered at the higher density than at the lower one. Handling time is a general component of a predator's behavior. It has an important effect on the functional response through its influence on prey attack rate (Holling, 1959). Predators may increase search and handling efficiency through learning as prey density increases (Holling, 1959). At lower densities, handling times may increase, not only because predators have not learned, but because they may spend a longer time with individual prey to extract as much available nutrients as possible. The shorter handling time of *M. basalis* in response to increased *P. citri* density could increase the level of biological control of mite populations in the field. However, previous theoretical and empirical studies indicate that the type III functional response where attack rates increase proportionally with prey density represents the only response with population regulating possibilities (Holling, 1965; Huffaker *et al*., 1971; Gotelli, 1995). Moreover, research on green lacewing species has shown that they exhibit a type II functional response (Nordlund and Morrison, 1990; Stewart *et al*., 2002), thus, the type of functional response that *M. basalis* has to the citrus and Kanzawa mites needs further research.

With increasing concerns about environmental issues, agricultural pest control has moved increasingly to a more integrated pest management approach with fewer or less chemical application being made. Phytoseiid mites have drawn a great deal of attention for use in the biological control of the phytophagous mites. Many phytoseiids have a shorter life cycle than their prey, equivalent reproductive potential, good searching capacity, and ability to survive on relatively few prey, but phytoseiids are limited in the amount of prey they can consume (Jeppson *et al*., 1975). Coccinellids in the genus *Stethorus* have also been considered for biological control of herbivorous mites, but they are unable to survive on low prey populations, which limits their ability to keep the prey at low density. Staphylinid beetles have too long of a developmental period and lack prey-searching ability. The life cycle of these larger predators is too long to match the reproductive potential of the plant-feeding mites. They consume a large number of prey and thus are capable of reducing high populations; but they are generally unable to prevent the development of injurious mite populations. Green lacewings, with their excellent searching ability, relatively short life cycle, and wide host range, have the potential to prevent the development of high mite populations.

This study demonstrated that a domesticated line of *M. basalis* possesses high prey acceptability to two papaya pest mites of all life stages, relatively short handling time on this two mites, and voracious prey consumption. In addition, they can be mass-produced on artificial diet in a cost-effective manner (USD 0.028 per adult including diet, labor, utility, and facility costs, and one female can produce an average of 736 eggs) (Chang, 2000; Lee, 2003). Chang and Huang (1995) reported that use of *M. basalis* for controlling *Tetranychus* mites on strawberry costs about USD 150 / ha, and is less expensive than chemical pesticides. Thus, *M. basalis* may be promising even as a biopesticide used for inundative release to control the papaya pest mites in screenhouses. However, their field performance, predatory behavior and prey preference in the field situation, and predator-prey release ratios need further investigation to insure the effectiveness of their application in the biological control programs.

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Figure 2-1 Relative foraging and predation efficiency of various larval instars of *M. basalis* on *T. kanzawai* life stages on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Means with different letters are significantly different at *P* < 0.05 (Fisher's protected LSD test). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis; the untransformed means are presented.

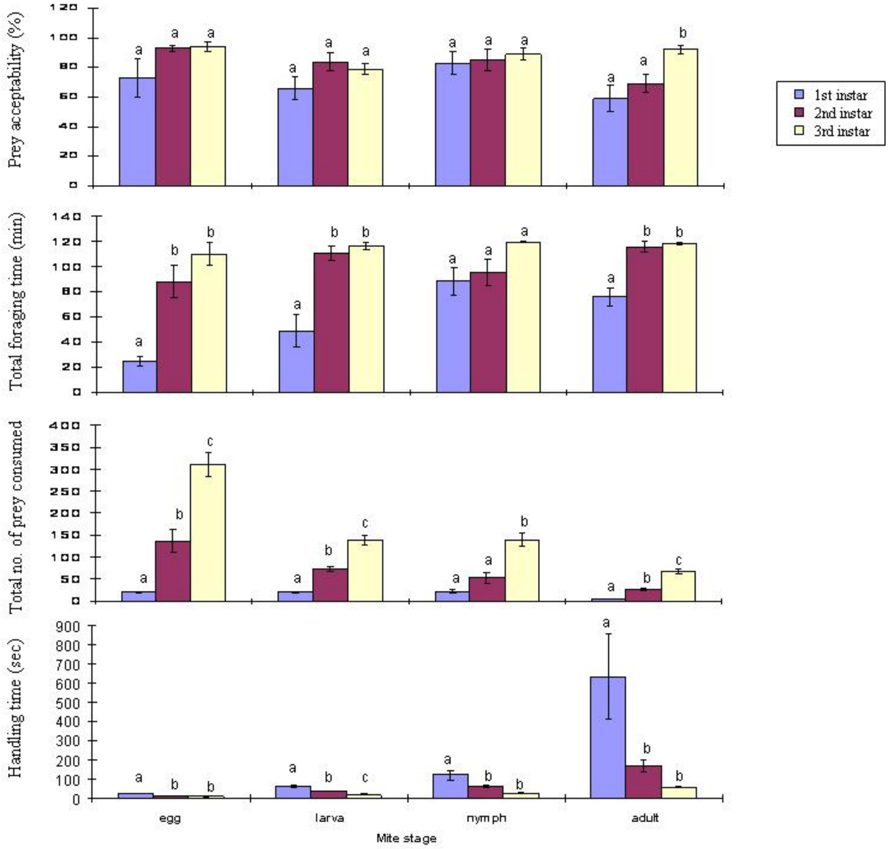

Figure 2-2 Relative foraging and predation efficiency of various larval instars of *M. basalis* on *P. citri* life stages (high density) on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Means with different letters are significantly different at *P* < 0.05 (Fisher's protected LSD test). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis; the untransformed means are presented.

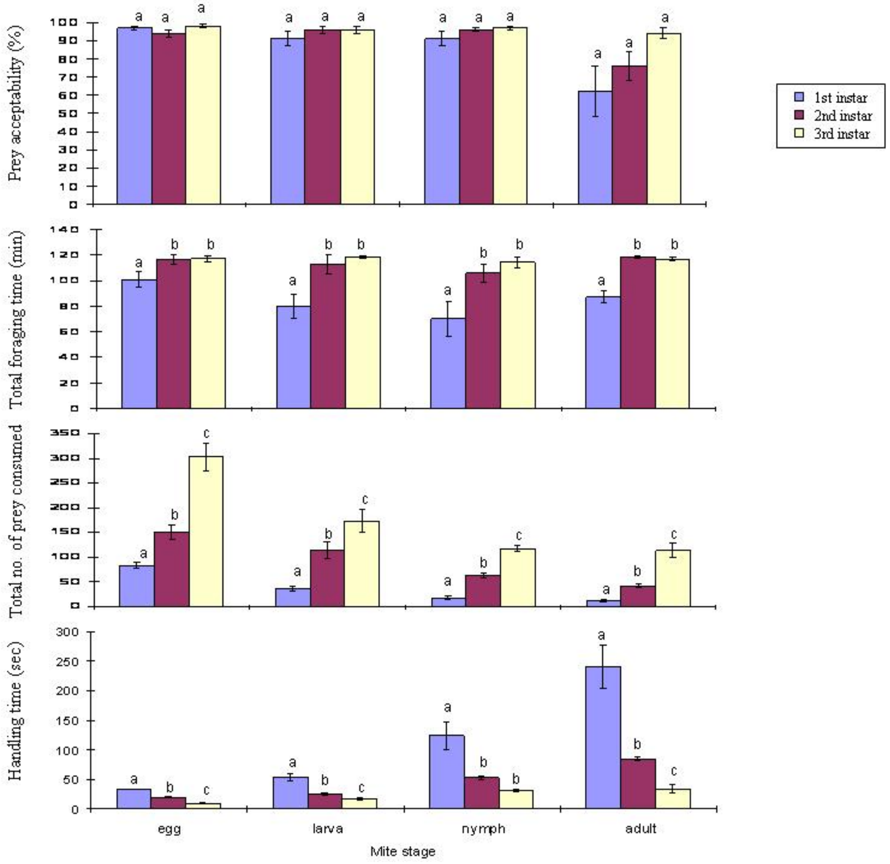

Figure 2-3 Relative foraging and predation efficiency of various larval instars of *M. basalis* on *P. citri* life stages (low density) on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Means with different letters are significantly different at *P* < 0.05 (Fisher's protected LSD test). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis; the untransformed means are presented.

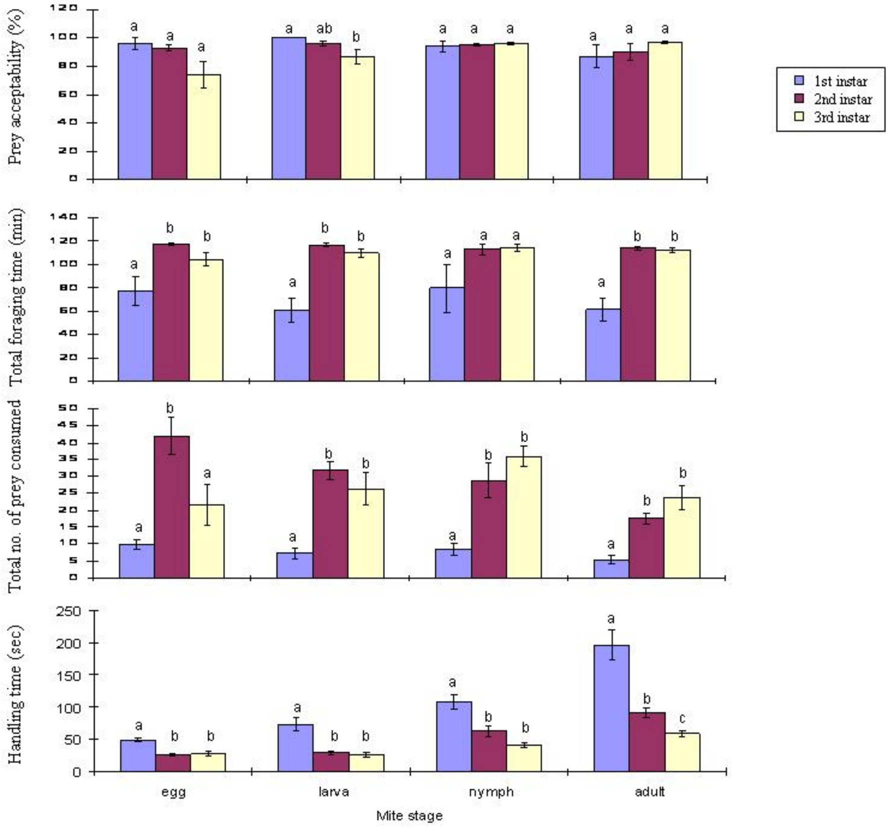

Figure 2-4 Influence of prey species (*T. kanzawai* and *P. citri*) on relative foraging and predation efficiency of first instar *M. basalis* on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Single asterisk indicates a significant difference at *P* < 0.05, and double asterisks indicate a significant difference at *P* < 0.01 (*t*-test for normally distributed data, and Mann-Whitney W test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis; the untransformed means are presented.

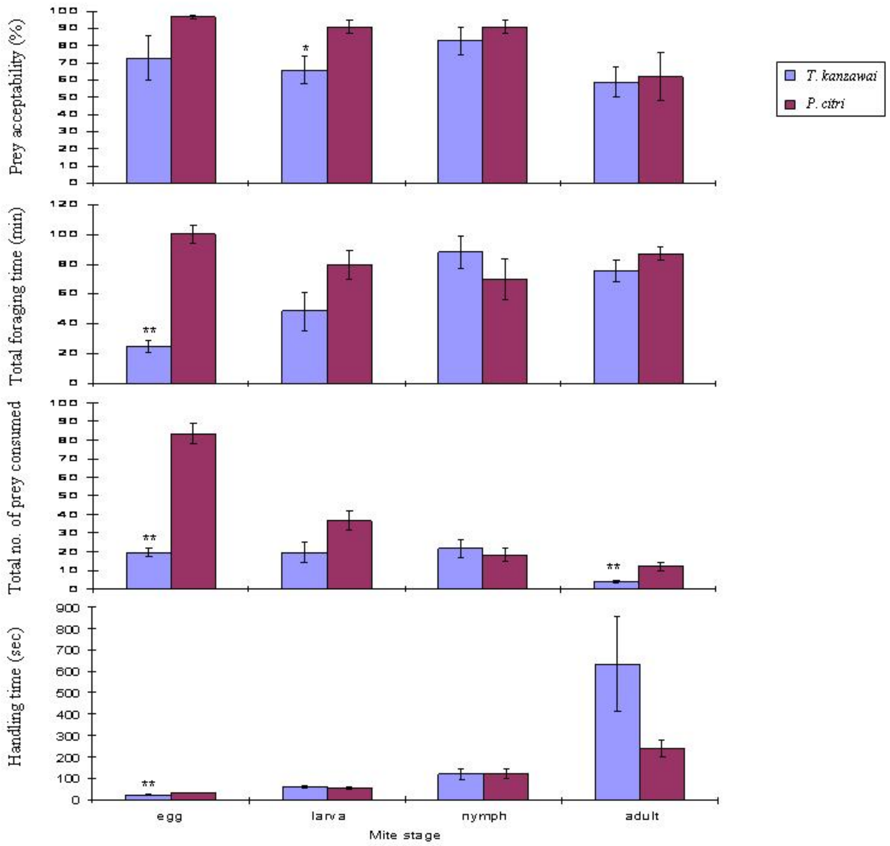

Figure 2-5 Influence of prey species (*T. kanzawai* and *P. citri*) on relative foraging and predation efficiency of second instar *M. basalis* on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Single asterisk indicates a significant difference at $P < 0.05$, and double asterisks indicate a significant difference at $P < 0.01$ (*t*-test for normally distributed data, and Mann-Whitney W test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Handling time were subjected to square root transformation before analysis; the untransformed means are presented.

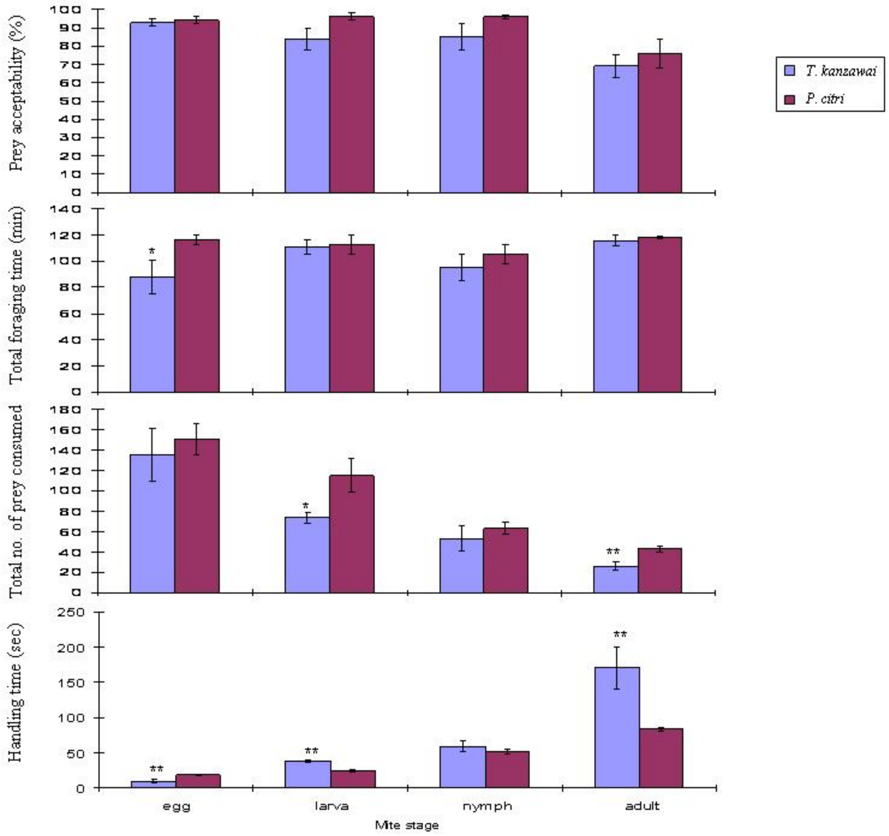

Figure 2-6 Influence of prey species (*T. kanzawai* and *P. citri*) on relative foraging and predation efficiency of third instar *M. basalis* on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Single asterisk indicates a significant difference at *P* < 0.05, and double asterisks indicate a significant difference at *P* < 0.01 (*t*-test for normally distributed data, and Mann-Whitney W test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis; the untransformed means are presented.

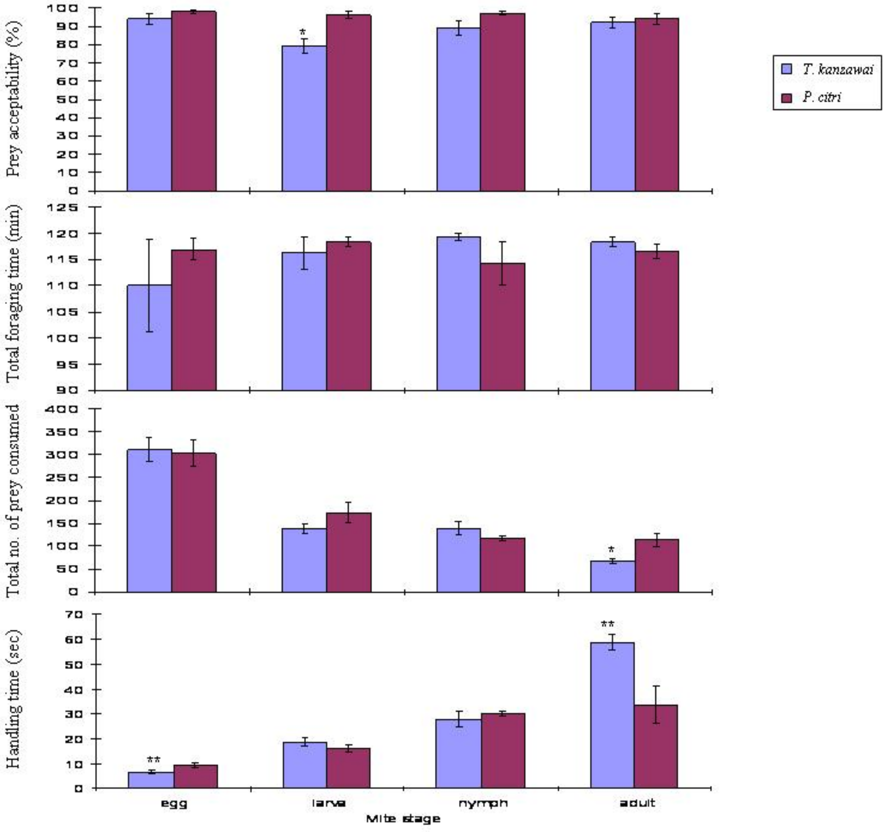

Figure 2-7 Influence of *P. citri* density on relative foraging and predation efficiency of first instar *M. basalis* on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Single asterisk indicates a significant difference at $P < 0.05$, and double asterisks indicate a significant difference at $P < 0.01$ (*t*-test for normally distributed data, and Mann-Whitney W test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis, and a *t*-test assuming unequal variance were used for the analysis. The untransformed means are presented.

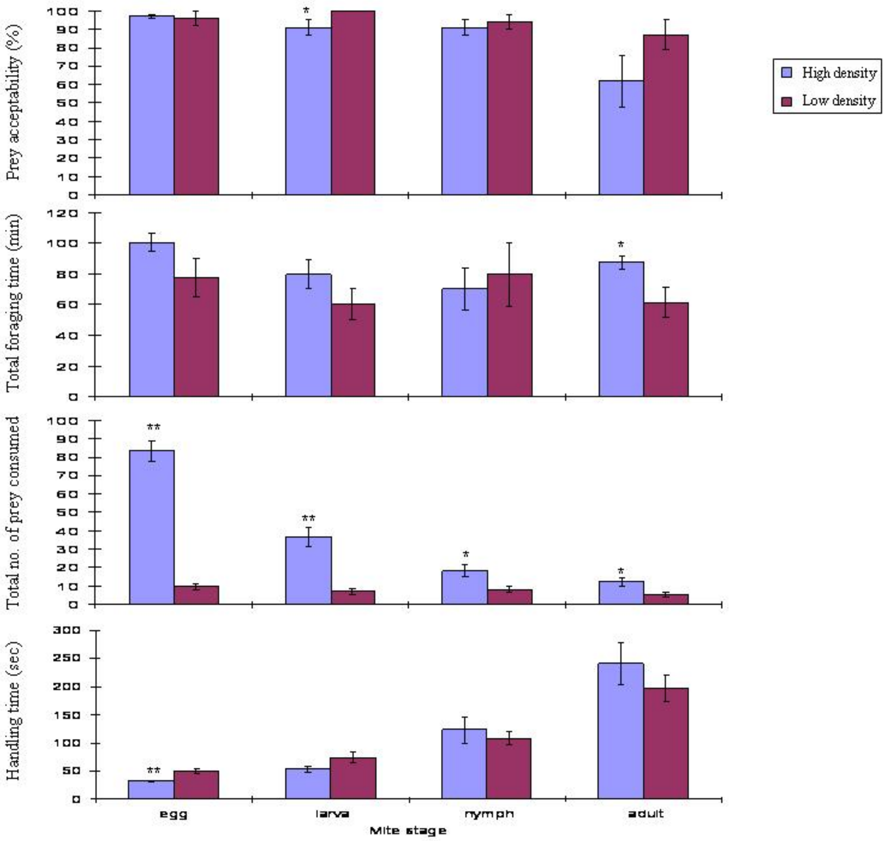

Figure 2-8 Influence of *P. citri* density on relative foraging and predation efficiency of second instar *M. basalis* on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Single asterisk indicates a significant difference at $P < 0.05$, and double asterisks indicate a significant difference at $P < 0.01$ (*t*-test for normally distributed data, and Mann-Whitney W test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis, and a *t*-test assuming unequal variance were used for the analysis. The untransformed means are presented.

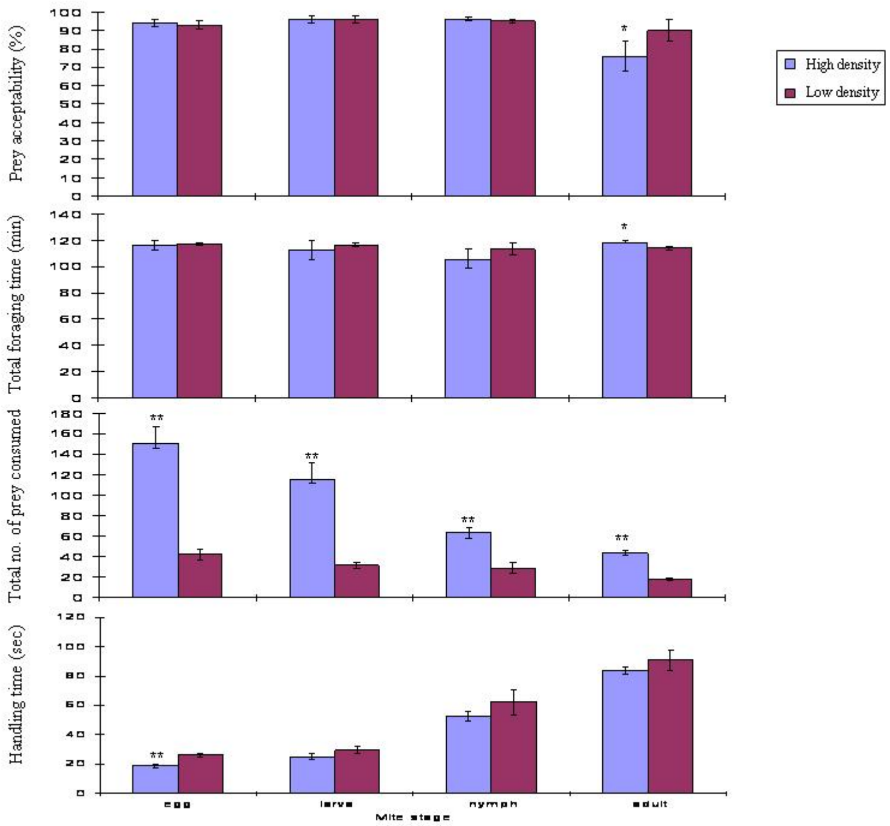

Figure 2-9 Influence of *P. citri* density on relative foraging and predation efficiency of third instar *M. basalis* on papaya (n = 5). Total observation duration = 2 hr. Prey acceptability denotes proportion of encountered prey that are attacked and consumed (including both fully and partially consumed). Total foraging time denotes total time spent by the predator for searching and handling prey. Handling time denotes the time from a prey encounter to consumption. Single asterisk indicates a significant difference at $P < 0.05$, and double asterisks indicate a significant difference at $P < 0.01$ (*t*-test for normally distributed data, and Mann-Whitney W test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Handling times were subjected to square root transformation before analysis, and a *t*-test assuming unequal variance were used for the analysis. The untransformed means are presented.

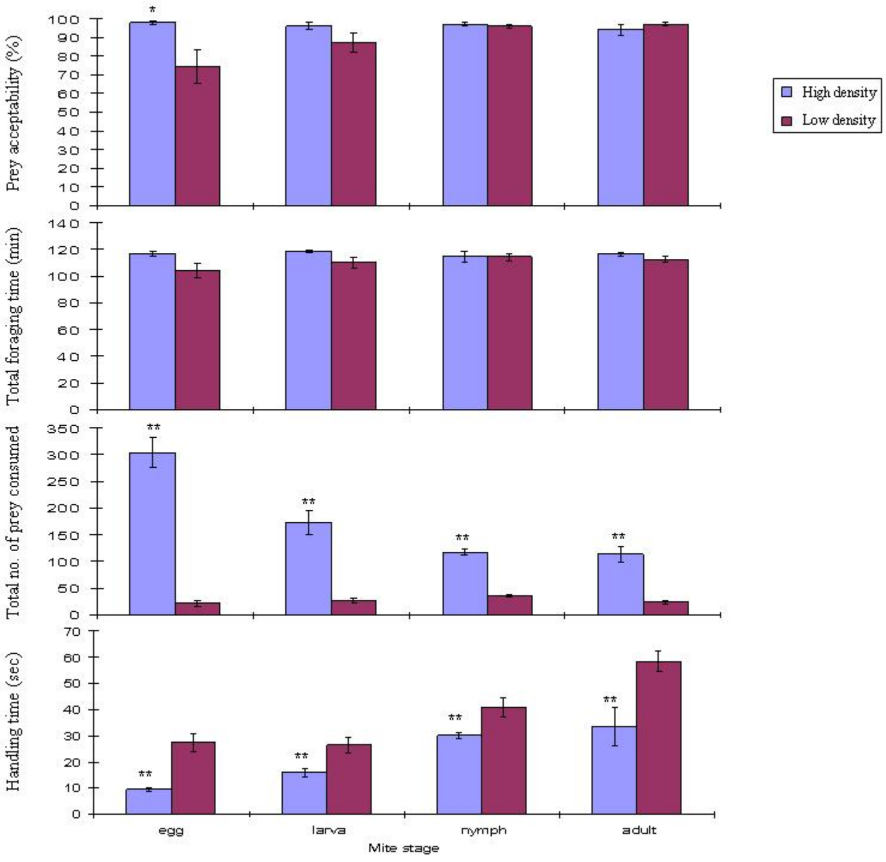

Table 2-1. Foraging behaviors of *M. basalis* larvae preying on *T. kanzawai* on papaya (n = 5)

Stage of *M. basalis*	Mite stage	Feeding behavioral parameter[1] (±SEM)			
		Prey acceptability[2]	Total foraging time[3] (min)	Total no. of prey consumed[4]	Handling time[5] (sec)
1st instar	egg	0.73 ± 0.13a	24.50 ± 4.01a	19.6 ± 2.0a	23.59 ± 2.43a
	larva	0.66 ± 0.08a	48.60 ± 12.99ab	19.6 ± 5.3a	60.95 ± 5.41a
	nymph	0.83 ± 0.08a	88.29 ± 11.24c	21.6 ± 4.9a	120.19 ± 24.09a
	adult	0.59 ± 0.09a	75.85 ± 7.47bc	4.0 ± 0.8b	633.43 ± 221.77b
2nd instar	egg	0.93 ± 0.02a	88.09 ± 12.73a	135.8 ± 26.3a	9.41 ± 2.74a
	larva	0.84 ± 0.06a	110.73 ± 5.52ab	73.6 ± 5.6b	38.39 ± 1.25b
	nymph	0.85 ± 0.07a	95.24 ± 10.20ab	53.4 ± 12.2bc	59.57 ± 7.14b
	adult	0.69 ± 0.06a	115.77 ± 4.23b	26.0 ± 3.7c	170.54 ± 30.73c
3rd instar	egg	0.94 ± 0.03a	110.04 ± 8.84a	311.4 ± 26.7a	6.67 ± 0.74a
	larva	0.79 ± 0.04a	116.22 ± 3.06a	138.2 ± 11.3b	18.76 ± 1.65b
	nymph	0.89 ± 0.04a	119.32 ± 0.68a	139.6 ± 14.2b	27.92 ± 2.94c
	adult	0.92 ± 0.03a	118.38 ± 0.99a	68.2 ± 4.9c	58.78 ± 2.91d

[1] Total observation duration = 2 hr.
[2] Proportion of encountered prey that are attacked and consumed (including both fully and partially consumed).
[3] The time spent searching and handling the prey.
[4] Number of prey that are fully or partially consumed.
[5] The time from a prey encounter to consumption.
Means within the same column of the same *M. basalis* stage followed by the same letter are not significantly different at $P < 0.05$ (Fisher’s protected LSD test; STATGRAPHICS Centurion XV, 2005). Data of handling time before analysis were subject to square root transformation; the untransformed means are presented.

Table 2-2. Foraging behaviors of *M. basalis* larvae preying on *P. citri* at high density on papaya (n = 5)

Stage of *M. basalis*	Mite stage	Feeding behavioral parameter[1] (±SEM)			
		Prey acceptability[2]	Total foraging time[3] (min)	Total no. of prey consumed[4]	Handling time[5] (sec)
1st instar	egg	0.97 ± 0.01a	100.53 ± 6.20a	83.4 ± 5.5a	32.33 ± 0.93a
	larva	0.91 ± 0.04a	79.71 ± 9.50a	36.6 ± 5.1b	53.09 ± 5.90a
	nymph	0.91 ± 0.04a	70.36 ± 13.65a	18.2 ± 3.5c	123.42 ± 23.50b
	adult	0.62 ± 0.14a	87.40 ± 4.57a	12.2 ± 2.2c	240.77 ± 37.75c
2nd instar	egg	0.94 ± 0.02a	116.32 ± 3.68a	150.8 ± 15.6a	18.78 ± 1.31a
	larva	0.96 ± 0.02a	112.49 ± 7.51a	114.8 ± 16.6b	25.06 ± 2.05b
	nymph	0.96 ± 0.01a	105.64 ± 7.24a	63.2 ± 5.6c	52.64 ± 3.41c
	adult	0.76 ± 0.08b	118.32 ± 0.76a	43.2 ± 3.1c	83.86 ± 2.72d
3rd instar	egg	0.98 ± 0.01a	116.91 ± 2.11a	303.0 ± 27.8a	9.35 ± 0.75a
	larva	0.96 ± 0.02a	118.35 ± 0.94a	173.0 ± 22.2b	16.00 ± 1.59a
	nymph	0.97 ± 0.01a	114.29 ± 4.14a	117.8 ± 6.2bc	30.11 ± 1.22b
	adult	0.94 ± 0.03a	116.57 ± 1.34a	114.0 ± 14.8c	33.62 ± 7.38b

[1] Total observation duration = 2 hr.

[2] Proportion of encountered prey that are attacked and consumed (including both fully and partially consumed).

[3] The time spent searching and handling the prey.

[4] Number of prey that are fully or partially consumed.

[5] The time from a prey encounter to consumption.

Means within the same column of the same *M. basalis* stage followed by the same letter are not significantly different at $P < 0.05$ (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005). Data of handling time before analysis were subject to square root transformation; the untransformed means are presented.

Table 2-3. Foraging behaviors of *M. basalis* larvae preying on *P. citri* at low density on papaya (n = 5)

Stage of *M. basalis*	Mite stage	Feeding behavioral parameter[1] (±SEM)			
		Prey acceptability[2]	Total foraging time[3] (min)	Total no. of prey consumed[4]	Handling time[5] (sec)
1st instar	egg	0.96 ± 0.04a	77.53 ± 12.20a	9.8 ± 1.5a	49.78 ± 3.59a
	larva	1.00 ± 0.00a	60.53 ± 10.26a	7.2 ± 1.7a	73.91 ± 9.85b
	nymph	0.94 ± 0.04a	79.78 ± 20.55a	8.4 ± 1.6a	107.75 ± 11.99b
	adult	0.87 ± 0.08a	61.36 ± 9.68a	5.4 ± 1.3a	196.30 ± 23.49c
2nd instar	egg	0.93 ± 0.02a	117.30 ± 1.04a	42.0 ± 5.6a	26.17 ± 2.00a
	larva	0.96 ± 0.02a	116.57 ± 1.40a	31.8 ± 2.8ab	29.46 ± 2.66a
	nymph	0.95 ± 0.01a	112.93 ± 4.50a	28.8 ± 5.1bc	62.20 ± 8.54b
	adult	0.90 ± 0.06a	113.98 ± 1.30a	17.6 ± 1.5c	90.80 ± 7.18c
3rd instar	egg	0.74 ± 0.09a	104.07 ± 5.72a	21.6 ± 5.9a	27.37 ± 3.57a
	larva	0.87 ± 0.05a	109.87 ± 3.65a	26.4 ± 4.8a	26.36 ± 2.95a
	nymph	0.96 ± 0.01a	114.27 ± 2.79a	36.0 ± 3.1a	40.87 ± 3.68b
	adult	0.97 ± 0.01a	112.52 ± 1.93a	23.8 ± 3.6a	58.50 ± 3.87c

[1] Total observation duration = 2 hr.

[2] Proportion of encountered prey that are attacked and consumed (including both fully and partially consumed).

[3] The time spent searching and handling the prey.

[4] Number of prey that are fully or partially consumed.

[5] The time from a prey encounter to consumption.

Means within the same column of the same *M. basalis* stage followed by the same letter are not significantly different at $P < 0.05$ (Fisher’s protected LSD test; STATGRAPHICS Centurion XV, 2005). Data of handling time before analysis were subject to square root transformation; the untransformed means are presented.

CHAPTER 3 - Prey preference of a generalist predator, *Mallada basalis* Walker (Neuroptera: Chrysopidae), between two species of papaya pest mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor) (Acari: Tetranychidae)

ABSTRACT

Prey preference of the generalist predator *Mallada basalis* Walker for two important papaya pest mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor), was investigated in the laboratory. Results of choice tests revealed that none of the three larval instars of *M. basalis* showed a preference for either species of mite or discriminated among the four mite life stages. Instead, lacewing larvae tended to consume whichever mite was encountered. Previous feeding experience on one mite species did not influence subsequent prey choice when lacewings were presented with both mite species. Absence of preference of the predator for the two mite pests found from this study indicates that *M. basalis* has potential as an effective biological control agent for both *T. kanzawai* and *P. citri* when the two mites occur simultaneously or subsequently in papaya plantations.

Key Words: prey choice; feeding behavior; feeding experience; biological control.

INTRODUCTION

Tetranychus kanzawai and *Panonychus citri* are important pests of papaya in Taiwan. *T. kanzawai* is an important pest mite throughout East and Southeast Asia, attacking over a hundred species of plants including many food crops and ornamental plants (Bolland *et al*., 1998; Zhang, 2003). It is normally an outdoor species, but can attack greenhouse plants as well. Mites pierce individual plant cells on the under surface of the leaf and feed by withdrawing chloroplasts. This results in the development of characteristic whitish or yellowish stippling on the upper leaf surface, which join to become brownish blotches that eventually envelope the entire leaf, reducing photosynthesis (Helle and Sabelis, 1985; Yamada and Tsutsumi, 1990; Zhang, 2003). Heavy damage may cause wilting and defoliation, which further impairs plant growth. *P. citri* has a worldwide distribution and is known to feed on over 80 plant species, including citrus, rose, almond, pear, castor bean, and several broadleaf evergreen ornamentals (Bolland *et al*., 1998; Zhang, 2003). This species can feed on both sides of leaves and produces a stippled appearance initially, which develops into pale patches later. With continuous feeding and damage, the leaves become grey, silver or yellow.

Presently, control of these two mite pests depends mainly on chemical applications. However, the intensive application of miticides in combination with the short life cycle and high reproductive rates of mites have led to the development of resistance in these two pest mites to many registered miticides (Cranham and Helle, 1985; Furuhashi, 1994; Masui *et al*., 1995; Yamamoto, *et al*., 1996; Goka, 1998; Aiki *et al*., 2005). In addition, many miticides produce unacceptable phytotoxicity to papaya (Lo, 2002). It is therefore necessary to search for alternative approaches for controlling papaya mite pests.

Mallada basalis (Walker) (Neuroptera: Chrysopidae) is a common predator in agricultural fields in Taiwan that has potential as a biological control agent against several species of arthropod pests, including *Phyllocnistis citrella*, *Aphis* spp, *Nipaecoccus filamentosus*, *Diaphorina citri*, and *P. citri* on citrus; *T. urticae* and *T. kanzawa* on strawberry; and *P. citri* on Indian jujube (Hao, *et al*., 1996; Lo, 1997; Hao, 2002). The larvae are generalist predators while the adults feed on nectar and honeydew (Wu, 1995). *M. basalis* can be successfully mass produced in a cost-effective manner using a microcapsulated artificial diet (Lee, 1994; 1995; 2003). Cold storage techniques have also been established for various stages, i.e., eggs, larvae, and pupae, which facilitates the scheduling of shipments and releases (Wu, 1992). In addition, research has demonstrated that *M. basalis* has some tolerance to selected insecticides, fungicides, and acaricides (Tzeng and Kao, 1996; Lo, 2002). All of these findings suggest that *M. basalis* may be a suitable candidate for augmentative biological control, and may be compatible for use in integrated pest management programs.

Evidence from field investigations suggest that *M. basalis* has some potential for use in biological control programs (Wu, 1992; Chang and Huang, 1995; Lo, 1997; Hao, 2002). In addition, I have investigated aspects of the feeding behavior of *M. basalis*, including foraging schedules, prey acceptance, handling times, and consumption rates, on the two major papaya pest mites, *T. kanzawai* and *P. citri* (see chapter 2). However, little is known about its prey preference. Generalist predators may exhibit prey preference in the presence of mixed prey species (Adashkevich *et al*., 1972; Mills, 1981; Dicke *et al*., 1989; Nordlund and Morrison, 1990; Obrycki and Orr, 1990; Hanna and Wilson, 1991; Hazzard and Ferro, 1991; Hemptinne *et al*., 1993; Legaspi *et al*., 1994). Preference may be based on differences in body size between predator and prey (Manly *et al*., 1972; Mollers and Pietruszka, 1987; Sabelis, 1992; Dean and Schuster, 1995), prey mobility (Allan *et al*, 1987; Schausberger, 1997; Shimoda *et al*., 1997; Eubanks and Denno, 2000), prey defense mechanisms (Hajek and Dahlsten, 1987; Hagler and Cohen, 1991; Shimoda *et al*., 1997), relative abundance of prey (Schmitt, 1987; Huang and Sih, 1990; Holt and Lawton, 1994), prey habitat (Hanna and Wilson, 1991; Hopkins and Dixon, 1997), prey nutritional value (Muma, 1957; Hydorn, 1971; Gagné *et al*., 2002), or the predator's specific nutritional needs (Hagen, 1962; Schausberger, 1997; Gnanvossou, 2002).

Prey preferences exhibited by biological control agents can affect their control efficacy to the target pest (Nordlund and Morrison, 1990; Legaspi, *et al*., 2006; Provost *et al*., 2006). The two pest mites, *T. kanzawai* and *P. citri*, can occur simultaneously at the same papaya plantation and on the same papaya leaves. Therefore, the purpose of this study was to investigate whether *M. basalis* shows a preference for one of the two species of pest mites as well as among different life stages of each mite species. Because preference may be a learned response, tests were also done to determine whether prey preference was linked to the lacewing's previous feeding experience on either of the two mite species.

MATERIALS AND METHODS

Insects and plants

Plants:

Papaya seedlings (*Carica papaya* L., 'Tainung No. 2') were purchased from a commercial nursery 3-4 weeks after germination. The seedlings were then transferred individually to 9-cm diameter pots, and maintained in a room at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D) with fluorescent lights at 7000 lux until they were approximately 25 cm tall and suitable for rearing mites. The seedlings were watered twice a week, but without any fertilization.

Green lacewings:

The *M. basalis* used for this study were from a laboratory colony that had been maintained since 1999 at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D) with fluorescent lights at 500 lux. No wild individuals had been introduced into the colony since then. Lacewing larvae were reared on a microencapsulated artificial diet developed by Lee (1994; 1995). The larval diet consisted of honey, sugar, Brewer's yeast, yeast autolysate, casein hydrolysate, egg yolk, honeybee larvae and distilled water and was produced with a machine developed by Lee (1994). The microcapsules had an average diameter of 465 μm and a thickness of 10 μm. The adult diet contained Brewer's yeast and honey in a 1:1 ratio.

The larvae were reared in plastic pans of 40 x 30 x 10.5 cm (L x W x H). Corrugated paper rolls (10 cm diameter and 1.5 cm thick) were first placed side-by-side in the pan, and then two tablespoons of sawdust, 25 ml of microencapsulated diet, and approximately 1,000 green lacewing eggs were added. Subsequently, diet was added three more times at 3-day intervals in the following amounts: 75, 100 and 25 ml. These amounts corresponded to relative feeding rates of larvae during growth and development. A piece of 200-mesh white screen was taped on the top of the rearing pan to prevent the escape of lacewing larvae and the invasion of their predators (ants, spiders, etc.). Most larvae pupated on or inside the corrugated paper rolls.

After the majority of larvae had pupated, pupae along with the paper rolls were removed and placed in a black acrylic box (45 x 45 x 45 cm) for collection of the adults. Attached to the top of the black box was a clear acrylic cylinder (15 cm diameter x 20 cm high). Upon emergence adult lacewings would fly up into the clear cylinder due to their attraction to light. The adults were then introduced into another acrylic cylinder which had a piece of white paper attached to the wall. The paper served as an oviposition site and was changed daily. Brewer's yeast and honey (1:1) were mixed, stuck on a piece of plastic slide, and hung inside the cylinder for adult food. Water was also provided with a wetted cotton ball.

Mites:

Tetranychus kanzawai were collected from papaya plantations in and around Nantou, Taiwan in 2003 and maintained in a rearing room on papaya seedlings at 26 ± 2°C, 70 ± 10% RH and a photoperiod of 14:10 (L:D) with fluorescent lights at 4000 lux. *P. citri* were also collected from the same fields at the same time and maintained under similar conditions as *T. kanzawai* but in a walk-in growth chamber. The temperature was slightly lower (25±1°C) with light intensity at 5000 lux.

Preference of larval M. basalis for different life stages of either T. kanzawai or P. citri

Separate preference tests were done for each mite species and for each of the three larval stages of *M. basalis*. A piece of papaya leaf (~ 270 mm^2) was floated on water (~ 4 ml) in a Petri dish (5 cm diameter) with the undersurface of the leaf facing up. For each test, a total of 400 mites (100 per life stage: egg, larva, nymph, and adult female) and one *M. basalis* larva were then introduced onto the leaf. Lacewings used for this test were in the second day of each instar, and were fed the microencapsulated artificial diet until tests began to avoid possible effects on prey preference due to hunger. This set-up confined the lacewing and the mites on the leaf throughout the experiment. The high mite densities allowed nearly equal encounter (defined by prey contact with the predator's mouthparts) rates of the lacewing with various life stages of the mites.

The feeding behaviors of the lacewing were observed under a microscope illuminated at an intensity of ~95 lux. During observations, the numbers of each prey life stage encountered and consumed by the lacewing were recorded. Observations were terminated when the total number of mites consumed by the lacewing reached 20. Mites were not replaced throughout the test. However, the initial numbers provided were far more than the 20 mites actually needed and made the change in encounter rates of the lacewing with the mites due to prey depletion negligible. Ten replications were used for each larval stage of *M. basalis* vs. each mite species.

The relative prey encounter rates were expressed as percentages, and were computed by dividing the number of each mite life stage encountered by the total number of mites of all life stages encountered (n = 20) x 100. The relative prey consumption rate was measured as the percentage of the individual life stage of the mites consumed in relation to total mites consumed (i.e., the number of the individual life stage of the mite consumed divided by the total number of mites consumed during each observation x 100). Prey acceptability for each prey life stage was measured as the percentage of encountered prey of each individual life stage that was consumed (i.e., for each individual mite life stage, the number consumed over the number encountered x 100).

Preference of M. basalis for T. kanzawai and P. citri nymphs: effect of relative prey abundance and previous feeding experience

The arena and experimental conditions were the same as for the previous experiment except that tests were done with one hundred nymphs each of *T. kanzawai* and *P. citri*, and one 2-d-old *M. basalis* 2nd instar larva. This *M. basalis* instar was selected as the representative predator life stage because it is intermediate larval stage, has a feeding period and stadial length that exceeds the test period, and can have feeding experience prior to tests. To initiate a test, one lacewing larva was introduced onto the leaf and the number of each species of the mite encountered and consumed by the lacewing was recorded. Each observation was terminated when a total of 20 mites were consumed. The test was repeated 10 times. As in the previous experiment, providing a surplus of each species of mite allowed *M. basalis* to exhibit preference without a limitation of prey.

To determine if offering different proportions of each prey species influenced prey preference in *M. basalis*, the procedure described above was used, but the ratio of *T. kanzawai to P. citri* nymphs was adjusted to achieve 160:40 nymphs and 40:160 nymphs. In addition, this study was repeated on 2nd instar *M. basalis* that had been conditioned with (i.e., had prior feeding experience on) one or the other mite species. This prior feeding experience occurred from hatching until tests were initiated (ca. 4 days). Tests with conditioned predators were done at the following *T. kanzawai:P. citri* ratios – 160:40, 40:160, 100:100. Each observation was terminated when a total of 20 mites were consumed. The test was repeated 10 times.

Data analyses

Relative encounter and consumption rate data for *M. basalis* were analyzed with χ^2 goodness of fit tests (Zar, 1984). Mann-Whitney W test (for two-sample comparisons) and Kruskal-Wallis test (conducted with STATGRAPHICS Centurion XV, software, 2005 (Statpoint, Inc.)) were used to analyze prey acceptability data because these data were not normally distributed.

RESULTS

M. basalis larvae exhibited little or no preference for different life stages of the two mites. Although there were some significant differences in the relative encounter and consumption rates of *M. basalis* larvae when given a choice of equal numbers of the various life stages of *Tetranychus kanzawai* or *Panonychus citri* (χ^2 = 9.23 to 76.31, P < 0.05, df = 3, n = 200; χ^2 goodness of fit test) (Fig. 1 & 2), both encounter and consumption rates corresponded to each other. Furthermore, there were generally no significant differences in prey acceptability of *M. basalis* among the various prey instars (Fig. 1 & 2), except that first instar *M. basalis* exhibited lower prey acceptability of *P. citri* adults than of the earlier life stages (H = 10.94, P = 0.01, df = 3; Kruskal-Wallis test) (Fig. 2).

M. basalis exhibited no preference for either *T. kanzawai* or *P. citri*. When lacewings were offered mixtures of various ratios of the two mites, the percentage of each mite species encountered and consumed corresponded with the proportions of each mite in the mixtures ($\chi^2 = 0.10$ to 2.53, $P > 0.05$, df = 1, n = 200; χ^2 goodness of fit test) (Table 1). In addition, *M. basalis* did not exhibit a change in prey preference following previous feeding experience. When lacewings were fed on either one of the two mite species prior to the tests, the encounter and consumption rates were still proportional to the relative abundance of the mites in the mixtures ($\chi^2 = 0.32$ to 3.13, $P > 0.05$, df = 1, n = 200; χ^2 goodness of fit test) (Table 1). Moreover, prior feeding experience did not influence percentage acceptability (range of means: 95.5 to 100%), as there were no significant differences between the two mite species (*W* ranging from -6.0 to 6.0; $P > 0.05$; Mann-Whitney W test) (Table 1). Direct observations showed that lacewings mostly consumed any mite they encountered.

DISCUSSION

A generalist predator is classified as one whose prey selection is proportional to the relative abundance of the prey species in its environment (Begon *et al*., 1996). However, some predators show prey preference regardless of the relative abundance of the prey (Cock, 1978; Hassell and Southwood, 1978). Green lacewings are generalist predators but are known to exhibit preferences for particular prey when they are simultaneously offered a number of different species. Adashkevich *et al*. (1972) found that in the presence of mixed pests, *Chrysopa* (= *Chrysoperla*) *carnea* attacked aphids first, then thrips, and finally tetranychid mites. Legaspi *et al*. (1994) reported that larvae of *Chrysoperla rufilabris* preferred eggs of *Sitotroga cerealella* and *Helicoverpa zea* over eggs of *Manduca sexta* and *Bemisia tabaci*. Nordlund and Morrison (1990) found that *C. rufilabris* prefer *Heliothis virescens* larvae over the cotton aphid, *Aphis gossypii,* but prefer *A. gossypii* over *H. virescens* eggs. However, in the current study *M. basalis* showed a statistically similar high prey acceptability to both mites, and encounter and consumption rates of *M. basalis* to the two papaya pest mites were proportional to the relative abundance of the mites in the mixture. These results agree with prey acceptability data shown for *M. basalis* when the two mite species were offered in no-choice tests (see chapter 2). These studies indicated that *M. basalis* exhibits no preference for either of the two mites. I observed that *T. kanzawai* and *P. citri* are approximately the same in terms of size, mobility, and ability to escape predators. These factors may account for the similarities in their acceptance by lacewing larvae. Furthermore, these two prey species may also provide similar nutritional value for the lacewing, but that is unknown.

Most organisms experience increases in body dimensions from birth to adulthood. Accompanying these ontogenetic changes, many species undergo extensive shifts in food and/or habitat use. Changes in prey preference associated with the age of the predator have been well documented among invertebrates, including mites (Turner, 1979; Polis, 1984; Hallas, 1988; Lubin *et al*., 1991; Rayor and Uetz, 1993) and insects (Fedorenko, 1975; Thompson, 1975; Johannsson, 1978; McArdle and Lawton, 1979; Lockwood, 1989; Rowe, 1992). Furthermore, the body size of the predator in relation to prey size is also an important factor in the foraging behavior of many predators (Sabelis, 1992). It has been reported that mean prey size increases with body size of the predator (Hespenheide, 1973; McArdle and Lawton, 1979; Rathet and Hurd, 1983; Werner and Gilliam, 1984; Cisneros and Rosenheim, 1997). However, my results showed that larval *M. basalis* exhibited no preference for different life stages of either *T. kanzawai* and *P. citri*, and the prey preference of the lacewing did not change with its age. My previous study also showed that there were generally no differences in prey acceptability of *M. basalis* to *T. kanzawai* and *P. citri* among the lacewing's ages as well as among the mites' life stages in no-choice tests (see chapter 2). The absence of prey preference of the lacewing for either mite species may be because the body dimensions of all the mite lifestages were far smaller than the lacewing's; thus, the effect of the prey size on the foraging behavior of the predator may be trivial in this case.

Investigations of the influence of predator's feeding experience on prey choice have not been extensive or conclusive. Rayor and Munson (2002) investigated the effect of a generalist predator's larval feeding experience on its adult acceptance of chemically-defended prey. The results showed that the adult predatory paper wasp, *Polistes dominulus*, which had experienced unpalatable Buckeye caterpillars (*Junonia coenia*), continued to attack and take back to the nest significantly more *J. coenia* than the wasps which had no experience on the unpalatable caterpillars. Houck (1986) showed that when the coccinellid *Stethorus punctum* (LeConte), an obligate predator of tetranychid mites, was exposed to different ratios of *Tetranychus urticae* and *Panonychus ulmi*, there was a weak but consistent preference for *T. urticae* following preconditioning to this species; but no preference was elicited when the beetle was conditioned to *P. ulmi*. My results showed that previous feeding experience of *M. basalis* on either *T. kanzawai* or *P. citri* had no effects on subsequent prey choice between these two mites. This finding could suggest that both mite species have similar enough characteristics that a generalist predator like *M. basalis* does not discriminate.

Tetranychus kanzawai and *P. citri* are the two most important acarine pests in papaya screenhouse plantations. Both mites can occur simultaneously at the same papaya plantation and on same papaya leaves. *M. basalis* exhibits no prey preference for either *T. kanzawai* or *P. citri* or for different life stages of the two papaya pest mites. These findings increase the probability that *M. basalis* could serve as an effective biological control agent for controlling both mite pests when they occur simultaneously in papaya plantations. In addition, the lacewing's previous feeding experience on one mite species would not affect their subsequent prey choice on the two mites. This would enable *M. basalis* to feed successively on different mite species (prey-switching) without reducing predation potential. It would also allow *M. basalis* to control the second pest mite in the beginning of its invasion since *T. kanzawai* and *P. citri* often occur sequentially in papaya plantations. However, the prey preference of a predator may also be affected by plant architecture and prey spatial distributions (Flaherty and Huffaker, 1970; Eveleigh and Chant, 1982; Gianino and Jones, 1989; Hanna and Wilson, 1991). *T. kanzawai* and *P. citri* have different spatial distribution patterns on the papaya, *T. kanzawai* have a more clumped distribution and aggregate more on the older leaves while *P. citri* have a more even distribution and spread more to the young leaves (Cheng, personal observations). Prey preference of *M. basalis* for the two papaya pest mites in the field needs further investigation before we can fully determine the control efficacy of this lacewing against these two important papaya pests.

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Figure 3-1 Relative prey encounter and consumption rates, and prey acceptability of larval *M. basalis* (A) 1st instar; (B) 2nd instar; (C) 3rd instar to a mixture of various life stages of *T. kanzawai*. Relative prey encounter rate (n = 200) = the number of the specific mite life stage encountered divided by the total number of the mites encountered during the observation x 100; relative prey consumption rate (n = 200) = the number of the specific mite life stage consumed divided by the total number of the mites consumed during the observation x 100; prey acceptability (n = 10) = the number of the specific mite life stage consumed divided by the number of the specific mite life stage encountered during the observation x 100. Asterisk indicates a significant difference in relative prey encounter and consumption rates among the four prey instars (P <0.05, χ^2 goodness of fit tests; Zar, 1984). There were no significant differences in prey acceptability (P <0.05, Kruskal-Wallis tests; STATGRAPHICS Centurion XV, 2005) of *M. basalis* among various life stages of the mites. Error bars represent ±SEM.

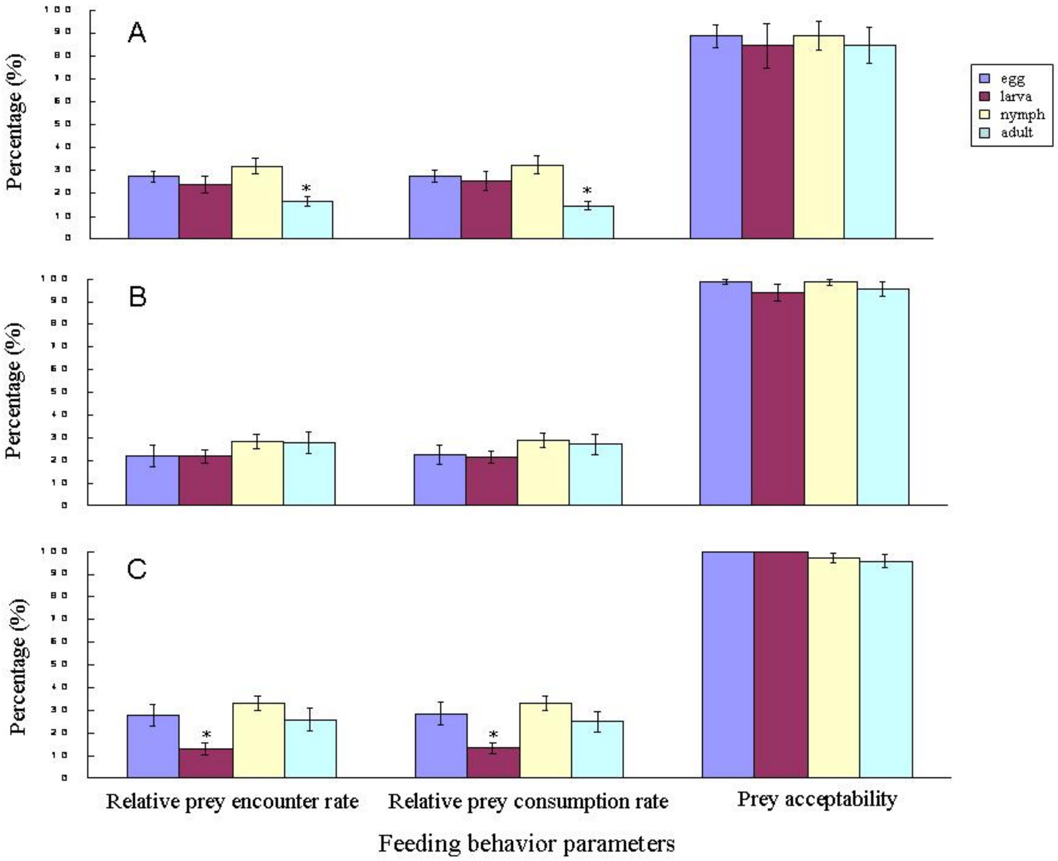

Figure 3-2 Relative prey encounter and consumption rates, and prey acceptability of larval *M. basalis* (A) 1st instar; (B) 2nd instar; (C) 3rd instar to a mixture of various life stages of *P. citri*. Relative prey encounter rate (n = 200) = (the number of the specific mite life stage encountered over the total number of the mites encountered during the observation) x 100; relative prey consumption rate (n = 200) = (the number of the specific mite life stage consumed over the total number of the mites consumed during the observation) x 100; prey acceptability (n= 10) = (the number of the specific mite life stage consumed over the number of the specific mite life stage encountered during the observation) x 100. Asterisk indicates a significant difference in relative prey encounter and consumption rates among the four prey instars at $P<0.05$ (χ^2 goodness of fit test; Zar, 1984). Means with different letters in prey acceptability are significantly different at $P < 0.05$ (Kruskal-Wallis test and Fisher's protected LSD procedure; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM.

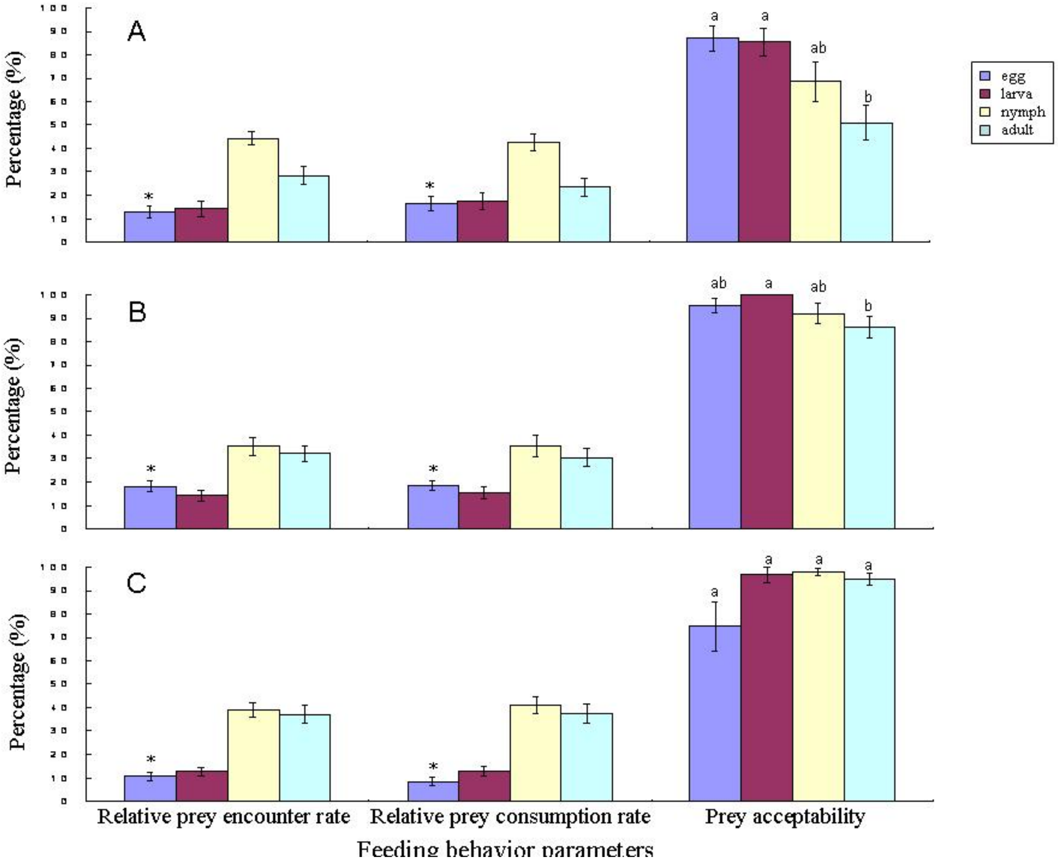

Table 3-1. Relative prey encounter rate, prey consumption rate, and prey acceptability of *M. basalis* larvae against a various ratios of *T. kanzawai* (Tk) and *P. citri* (Pc) nymphs after being conditioned on different foods (artifical diet, Tk, or Pc). The relative encounter and consumption rates of *M. basalis* to the two mites were statistically proportional to the mites ratios offered (χ^2 goodness of fit tests; Zar, 1984), and there were no significant differences in the prey acceptability of *M. basalis* between the two mites of specific ratios (Mann-Whitney W tests; STATGRAPHICS Centurion XV, 2005)

Previous food	Prey provided	% Encounter[1]		% Consumption[2]		% Acceptability[3]	
		Tk	Pc	Tk	Pc	Tk	Pc
Diet	50% Tk & 50% Pc	46.4 ± 2.9	53.6 ± 2.9	46.5 ± 3.0	53.5 ± 3.0	97.5 ± 1.7	97.0 ± 2.1
	20% Tk & 80% Pc	20.9 ± 2.3	79.1 ± 2.3	21.0 ± 2.2	79.0 ± 2.2	100.0 ± 0.0	99.0 ± 1.1
	80% Tk & 20% Pc	75.6 ± 3.6	24.4 ± 3.6	75.5 ± 3.6	24.5 ± 3.6	98.6 ± 1.4	98.9 ± 1.1
Tk	50% Tk & 50% Pc	52.5 ± 3.6	47.5 ± 3.6	52.5 ± 3.6	47.5 ± 3.6	100.0 ± 0.0	100.0 ± 0.0
	20% Tk & 80% Pc	23.0 ± 2.3	77.0 ± 2.3	22.0 ± 2.0	78.0 ± 2.0	95.5 ± 3.0	100.0 ± 0.0
	80% Tk & 20% Pc	75.0 ± 2.6	25.0 ± 2.6	75.0 ± 2.6	25.0 ± 2.6	100.0 ± 0.0	100.0 ± 0.0
Pc	50% Tk & 50% Pc	47.9 ± 4.2	52.1 ± 4.2	48.0 ± 4.1	52.0 ± 4.1	99.3 ± 0.7	99.1 ± 0.9
	20% Tk & 80% Pc	23.7 ± 3.1	76.3 ± 3.1	24.0 ± 3.1	76.0 ± 3.1	100.0 ± 0.0	98.7 ± 0.9
	80% Tk & 20% Pc	77.8 ± 1.8	22.2 ± 1.8	78.0 ± 1.7	22.0 ± 1.7	99.4 ± 0.6	98.3 ± 1.7

[1] (the number of the specific mite species encountered divided by the total number of the two mite species encountered during the observation) x 100; n = 200.

[2] (the number of the specific mite species consumed divided by the total number of the two mite species consumed during the observation) x 100; n = 200.

[3] (the number of the specific mite species consumed divided by the number of the specific mite species encountered during the observation) x 100; n = 10.

CHAPTER 4 - Efficacy of the green lacewing *Mallada basalis* Walker (Neuroptera: Chrysopidae) on two species of papaya mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor) (Acari: Tetranychidae), at different predator:prey release ratios

ABSTRACT

Population suppression of the phytophagous mites, *Tetranychus kanzawai* and *Panonychus citri*, by the green lacewing, *Mallada basalis*, was compared at various predator:prey release ratios on papaya in the laboratory. When each pest mite species was tested separately at a density of ~ 30 mites per seedling, three-day results showed that predator:prey ratios of 1:30, 1:15, and 1:10 resulted to reductions of *T. kanzawai* by 66.8%, 82.6%, and 83.3%, respectively, and reductions of *P. citri* by 41.8%, 75.5%, and 77.2%, respectively. When the two mite species were present simultaneously, total mite reduction were 48.5%, 71.9%, and 74.5% at ratios of 1:30, 1:15, and 1:10, respectively. At predator:prey ratios of 1:30, 1:15, and 1:10 with both mite species present, *T. kanzawai* was reduced by 50.5%, 77.4%, and 79.5%, respectively, and *P. citri* was reduced by 44.1%, 60.3%, and 63.2%, respectively. This study suggests that *M. basalis* could suppress both *T. kanzawai* and *P. citri* of various life stages, and on both sides of papaya leaves. However, *M. basalis* provided relatively greater control of *T. kanzawai* than *P. citri* when the two mites occurred together and when they were offered to the predators separately.

Key Words: biological control; integrated pest management; augmentation; natural enemy; phytophagous mites; predator-prey interactions

INTRODUCTION

Papaya is an important fruit crop in Taiwan, occupying about 3,800 hectares and with an annual production of 126,500 tons (Anonymous, 2006). 'Tainung No. 2' is the principle papaya variety cultivated in Taiwan (Wang, 1991). However, this cultivar is susceptible to papaya ringspot potyvirus (Lin *et al*., 1989), one of the most destructive diseases of papaya (Purcifull *et al*., 1984). This disease is nonpersistently transmitted by a number of aphid species, (Jensen, 1949; Zetter, *et al*., 1968; Wang, 1981; Purcifull *et al*., 1984). Screenhouse cultivation has been developed as an effective means of protecting papayas from aphids and virus infection, with demonstrated rates of protection reaching up to 97% (Shi *et al*., 1990). Therefore, most of the papayas in Taiwan are now cultivated in screenhouses. However, these unventilated structures result in consistently warm conditions which favor outbreaks of acarine pests (Hao *et al*., 1996).

The Kanzawa spider mite, *Tetranychus kanzawai* Kishida, and the citrus red mite, *Panonychus citri* (McGregor), are major pests of papayas in screenhouses (Ho *et al*., 1997), and both occur year round in Taiwan (Anonymous, 2002). *Tetranychus kanzawai* lays eggs on the undersides of leaves where larvae and adults feed on chloroplast cells. This feeding causes upper leaf surfaces to develop characteristic whitish or yellowish stippling, which joins and becomes brownish as mite feeding continues. Heavy damage causes wilting and defoliation, which further reduces plant growth. *Panonychus citri* feeds on both sides of the leaves and produces a stippled appearance initially, which develops into pale patches later. With continuous feeding and damage, the leaves become grey, silver or yellow.

Presently control of these two mite pests depends mainly on chemical applications. However, a growing public concern about the impacts of chemicals on the environment, pest resurgence, secondary pest outbreaks, and increased resistance of arthropods to pesticides has led to a more integrated pest management approach. By combining the advantages of chemical, cultural, and biological control methods, greater permanence of pest suppression may be obtained. In an enclosed environment, it is easier to establish sufficient populations of natural enemy through inoculative or inundative releases so that desired levels of pest control can be achieved without the detrimental effects of chemical pesticides.

The green lacewing, *Mallada basalis* (Walker), is one of the most common chrysopid species in agricultural fields in Taiwan. Previously, investigators have suggested its potential as a biological control agent against several species of arthropods, such as *Phyllocnistis citrella*, *Aphis* spp, *Nipaecoccus filamentosus*, *Diaphorina citri*, and *P. citri* on citrus; *T. urticae* and *T. kanzawa* on strawberry; and *P. citri* on Indian jujube (Lo, 1997). *Mallada basalis* has been successfully mass produced in a cost-effective manner on a microcapsulated artificial diet (Lee, 1995; 2003), and cold storage techniques have been established for various life stages of this predator, which helps in shipping and making scheduled releases (Wu, 1992). *Mallada basalis* also exhibits tolerance to some insecticides, fungicides, and acaricides (Tzeng and Kao, 1996; Lo, 2002). All of these points suggest that *M. basalis* is compatible for use in integrated pest management programs. In addition to many field evaluations documenting its potential as a biological control agent for a number of pests (Hao, *et al*., 1996; Lo, 1997; Hao, 2002), my previous behavioral studies also suggested that *M. basalis* possesses great potential for simultaneously controlling both *T. kanzawai* and *P. citri* on papayas (see chapter 2 and 3). However, information about which predator-to-prey release ratios are effective is lacking. Therefore, this study was designed to determine and compare control efficacies of different predator:prey release ratios of *M. basalis* for *T. kanzawai* and *P. citri* separately, and as a mixture of the two mite species. Information from this study should suggest effective predator:prey release ratios for application of *M. basalis* in augmentative biological control programs on papayas.

MATERIALS AND METHODS

Insects and plants

A laboratory colony of *Mallada basalis* was used for this study. This colony has been reared continuously since 1999 at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D) with microcapsulated artificial diets for larvae (Lee, 1994; 1995), and Brewer's yeast and honey (1:1) for adults. No wild individuals have been introduced into the colony since its inception. The microcapsulated larval diets contained honey, sugar, Brewer's yeast, yeast autolysate, casein hydrolysate, egg yolk, honeybee larvae and distilled water (Lee 1994). The microcapsules were 465±68 μm in diameter and had a thickness of ~10 μm. The larvae were reared in plastic pans (40 x 30 x 10.5 cm (L x W x H)). Corrugated paper rolls (10 cm diameter x 1.5 cm thick) were first placed in the pan, and two tablespoons of sawdust, 25 ml of microcapsulated diet, and approximately 1,000 green lacewing eggs were then introduced into the pan. The diet was added once every three days for a total of four times including the initial one. Amounts of diet provided were 25, 75, 100 and 25 ml, respectively, for the successive feedings. A piece of 200-mesh white screen was taped on the top of the rearing pan to prevent the escape of lacewing larvae and the invasion of predators such as ants or spiders. Most of the pupation occurred on or inside the corrugated paper rolls. After the majority of lacewings pupated, they were removed, along with the corrugated paper rolls, and placed in a black acrylic box (45 x 45x 45 cm) to await adult emergence. The black box consisted of a clear acrylic cylinder (15 cm diameter and 20 cm height) on the top. Upon emerging, the positively phototaxic adults would fly up into the clear cylinder. The adults were moved to another acrylic cylinder which was lined with a piece of white paper on the inside wall for oviposition. The white paper was changed daily. Brewer's yeast and honey (1:1) were mixed, stuck on a piece of plastic slide, and hung inside the cylinder for adult food; water was also provided on a wetted cotton ball.

Tetranychus kanzawai and *P. citri* were collected from the papaya plantations in the Nantou areas of Taiwan in 2003, and maintained on papaya seedlings in separate rooms at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D). Papaya seedlings were maintained in a room at 26±2°C, 70±10% RH and a photoperiod of 14:10 (L:D).

General experimental procedures

Papaya seedlings about 22 cm tall were each infested with approximately 12 *T. kanzawai* (mostly nymphs plus a few female adults) by placing a piece of mite-infested papaya leaf on each seedling. The number of mites with which the seedlings were infested was determined in preliminary tests to generate an initial mite density of about 30 mites per seedling. Two days after infestation, 25 seedlings were selected based on homogenous mite infestation. Five seedlings were then picked at random and the total number of mites on each seedling was counted to estimate the initial average mite density at the beginning of the experiment. The remaining 20 seedlings were placed individually in separate acrylic cages (40 x 40 x 40 cm), and 5 were randomly assigned to each of the three predator:prey ratios and a no-predator treatment, which served as a control. All experimental units were then arranged and kept on shelves with a RCBD experimental design with the blocking factor of different shelves in a walk-in growth chamber (3.6 x 2.7x 2.5 m) at 25±1^{o}C, 70±10% RH and a photoperiod of 14:10 (L:D).

The three predator:prey ratios were created by introducing one, two, or three *M. basalis* 2nd instars to each of the assigned papaya seedlings. The lacewings were initially placed on the upper leaf surface near the top of each seedling. Observations indicated that the lacewings began foraging immediately. Three days after predators were released, the live mites on each of the papaya seedlings were counted and the numbers were recorded for various life stages and for *P. citri* on different sides of papaya leaves, respectively. The experiment was repeated five times for a total of 25 replications per treatment. The same procedures used for *T. kanzawai* were applied to tests with *P. citri*, and for the experiment in which *M. basalis* was exposed to a mixture of *T. kanzawai* and *P. citri*. However, in the latter tests, each papaya seedling was infested with a piece of papaya leaf containing approximately 6 *T. kanzawai* and 6 *P. citri* to generate approximately the same pre-treatment mite density (~ 30 mites per seedling) as in the tests with *T. kanzawai* and *P. citri* separately. Control efficacy was computed as (number mites in untreated check – number mites in specific release ratio treatment) / number mites in untreated check).

Data analysis

Mite data were analyzed with analysis of variance (ANOVA), and significantly different means were separated with Fisher's protected LSD procedures. Mite age class and locality distribution data were analyzed with ANOVA if normally distributed, or with the Kruskal-Wallis test if non-normally distributed. All data were subjected to square root transformation prior to analysis. All analyses were conducted using STATGRAPHICS Centurion XV, software, 2005 (Statpoint, Inc).

RESULTS AND DISCUSSION

Results showed that at all three predator:prey ratios, lacewings significantly reduced the number of *T. kanzawai* alone ($H = 61.10$; df = 124; $P < 0.0001$) (Table 1), *P. citri* alone ($H = 43.69$; df = 124; $P < 0.0001$) (Table 2), and the two mite species together ($H = 47.84$; df = 124; $P < 0.0001$) (Table 3), within three days compared to the untreated check. However, at predator:prey ratios of 1:15 and 1:10, mites numbers were significantly lower than at the 1:30 ratio.

Most studies that have reported on the release of green lacewings for pest management have cited predator to prey ratios between 1:5 and 1:30 (see review by Tulisalo, 1984b). Furthermore, Chang and Huang (1995) reported that *M. basalis* released at the rate of 5 first instar larvae per plant once every three weeks for a total of three releases could provide over 60% control of *T. kanzawai* on strawberry. Hao (2002) indicated that *M. basalis* released at 200 eggs per plant once every 7 – 10 days (9 successive releases) could provide 90% control of *P. citri* on Indian jujube in net houses. Wu (1992) demonstrated that *M. basalis*, when released at 1,000 eggs per tree, could effectively reduce *P. citri* on citrus. Although the latter studies have investigated the application of *M. basalis* against *T. kanzawai* and *P. citri* in the field, none of them were carried out on papayas. My study on papaya indicated that *M. basalis* could significantly reduce both *T. kanzawai* and *P. citri* densities under laboratory conditions with predator:prey ratio of 1:30. A higher release rate of 2 lacewings per 30 mites (1:15 predator:prey) elicited over 80% control of *T. kanzawai*, or about 75% control of *P. citri*, but 3 lacewings per 30 mites (1:10 predator:prey) did not result in any greater effectiveness than the 1:15 ratio, perhaps due to cannibalism or other negative interactions among the predators.

My results also showed that at the time counts were made, the majority of the mites were eggs, and there were no differences in the age class distributions of the mite populations among almost all treatments, including the control ($H = 2.73 – 7.62$; df = 98; $P > 0.05$) (Figs. 1-2). Although the populations of *P. citri* in the 1:15 and 1:10 treatments consisted of fewer eggs than in the 1:30 treatment and the untreated check ($H = 11.00$; df = 98; $P = 0.0117$) (Fig. 2), the same phenomenon was not observed when *P. citri* was presented simultaneously with *T. kanzawai* ($H = 0.47 – 3.31$; df = 97; $P > 0.05$) (Fig. 3).

This implies that *M. basalis* exerted the same level of predation on all age classes of both mite species. This result agrees with my previous finding that *M. basalis* exhibits no preference for different life stages of the two mites (see chapter 3).

Previously, no-choice tests revealed that *M. basalis* had a shorter handling time on *P. citri* than on *T. kanzawai*, which resulted in a greater consumption rate on *P. citri* (see chapter 2). Furthermore, choice tests indicated that *M. basalis* has no preference for either mite species (see chapter 3). It is therefore interesting that in the current study, *M. basalis* controlled *T. kanzawai* more effectively than it did *P. citri* when the two mite species were offered as a mixture (Table 3). One explanation may be that my previous study was conducted on a very small spatial scale (i.e., a leaf area of 270 mm^2) and was of short duration (observations ended when a total of 20 mites were consumed). In contrast, the current study was done over 6 days and was conducted on a larger scale (20-cm seedling). These differences allowed for changes in population density between the two mite species as well as different spatial distributions when they co-occurred on the same papaya leaves. For example, we found that when papaya seedlings were infested with approximately the same amount of both *T. kanzawai* and *P. citri* without introducing lacewings, the population density of *T. kanzawai* was always higher than that of *P. citri*. I observed a similar trend on papayas in the field (Cheng, personal observation). I also noted that in tests with individual mite species, *T. kanzawai* were mostly distributed on the undersurfaces of the papaya leaves, while *P. citri* was distributed about equally on both sides of the papaya leaves. However, when papaya seedlings were infested with both *T. kanzawai* and *P. citri* at approximately the same initial density, *T. kanzawai* became the dominant species and distributed itself on the undersurfaces of the leaf while *P. citri* became the secondary one, and was distributed mainly on the upper surfaces. However, the local distribution of the two mite species probably does not explain differences in observed predation rates because results (Fig. 4) showed that there were no differences in mite populations on either side of the leaf (H = 5.10 and 2.00; df = 98; P = 0.16 and 0.58 for undersurfaces and uppersurfaces of the leaf, respectively), suggesting that *M. basalis* produced the same degree of control on both leaf surfaces.

When two species of prey have a shared enemy, the enemy might attack the one with the higher density to a greater degree than the one at lower density (Holt, 1977; Janssen *et al.*, 1998; Liu, 2006) because of more frequent encounters of the more abundant species and possibly adaptation or learning. These arguments likely explain why *M. basalis* attacked *T. kanzawai* more than *P. citri*. Besides, *T. kanzawai* exhibited a more clumped distribution whereas *P. citri* was distributed more evenly on papaya leaves. Therefore, lacewings may have foraged more efficiently on prey with a clumped distribution, but this remains to be determined experimentally. In addition to the different spatial distribution patterns of the two mites on a papaya leaf, *T. kanzawai* are more likely to be found on older leaves in the field (Chang and Huang, 1995). Conversely, *P. citri* are found more often on younger leaves (Cheng, 1966). In papaya plantations, this additional difference in prey location could have an added influence on predator foraging efficiency and predator-prey dynamics as leaves of different maturity occupy different heights on larger papaya trees. How the interactions among the predator and prey, and the different distribution patterns of the two mites on papayas at different spatial scales would influence the biological control capability of *M. basalis* needs further investigation.

The environmental conditions of screenhouses are easier to manipulate than those in the open field. This capability could increase the success of biological control applications. For example, previous researchers have suggested that the use of lacewings is best suited to glasshouses or other enclosed systems (Daane *et al.*, 1997). Chang and Huang (1995) reported that use of *M. basalis* for controlling *Tetranychus spp.* mites on strawberry costs about USD 150 / ha, and is cheaper than use of the chemical means. Although it has been indicated that fecundity, longevity, feeding and searching ability of green lacewings were decreased with the number of generations in mass rearing, the common green lacewing has been proven to be a resilient laboratory insect which when reared on a diet of *Sitotroga* eggs, yeast hydrolysate, and sugar, retain their properties rather well through many generations (Tulisalo and Tuovinen, 1975; Ushchekov, 1976; Shuvakhina, 1977; Radzivilovskaya, 1980; Tulisalo, 1984a). The current study demonstrated that the domesticated line of *M. basalis* could suppress both *T. kanzawai* and *P. citri* populations in laboratory cages. However, how they will survive under field conditions, and what their predatory potential might be is unknown and needs further investigation. My study showed that *M. basalis* at predator:prey ratio of 1:30 could provide significant control of both *T. kanzawai* and *P. citri*. But, it also indicated that a higher release rate is needed when this two mites occur simultaneously. I found less than half the released lacewings inside the cages at the end of the tests, which reflects the kind of losses observed under field conditions. However, field conditions are even more complicated because dispersal, intraguild predation, parasitism, and starvation all can influence the effectiveness of the augmentation program. Evaluations in real agricultural settings with higher predator: prey ratios than those used in our laboratory tests are needed before recommendations can be made to growers.

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Figure 4-1 Age class distribution (shown as the percentage of each of the 4 mite instars) of *T. kanzawai* among various predator:prey ratios of 1:30, 1:15, 1:10 and an untreated check (n = 24-25) 3 days after release of *M. basalis*. Means with the same letters are not significantly different at *P* < 0.05 (*F*-test for normally distributed data, Kruskal-Wallis test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Data were subjected to square root transformation before analysis; untransformed means are presented.

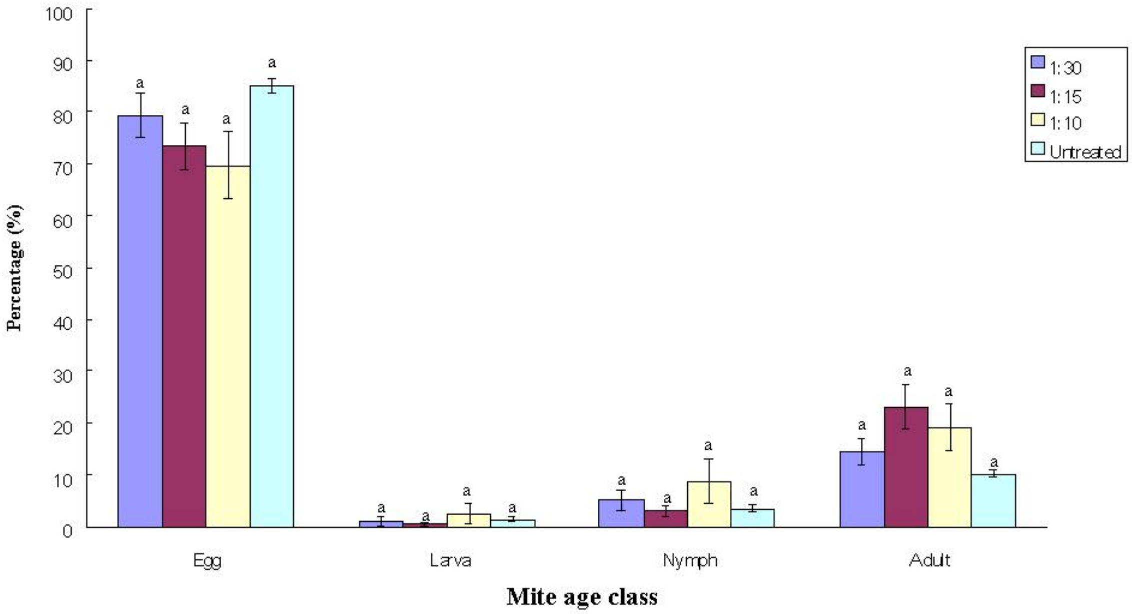

Fig. 1.

Figure 4-2 Age class distribution (shown as the percentage of each of the 4 mite instars) of *P. citri* among various predator:prey ratios of 1:30, 1:15, 1:10 and an untreated check (n = 24-25) 3 days after release of *M. basalis*. Means with different letters are significantly different at *P* < 0.05 (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Data were subjected to square root transformation before analysis; untransformed means are presented.

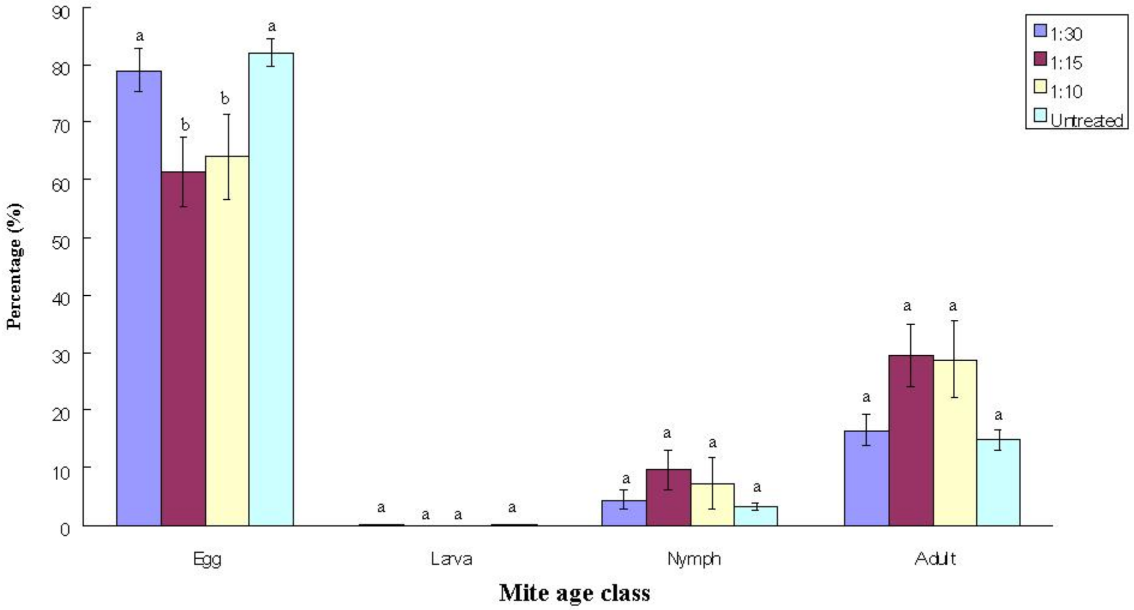

Fig. 2.

Figure 4-3 Age class distribution (shown as the percentage of each of the 4 mite instars) of *T. kanzawai* (A) and *P. citri* (B) among various predator:prey ratios of 1:30, 1:15, 1:10, and an untreated check when the two mites present simultaneously (n = 24-25) 3 days after release of *M. basalis*. Means with the same letters are not significantly different at $P < 0.05$ (*F*-test for normally distributed data, Kruskal-Wallis test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Data were subjected to square root transformation before analysis; untransformed means are presented.

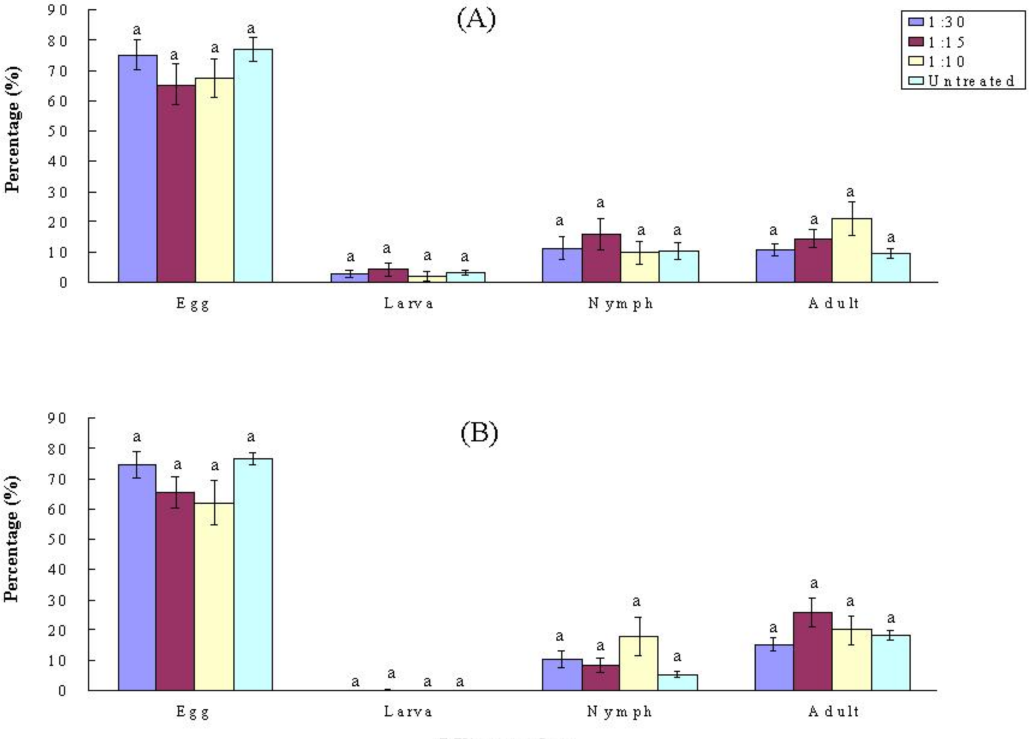

Fig. 3.

Figure 4-4 Locality distribution (shown as percentages) of *P. citri* on papaya leaves among various predator:prey ratios of 1:30, 1:15, 1:10, and an untreated check (n = 24-25) 3 days after release of *M. basalis*. Means with the same letters are not significantly different at $P < 0.05$ (*F*-test for normally distributed data, Kruskal-Wallis test for non-normally distributed data; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM. Data were subjected to square root transformation before analysis; untransformed means are presented.

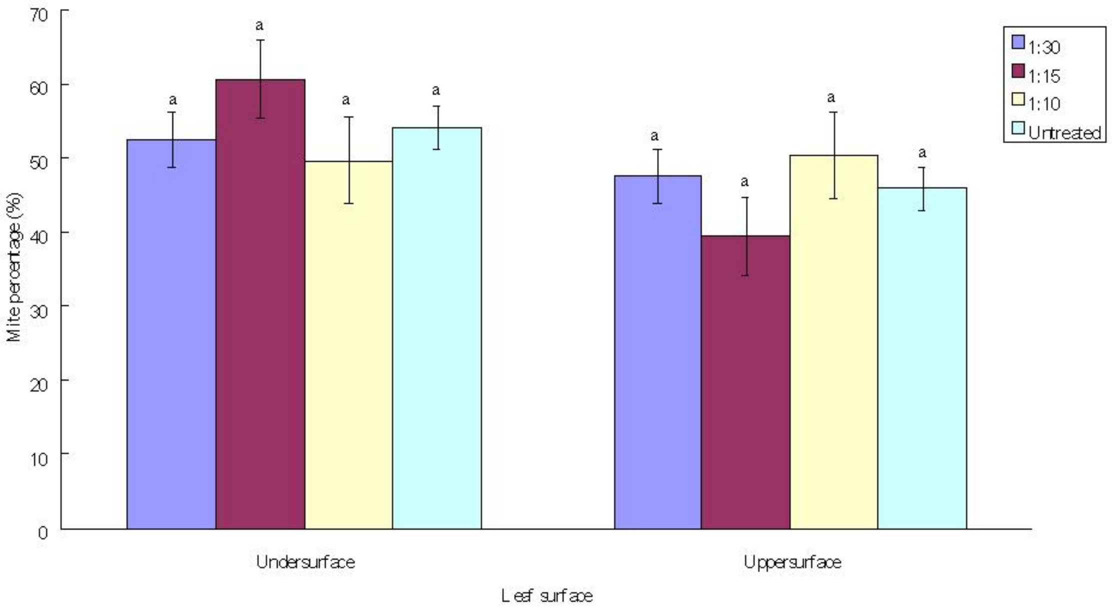

Fig. 4.

Table 4-1. Control efficacy of different predator:prey release ratios of *M. basalis* to *T. kanzawai* (n = 25)

Predator:prey ratio	Mean no. mites / seedling (±SEM)[1]	Control efficacy
1 : 30	42.4 ± 9.0b	66.8%
2 : 30	22.2 ± 4.7c	82.6%
3 : 30	21.3 ± 4.0c	83.3%
Untreated Check	127.7 ± 7.8a	

[1] Mean no. mites per seedling followed by the same letter are not significantly different at $P < 0.05$ (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005). Data were subject to square root transformation prior to analysis. Untransformed means are presented.

Table 4-2. Control efficacy of different predator:prey release ratios of *M. basalis* to *P. citri* (n = 25)

Predator:prey ratio	Mean no. mites / seedling (±SEM)[1]	Control efficacy
1 : 30	67.0 ± 14.5b	41.8%
2 : 30	28.3 ± 6.7c	75.5%
3 : 30	26.2 ± 8.0c	77.2%
Untreated Check	115.1 ± 18.3a	

[1] Mean no. mites per seedling followed by the same letter are not significantly different at $P < 0.05$ (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005). Data were subject to square root transformation prior to analysis. Untransformed means are presented.

Table 4-3. Control efficacy of different predator:prey release ratios of *M. basalis* to mixtures of *T. kanzawai* (Tk) and *P. citri (Pc)* (n = 25)

Predator:prey ratio	Mean no. mites / seedling (±SEM)[1]			Control efficacy		
	Tk	Pc	Total	Tk	Pc	Total
1 : 30	42.8 ± 0.3b	22.8 ± 3.0b	65.6 ± 11.0b	50.5%	44.1%	48.5%
2 : 30	19.6 ± 4.0c	16.2 ± 2.6bc	35.8 ± 4.7c	77.4%	60.3%	71.9%
3 : 30	17.8 ± 5.8c	15.0 ± 2.5c	32.7 ± 6.1c	79.5%	63.2%	74.3%
Untreated Check	86.6 ± 11.7a	40.7 ± 4.3a	127.3 ± 12.0a			

[1] Mean no. mites per seedling followed by the same letter are not significantly different at $P < 0.05$ (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005). Data were subject to square root transformation prior to analysis. Untransformed means are presented.

CHAPTER 5 - Effect of temperature on prey consumption rate of the green lacewing *Mallada basalis* Walker (Neuroptera: Chrysopidae) to two species of pest mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor) (Acari: Tetranychidae)

ABSTRACT

The green lacewing, *Mallada basalis*, has been shown to have high potential as a biological control agent against two mites species of economic-importance on papaya: the Kanzawa mite, *Tetranychus kanzawai*, and the citrus mite, *Panonychus citri*. However, the impact that this predator can have on mite populations is dependent on prevailing environmental temperatures, which influence predator-prey dynamics by affecting developmental rates, survival, reproduction, and longevity. This study investigated the consumption rates of 2nd instar *M. basalis* on *T. kanzawai* and *P. citri* at five temperatures (15, 20, 25, 30, and 35 ^{o}C) in the laboratory. Results indicated that prey consumption by 2nd instar lacewings was temperature-dependent between 15 and 30 ^{o}C for both mite species, but consumption declined at 35 ^{o}C. Numbers of *T. kanzawai* nymphs consumed in a 30-min trial ranged from 16.3 ± 1.0 at 15 ^{o}C to 45.7 ± 2.5 at 30 ^{o}C. On *P. citri*, predators consumed 26.4 ± 1.8 nymphs at 15 ^{o}C and 48.0 ± 3.3 at 30 ^{o}C. There were slightly different trends in the consumption rate of the lacewing in response to the five temperatures between the two mites, and this might be the result of the different spatial distribution patterns of the two mites as well as the different handling times of the lacewing for the two mites. Considerably high prey consumption rates at a wide temperature range including the temperature as low as 15 ^{o}C suggests that *M. basalis* may be suitable for year-round application in Taiwan against both *T. kanzawai* and *P. citri*. However, further investigations on the effect of temperature on the predatory potential of *M. basalis* under field conditions are needed for effective application of this lacewing in papaya mite management programs.

Key Words: phytophagous mites; predator-prey interaction; feeding behavior; predation rate; biological control

INTRODUCTION

The Kanzawa spider mite, *Tetranychus kanzawai* Kishida, and the citrus red mite, *Panonychus citri* (McGregor), are two important acarine pests of a wide range of crops in many parts of the world (Bolland *et al*., 1998; Zhang, 2003). They cause injury by penetrating their stylets into plant tissue to feed on cell chloroplasts. This results in leaf stippling, wilting, and defoliation, which ultimately reduces plant growth and productivity. Intensive application of miticides, combined with short life cycle and strong fertility of the mites, have led to the development of resistance to most registered miticides (Cranham and Helle, 1985; Furuhashi, 1994; Masui *et al*., 1995; Yamamoto, *et al*., 1996; Goka, 1998; Aiki *et al*., 2005). Therefore, the search for alternative control measures has become essential.

Mallada basalis (Walker) is a common chrysopid in agricultural fields in Taiwan. Previous investigations have suggested its potential for controlling several species of arthropods. These include *Phyllocnistis citrella*, *Aphis* spp, *Nipaecoccus filamentosus*, *Diaphorina citri*, and *P. citri* on citrus; *T. urticae* and *T. kanzawa* on strawberry; and *P. citri* on Indian jujube (Hao, *et al*., 1996; Lo, 1997; Hao, 2002). A further benefit is that *M. basalis* can be mass-produced on a microcapsulated artificial diet in a cost-effective manner (Lee, 1995; 2003). In addition, cold storage techniques have been established to store immature life stages for shipment and scheduled releases (Wu, 1992). Finally, research has demonstrated tolerance in *M. basalis* to some insecticides, fungicides, and acaricides (Tzeng and Kao, 1996; Lo, 2002). All of these suggest that *M. basalis* is very compatible for use in integrated pest management.

My earlier studies have provided further support that *M. basalis* has high potential as a biological control agent for both *T. kanzawai* and *P. citri* on papaya (see chapters 2 – 4). However, one factor that has not been investigated is how temperature influences predator-prey interactions between *M. basalis* and papaya mites. In general, temperature plays a crucial role in the bioecology of insects. Studies have demonstrated effects of temperature on development and population growth (Obrycki and Tauber, 1982; Tauber *et al*. 1987; Lopez-Arroyo *et al*. 1999; Pervez, 2004), foraging behavior, functional response, and predation capability of a number of insect species (Dreisig, 1981; Flinn, 1991; Runjie *et al*., 1996; Cocuzza *et al*., 1997; Nielsen, 1999; Mohaghegh *et al*., 2001; Flinn and Hagstrum, 2002; Menon *et al*., 2002; Perdikis *et al*., 2004; Simmons and Legaspi, 2004; Mahdian *et al*., 2006; Parajulee *et al*., 2006). This study investigated the effect of temperature on the consumption rate of *M. basalis* to two species of pest mites, *T. kanzawai* and *P. citri*, to provide information for understanding and effectively applying *M. basalis* in augmentative biological control programs for these two pest mites.

MATERIALS AND METHODS

Insects and plants

Green lacewings:

A laboratory colony of *Mallada basalis* was used for this study. This colony has been reared continuously, with no introduction of wild individual, since 1999 at 26±2 ^{o}C, 70±10% RH and a photoperiod of 14:10 (L:D) on microcapsulated artificial diets developed for larvae (Lee, 1994; 1995), and a Brewer's yeast and honey (1:1) diet for adults. The larvae were reared in plastic pans of 40 x 30 x 10.5 cm (L x W x H). Corrugated paper rolls (10 cm diameter and 1.5 cm thick) were first placed in the pan, after which two tablespoons of sawdust, 25 ml of microcapsulated diet, and approximately 1,000 green lacewing eggs were added. The diets were replenished three times with 75, 100 and 25 ml of diet being added on a 3-day schedule. A piece of 200-mesh white screen was taped on the top of the rearing pan to prevent the escape of lacewing larvae and to prevent invasion by their predators (e.g., ants, spiders, etc).

After the majority of the larvae formed cocoons, they were removed along with the paper rolls to a black acrylic box (45 x 45x 45 cm). A clear acrylic cylinder (15 cm diameter and 20 cm high) was attached to the top of the black box. Upon emergence, adults would fly into the clear cylinder. Adults were then introduced into another acrylic cylinder that was lined on the inside wall with a piece of white paper, which served as a substrate for oviposition. The paper was changed daily. Brewer's yeast and honey (1:1) were mixed, stuck on a piece of plastic slide, and hung inside the cylinder for adult food, and the water was also provided through a wetted cotton ball.

Mites:

Tetranychus kanzawai were collected from the papaya plantations in Nantou areas, Taiwan in 2003, and maintained on papaya seedlings at 26 ± 2 °C, 70 ± 10% RH and a photoperiod of 14:10 (L:D). *Panonychus citri* were also collected from the same fields at the same time as mentioned above, and maintained in a walk-in growth chamber on papaya seedlings at 25±1 °C, 70±10% RH and a photoperiod of 14:10 (L:D).

Plants:

Papaya seedlings (*Carica papaya* L., 'Tainung No. 2') were purchased from a commercial nursery 3-4 weeks after germination. The seedlings were then transferred individually to 9-cm diameter pots, and maintained in a room at 26±2 °C, 70±10% RH and a photoperiod of 14:10 (L:D) until they were approximately 25 cm tall and suitable for rearing mites. The seedlings were watered twice a week, but without any fertilization.

Experimental procedures

A piece of papaya leaf (~ 470 mm^2) with the undersurface facing up was floated on water (~ 4 ml) in a 5-cm diameter Petri dish. One hundred mite nymphs (either *T. kanzawai* or *P. citri*) were introduced onto the leaf and the unit was then placed in a growth chamber at 70 ± 10% RH and one of the following temperatures: 15, 20, 25, 30 and 35 °C. One green lacewing second instar larva (at their 2nd day) which had been starved and kept in the growth chamber for 4 h prior to the test was then added onto the leaf in the Petri dish. The Petri dish was then covered with the lid. Thirty minutes later, the number of the mites consumed by the lacewing was recorded. Tests for each mite species and at each temperature were replicated at least 20 times. Because of a limited numbers of growth chambers, tests were blocked over time and the order was randomized for each block.

Data analysis

Extreme data (where total consumption was less than 10 mites for both mite species) were excluded from the analysis. To equalize the variance among temperatures, the first 20 sets of data for each species were used for the analysis. Since the shape of the data was not consistent with an assumption of normality, the Kruskal-Wallis test was used to test for differences among the distributions. For those situations where the hypothesis of equal distributions was rejected at the type one error rate 0.05, means were separated with Fisher's protected LSD procedures using STATGRAPHICS Centurion XV, software, 2005 (Statpoint, Inc).

RESULTS AND DISCUSSION

On both *T. kanzawai* and *P. citri*, prey consumption by 2nd instar *M. basalis* increased between 15 and 30°C, and then declined between 30 and 35°C (Fig. 1). Except at the highest temperature (35°C), consumption was consistently higher on *P. citri* than on *T. kanzawai* (Table 1). On *T. kanzawai*, the lacewing exhibited a statistically nonsignificant prey consumption rate between 15 and 20 °C (mean separation = 7.1; LSD = 7.8). Consumption then increased significantly with increasing temperature to 30 °C ($H = 47.05$; df = 99; $P < 0.0001$). Whereas on *P. citri*, the lacewing's prey consumption rate at 20 °C was significantly higher than at 15 °C (mean separation = 9.0; LSD = 8.15), but was similar between 20 and 25 °C. Consumption then increased significantly between 20 and 30 °C. In both species, the consumption rate decreased between 30 and 35 °C, but the difference was only significant in *P. citri* (mean separation = 9.1; LSD = 8.15) (Table 1). The slightly different trend in consumption rate of *M. basalis* in response to temperature between the two mites may be due to the different spatial distribution patterns of the two mites, as well as the different handling times of the lacewing to the two mites. *T. kanzawai* has a clumped distribution, but *P. citri* is more evenly distributed. This difference in spatial distribution between these two mite species is quite significant. At the lower temperature (e.g., 15 °C), the lacewing might have a lower mobility. The effect of temperature on the lacewing's consumption rate might be less pronounced with species that have a clumped distribution because the lacewing does not have to move much to forage. This would assume that movement is limited to a greater degree by low temperature than prey handling. In a separate study, I had demonstrated that the handling time of *M. basalis* with *P. citri* was shorter than with *T. kanzawai* (see Chapter 2). Thus, at higher temperatures (e.g., between 30 and 35 ^{o}C), the comparatively shorter handling times might make the effect of temperature on the consumption rate of *M. basalis* more pronounced with *P. citri*. The shorter handling time might also provide an explanation for the higher consumption rate of *P. citri* compared with *T. kanzawai* in this study. In addition, the effect of temperature on predator metabolism may also play a role in the consumption rates among various temperatures.

A number of studies have shown the relationship between temperature and various responses in predators, including green lacewings (Harbaugh and Mattson, 1973; Dreisig, 1981; Obrycki and Tauber, 1982; Nee, 1983; Ding and Chen, 1986; Tauber *et al.*, 1987; Cocuzza *et al.*, 1997; Lopez-Arroyo *et al.*, 1999; Nielsen, 1999; Mohaghegh *et al.*, 2001; Pervez, 2004; Simmons and Legaspi, 2004; Mahdian *et al.*, 2006; Parajulee *et al.*, 2006). For natural enemies in general, it has been suggested that increased feeding activity and search rates at high temperatures, as well as decreased handling times, enhance the functional response and, thus, have important impacts on the potential of natural enemies to control target pests (Dreisig, 1981; Flinn, 1991; Runjie *et al.*, 1996; Flinn and Hagstrum, 2002; Mohaghegh *et al.*, 2001; Menon *et al.*, 2002; Skirvin and Fenlon, 2003; Xia *et al.*, 2003; Mahdian *et al.*, 2006; Parajulee *et al.*, 2006).

In a study with *M. basalis*, Chang (2000) indicated that the effective temperature range for larvae is about 15 to 43 ^{o}C. The current study demonstrated that prey consumption by *M. basalis* increased within a narrower range of temperature, and that temperatures above 30 ^{o}C were not optimal for prey consumption. Although *M. basalis* exhibited lower predation rates at the lower temperatures of 15 and 20 ^{o}C, at these temperatures both pest mites also have lower development rates. While *P. citri* has an optimal population growth rate at 25 ^{o}C (Zhang, 2003), and *T. kanzawai* at 34 ^{o}C (Chang, 2000), *M. basalis* showed increased predation rates at these temperatures. My other studies have provided further support that *M. basalis* has strong potential as a biological control agent against both *T. kanzawai* and *P. citri* (see chapter 2 – 4). Based on the current study, it would appear that *M. basalis* is suitable for year-round application in

Taiwan because mean monthly temperatures in Taiwan range between 16 and 30 ^{o}C. However, my tests were conducted in small arenas and over a short period. Effects of temperature on the predator's search rate and the prey's ability to escape predation, and effects of prey spatial distribution on the predator's foraging efficiency, would be more prominent in field conditions. In addition, temperature fluctuations in the field may affect predator responses differently than the constant temperature conditions used for the laboratory investigation. Therefore, how temperature would affect the overall predatory potential of *M. basalis* in the field needs further investigation before this natural enemy can be effectively applied in pest management programs against mites.

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Figure 5-1 Prey consumption of *T. kanzawai* and *P. citri* nymphs by *M. basalis* second instar larvae at various temperatures (total duration = 30 minutes) (n = 20). Means with different letters are significantly different at *P* ≤ 0.05 within a species (LSD = 7.80 and 8.15 for *T. kanzawai* and *P. citri*, respectively) (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005). Error bars represent ±SEM.

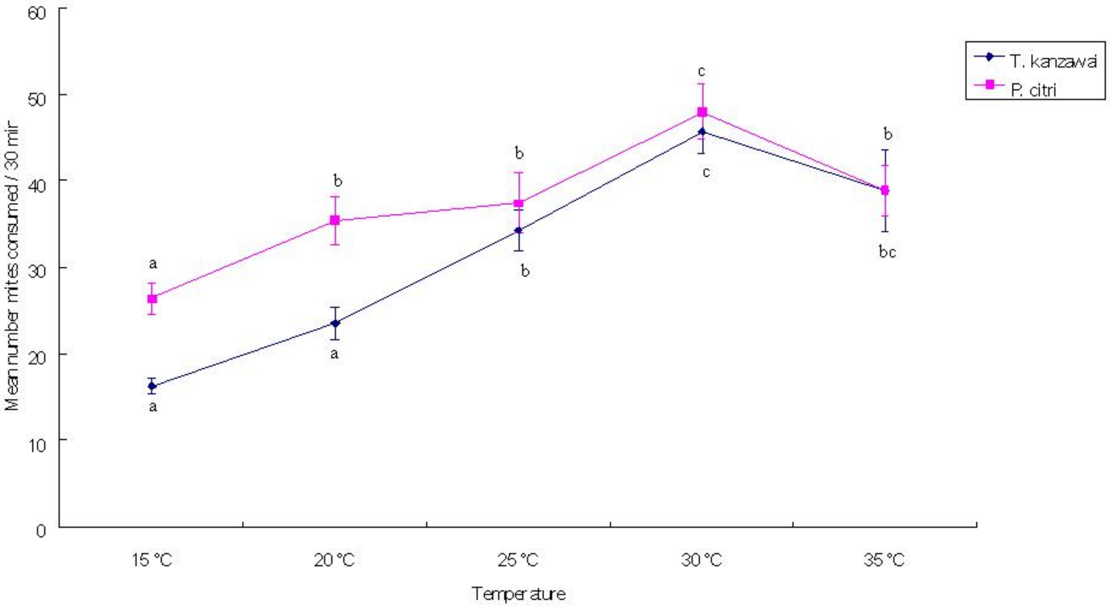

Table 5-1. Prey consumption of *M. basalis* second instar larvae to *T. kanzawai* and *P. citri* nymphs at various temperatures (total duration = 30 minutes) (n = 20)

Temperature °C	Mean (±SEM) number mites consumed	
	T. kanzawai	*P. citri*
15	16.3 ± 1.0a	26.4 ± 1.8a
20	23.5 ± 1.9a	35.4 ± 2.8b
25	34.3 ± 2.4b	37.5 ± 3.5b
30	45.7 ± 2.5c	48.0 ± 3.3c
35	38.8 ± 4.7bc	38.9 ± 2.9b

Means within the same column of the same *M. basalis* stage followed by the same letter are not significantly different at $P \leq 0.05$ (LSD = 7.80 and 8.15 for *T. kanzawai* and *P. citri*, respectively) (Fisher's protected LSD test; STATGRAPHICS Centurion XV, 2005).

SUMMARY

Environmentally-friendly approaches have been the trend in agricultural pest management for the past few decades. The aims of these alternative approaches are to reduce adverse impacts of pest control on natural and managed environments, and to foster a more sustainable means of producing crops. Glasshouse/screenhouse cultivation is an environmentally-supportive practice because it serves as a partial physical barrier to insect pests and diseases, thus, reducing reliance on chemical pesticides for producing high-quality crops. Currently, most papayas in Taiwan are cultivated in screenhouses for protection against aphids which vector papaya ringspot potyvirus. However, the warm screenhouse conditions induce outbreaks of two pest mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* **(**McGregor). Pressure from mites, and overreliance on chemicals to control them, has brought about a predicted, but undesirable result: many mite populations are resistant to most if not all of the registered miticides. This situation has made it necessary to seek alternative forms of papaya mite management.

Biological control, which utilizes natural enemies to suppress pest populations, is considered an environmentally-safe method and a viable alternative to pesticides. When done in glasshouses or screenhouses, the effectiveness of biological control may be greater than in open fields because environmental conditions are more moderate and can be controlled. Among the natural enemies used in augmentative biological control programs against tetranychid mite pests, phytoseiid mites have gained much attention because they specialize on tetranychids, have favorable attributes relative to the pest, and are commercially available at relatively low cost. Green lacewings, which have been demonstrated as a generalist predator of many important agricultural pests, provide another option.

Mallada basalis Walker is a common Chrysopid in Taiwan agricultural fields. Results of previous research have suggested that this green lacewing may have potential as a biological control agent against several species of arthropod pests, including tetranychid mites such as *T. kanzawai*, *P. citri*, and *T. urticae*. Its tolerance to some

insecticides, fungicides, and acaricides has also been reported. In addition, cold storage techniques were established to store its various stages, i.e., eggs, larvae, and pupae, for shipment and scheduled release. All of these enhance the promise of *M. basalis* as a biological control agent. However, very little is known about the predatory response of *M. basalis* to *T. kanzawai* or *P. citri*. In general, behavioral and ecological studies provide information on natural enemy-pest interactions that it is crucial for the effective application of biological control agents. More specifically, laboratory assessments provide data that is helpful in understanding basic mechanisms by which natural enemies control pests, thus contributing essential knowledge for further field investigations. For these reasons, I conducted a series of experiments involving predator foraging behavior and prey-selection involving a domesticated line of *M. basalis* and the two primary mite pests on papaya, *T. kanzawai* and *P. citri*.

In no-choice tests, I showed that all larval instars of this green lacewing were active searchers, exhibited considerably high prey acceptability of both *T. kanzawai* and *P. citri*, and had relatively short handling times, and voraciously consumed all life stages of both mites. The magnitude of *M. basalis*' responses varied depending on the life stage of the predator and prey, as well as which mite species was available as prey. The handling time decreased, and the consumption rate increased as age of the predator increased, and as prey age decreased. Handling times were shorter and consumption rates were greater at higher than lower *P. citri* density, and *M. basalis* consumed more *P. citri* than *T. kanzawai*.

In choice tests, *M. basalis* did not show an age-class preference for either species of prey mite. They also did not prefer one mite species over the other, and prior feeding experience of the lacewing on one mite species did not affect their subsequent prey choice.

A laboratory assessment of the ability of *M. basalis* to suppression populations of the two mites, showed that a predator:prey ratio of 1:30 significantly reduced both *T. kanzawai* and *P. citri* densities of all life stages whenever the two mites occurred singly or simultaneously. However, population suppression was similar but better at the two higher predator-prey ratios (1:15 and 1:10).

Finally, I investigated the relationship between temperature and consumption rate of *T. kanzawai* and *P. citri* by *M. basalis*. Results showed that *M. basalis* is capable of preying on the mites at temperatures as low as 15 °C, and prey consumption increases with temperature up to 30 °C after which rates decline. The consumption-temperature curves differed for the two mite species suggesting that differences in the spatial distribution and handling times of the prey species may have had effects on foraging efficiency that interacted with temperature effects.

Tetranychus kanzawai and *P. citri* can occur simultaneously at the same papaya plantation and on same papaya leaves. The high prey acceptability and voracious prey consumption of *M. basalis* to all life stages of both mites suggest the potential of *M. basalis* to serve as a useful biological control agent regardless of which papaya mite pest is present. No preference in *M. basalis* between the two mites even with previous feeding experience enhances the capability of *M. basalis* against this two mites when they occur simultaneously or sequentially. The positive density-dependent responses – decreased handling time and increased consumption rate with increasing mite density – further suggest that *M. basalis* may be capable of responding to, and contain, pest populations. Finally, the relatively high consumption of both mites across a range of temperatures, which include those found seasonally in screenhouses, suggests that *M. basalis* could be applied as an effective augmentative biological control agent year-round in Taiwan.

The promise of a natural enemy for biological control programs depends not only on its predatory/parasitizing potential, but also on its ability to be mass-produced and the field performance of those mass-produced individuals. *M. basalis* can be mass-produced on artificial diet in a cost-effective manner. With the current techniques, production of a *M. basalis* adult has been estimated being about 0.028 USD including diets, labor, utility, and facility, and one female could produce an average of 736.3 eggs. It was also reported that use of *M. basalis* for controlling *Tetranychus* mites on strawberry costs about 150 USD / ha. It is cheaper than use of the chemical means. My current study indicates that laboratory colonies of *M. basalis* continue to possess high predatory capability even after 10 years. My research, combined with prior knowledge, provides an expanding basis on which to promote the use of *M. basalis* as a biological control agent for the two important papaya pest mites. However, as field conditions are much more complicated than the laboratory, and factors such as plant architectural structures, predator and prey spatial distributions, varying prey population densities, cannibalism, and changes in climatic conditions all influence predator-prey interactions in a dynamic manner, the performance of mass-produced *M. basalis* under more realistic field settings needs to be investigated before an effective papaya pest mite biological control program can be established.

Appendix A - Tables of Statistics

Table A-1 Statistics of comparisons on feeding behavioral parameters of *M. basalis* larvae preying on various life stages of *T. kanzawai* on papaya (Table 1 / Chapter 2)

Stage of *M. basalis*	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
1st instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	*F* = 1.13	*F* = 8.73	*F* = 4.71	*F* = 17.35
	P	0.3669	0.0012	0.0153	$<$ 0.0001
2nd instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	*F* = 3.21	*H* = 7.87	*F* = 9.85	*F* = 39.00
	P	0.0514	0.0488	0.0006	$<$ 0.0001
3rd instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	*F* = 2.99	*H* = 2.1431	*F* = 40.19	*F* = 102.88
	P	0.0622	0.5432	$<$ 0.0001	$<$ 0.0001

* *F* for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-2 Statistics of comparisons on feeding behavioral parameters of *M. basalis* larvae preying on various life stages of *P. citri* at high density on papaya (Table 2 / Chapter 2)

Stage of *M. basalis*	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
1st instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	$H = 4.6166$	$F = 1.94$	$F = 58.93$	$F = 26.28$
	P	0.2021	0.1640	< 0.0001	< 0.0001
2nd instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	$H = 8.9599$	$H = 2.3368$	$F = 17.12$	$F = 140.02$
	P	0.0298	0.5055	< 0.0001	< 0.0001
3rd instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	$H = 2.9353$	$F = 0.47$	$F = 20.47$	$F = 14.94$
	P	0.4017	0.7095	< 0.0001	< 0.0001

* *F* for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-3 Statistics of comparisons on feeding behavioral parameters of *M. basalis* larvae preying on various life stages of *P. citri* at low density on papaya (Table 3 / Chapter 2)

Stage of *M. basalis*	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
1st instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	$H = 2.8920$	$F = 0.55$	$H = 4.7877$	$F = 24.47$
	P	0.4086	0.6567	0.1880	< 0.0001
2nd instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	$F = 1.28$	$H = 3.8457$	$F = 5.97$	$F = 33.26$
	P	0.3162	0.2786	0.0062	< 0.0001
3rd instar	n	5	5	5	5
	df	19	19	19	19
	Test statistic*	$H = 5.8267$	$F = 1.38$	$F = 1.99$	$F = 16.38$
	P	0.1204	0.2843	0.1556	< 0.0001

[*] *F* for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-4 Statistics of comparisons on feeding behavioral parameters of various *M. basalis* larval instars preying on *T. kanzawai* on papaya (Figure 1 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	14	14	14	19
	Test statistic[*]	$F = 2.37$	$H = 10.82$	$F = 45.91$	$F = 18.11$
	P	0.1356	0.0045	< 0.0001	< 0.0001
larva	n	5	5	5	5
	df	14	14	14	19
	Test statistic[*]	$F = 2.11$	$F = 20.29$	$F = 56.82$	$F = 48.68$
	P	0.1645	0.0001	< 0.0001	< 0.0001
nymph	n	5	5	5	5
	df	14	14	14	19
	Test statistic[*]	$F = 0.22$	$H = 6.9067$	$F = 29.91$	$F = 14.99$
	P	0.8026	0.0316	< 0.0001	< 0.0001
adult	n	5	5	5	5
	df	14	14	14	19
	Test statistic[*]	$F =6.53$	$H = 9.6222$	$F = 82.86$	$F = 12.68$
	P	0.0121	0.0081	< 0.0001	< 0.0001

[*] *F* for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-5 Statistics of comparisons on feeding behavioral parameters of various *M. basalis* larval instars preying on *P. citri* at high density on papaya (Figure 2 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	*F* = 1.82	*F* = 4.58	*F* = 36.45	*F* = 119.59
	P	0.2041	0.0332	< 0.0001	< 0.0001
larva	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	*H* = 1.4539	*H* = 8.8563	*F* = 17.72	*F* = 34.19
	P	0.4834	0.0119	0.0003	< 0.0001
nymph	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	*F* = 1.75	*F* = 6.35	*F* = 90.22	*F* = 17.65
	P	0.2147	0.0132	< 0.0001	< 0.0001
adult	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	*F* = 2.98	*F* = 38.97	*F* = 34.79	*F* = 40.11
	P	0.0888	< 0.0001	< 0.0001	< 0.0001

* *F* for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-6 Statistics of comparisons on feeding behavioral parameters of various *M. basalis* larval instars preying on *P. citri* at low density on papaya (Figure 3 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	$H = 4.9985$	$F = 6.73$	$H = 9.1164$	$F = 16.53$
	P	0.0821	0.0109	0.0105	$<$ 0.0001
larva	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	$H = 6.832$	$H = 10.5$	$F = 14.82$	$F = 25.42$
	P	0.0328	0.0052	0.0006	$<$ 0.0001
nymph	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	$F = 0.13$	$H = 2.24$	$F = 16.05$	$F = 16.03$
	P	0.8827	0.3263	0.0004	$<$ 0.0001
adult	n	5	5	5	5
	df	14	14	14	19
	Test statistic*	$F = 1.31$	$F = 27.17$	$F = 15.32$	$F = 34.08$
	P	0.3069	$<$ 0.0001	0.0005	$<$ 0.0001

F for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-7 Statistics of comparisons on feeding behavioral parameters of 1st instar *M. basalis* larvae between preying on *T. kanzawai* and *P. citri* on papaya (Figure 4 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 1.8922$	$t = 9.8341$	$t = 11.4001$	$t = - 4.11$
	P	0.0951	< 0.0001	< 0.0001	0.0147
larva	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 2.8263$	$t = 1.9329$	$t = 2.3002$	$t = 0.78$
	P	0.0223	0.0893	0.0505	0.4791
nymph	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 0.8237$	$t = -1.0128$	$t = -0.5651$	$t = - 0.09$
	P	0.4340	0.3408	0.5875	0.9300
adult	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 0.1443$	$t = 1.3195$	$t = 3.5485$	$t = 2.12$
	P	0.8888	0.2235	0.0075	0.1019

* *t* for normally distributed data with a *t* test; *W* for non-normally distributed data with Mann-Whitney *W* test.

Table A-8 Statistics of comparisons on feeding behavioral parameters of 2nd instar *M. basalis* larvae between preying on *T. kanzawai* and *P. citri* on papaya (Figure 5 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 0.1855$	$W = -10.5$	$t = 0.4903$	$t = -4.93$
	P	0.8574	0.0311	0.6371	0.0079
larva	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$W = -6.5$	$W = -3.5$	$t = 2.3564$	$t = 4.39$
	P	0.2087	0.4802	0.0462	0.0118
nymph	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 1.4563$	$t = 0.8314$	$t = 0.7313$	$t = 1.06$
	P	0.1834	0.4299	0.4855	0.3483
adult	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 0.7221$	$W = 3.5$	$t = 3.5526$	$t = 3.05$
	P	0.4908	0.4802	0.0075	0.0382

t for normally distributed data with a *t* test; *W* for non-normally distributed data with Mann-Whitney *W* test.

Table A-9 Statistics of comparisons on feeding behavioral parameters of 3rd instar *M. basalis* larvae between preying on *T. kanzawai* and *P. citri* on papaya (Figure 6 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 1.4322$	$W = -1.5$	$t = -0.2180$	$t = -4.04$
	P	0.1900	0.8325	0.8329	0.0156
larva	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$W = -11.5$	$W = -1.5$	$t = -1.1673$	$t = 1.61$
	P	0.0208	0.7972	0.2767	0.1822
nymph	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 1.6802$	$W = 7.5$	$t = -1.4048$	$t = -0.84$
	P	0.1314	0.1188	0.1977	0.4465
adult	n	5	5	5	5
	df	4	4	4	4
	Test statistic*	$t = 0.4495$	$t = -1.0905$	$t = 2.9288$	$t = 3.96$
	P	0.6650	0.3072	0.0190	0.0167

* *t* for normally distributed data with a *t* test; *W* for non-normally distributed data with Mann-Whitney *W* test.

Table A-10 Statistics of comparisons on feeding behavioral parameters of 1st instar *M. basalis* larvae between preying on high and low densities of *P. citri* on papaya (Figure 7 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	4	4	4	5
	Test statistic[*]	*W* = 5.5	*t* = 1.6805	*W* = -12.5	*t* = - 4.9927
4.	*P*	0.2636	0.1314	0.0111	0.0041
larva	n	5	5	5	5
	df	4	4	4	5
	Test statistic[*]	*W* = 9.5	*t* = 1.3718	*t* = 5.4501	*t* = - 1.92
	P	0.0449	0.2074	0.0006	0.0963
nymph	n	5	5	5	5
	df	4	4	4	5
	Test statistic[*]	*t* = -0.6736	*t* = -0.3817	*t* = 2.5560	*t* = 0.4586
	P	0.5195	0.7126	0.0339	0.6626
adult	n	5	5	5	5
	df	4	4	4	5
	Test statistic[*]	*t* = -1.5828	*t* = 2.4332	*t* = 2.7092	*t* = 0.9787
	P	0.1521	0.0410	0.0267	0.3603

[*] *t* for normally distributed data with a *t* test; *W* for non-normally distributed data with Mann-Whitney *W* test.

Table A-11 Statistics of comparisons on feeding behavioral parameters of 2nd instar *M. basalis* larvae between preying on high and low densities of *P. citri* on papaya (Figure 8 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	4	4	4	8
	Test statistic*	*t* = 0.5020	*W* = -5.5	*t* = 6.5628	*t* = - 3.2883
	P	0.6292	0.2652	0.0002	0.0111
larva	n	5	5	5	5
	df	4	4	4	8
	Test statistic*	*W* = 0.5	*W* = -7.5	*t* = 4.9366	*t* = - 1.3383
	P	> 0.9999	0.1314	0.0011	0.2176
nymph	n	5	5	5	5
	df	4	4	4	5
	Test statistic*	*t* = 0.1907	*W* = 1.5	*t* = 4.5295	*t* = - 0.9789
	P	0.8535	0.8340	0.0019	0.3726
adult	n	5	5	5	5
	df	4	4	4	5
	Test statistic*	*t* = -2.6546	*t* = 2.8914	*t* = 7.3901	*t* = - 0.8469
	P	0.0290	0.0202	0.0001	0.4357

* *t* for normally distributed data with a *t* test; *W* for non-normally distributed data with Mann-Whitney *W* test.

Table A-12 Statistics of comparisons on feeding behavioral parameters of 3rd instar *M. basalis* larvae between preying on high and low densities of *P. citri* on papaya (Figure 9 / Chapter 2)

Mite stage	Statistics	Feeding behavioral parameter			
		Prey acceptability	Total foraging time	Total no. of prey consumed	Handling time
egg	n	5	5	5	5
	df	4	4	4	5
	Test statistic*	$t = 2.6315$	$t = 2.1071$	$t = 9.9158$	$t = -5.9218$
	P	0.0301	0.0682	< 0.0001	0.0020
larva	n	5	5	5	5
	df	4	4	4	7
	Test statistic*	$W = -6.0$	$t = 2.2502$	$t = 6.4578$	$t = -3.2095$
	P	0.2463	0.0546	0.0002	0.0149
nymph	n	5	5	5	5
	df	4	4	4	5
	Test statistic*	$t = 0.4666$	$t = 0.0027$	$t = 11.73$	$t = -2.8623$
	P	0.6533	0.9979	< 0.0001	0.0353
adult	n	5	5	5	5
	df	4	4	4	5
	Test statistic*	$t = -0.9682$	$t = 1.7221$	$t = 5.9011$	$t = -3.0164$
	P	0.3613	0.1234	0.0004	0.0295

* *t* for normally distributed data with a *t* test; *W* for non-normally distributed data with Mann-Whitney *W* test.

Table A-13 Statistics of comparisons on relative prey encounter and consumption rates, and prey acceptability of *M. basalis* larvae conditioned with different diet to a mixture of *T. kanzawai* and *P. citri* nymphs at various ratios (Table 1 / Chapter 3)

Previous food	Prey provided	% Encounter (n = 200; df = 1)	% Consumption (n = 200; df = 1)	% Acceptability (n = 10; df = 9)	
		χ^2	χ^2	W[*]	P
Diet	50% Tk & 50% Pc	1.037	0.98	0.0	0.9569
	20% Tk & 80% Pc	0.1013	0.125	-0.5	> 0.9999
	80% Tk & 20% Pc	2.42	2.531	0.5	> 0.9999
Tk	50% Tk & 50% Pc	0.5	0.5	0.0	0.9421
	20% Tk & 80% Pc	1.125	0.5	6.0	0.5036
	80% Tk & 20% Pc	3.125	3.125	0.0	0.9421
Pc	50% Tk & 50% Pc	0.3528	0.32	-0.5	> 0.9999
	20% Tk & 80% Pc	1.7113	2.0	-6.0	0.5036
	80% Tk & 20% Pc	0.605	0.5	-0.5	> 0.9999

[*] Mann-Whitney *W* test.

Table A-14 Statistics of comparisons on relative prey encounter and consumption rates, and prey acceptability of *M. basalis* larvae to a mixture of various life stages of *T. kanzawai* (Figure 1 / Chapter 3)

Stage of *M. basalis*	% Encounter (n = 200; df = 3)	% Consumption (n = 200; df = 3)	% Acceptability (n = 10; df = 39)	
	χ^2	χ^2	H^*	*P*
1st instar	9.23	13.84	0.1890	0.9793
2nd instar	3.22	3.08	2.1544	0.5410
3rd instar	17.68	16.68	1.1009	0.7769

[*] Kruskal-Wallis test.

Table A-15 Statistics of comparisons on relative prey encounter and consumption rates, and prey acceptability of *M. basalis* larvae to a mixture of various life stages of *P. citri* (Figure 2 / Chapter 3)

Stage of *M. basalis*	% Encounter (n = 200; df = 3)	% Consumption (n = 200; df = 3)	% Acceptability (n = 10; df = 39)	
	χ^2	χ^2	*H**	*P*
1st instar	76.31	34.94	10.9428	0.0120
2nd instar	28.36	21.84	7.9836	0.0464
3rd instar	61.03	66.28	5.9010	0.1165

* Kruskal-Wallis test.

Table A-16 Statistics of comparisons on mean number mites of various predator:prey ratio treatments of *M. basalis* to *T. kanzawai* (Table 1 / Chapter 4)

Statistics	
n	25
df	124
H[*]	61.1006
P	< 0.0001

[*] Kruskal-Wallis test.

Table A-17 Statistics of comparisons on mean number mites of various predator:prey ratio treatments of *M. basalis* to *P. citri* (Table 2 / Chapter 4)

Statistics	
n	25
df	124
H^*	43.6854
P	< 0.0001

[*] Kruskal-Wallis test.

Table A-18 Statistics of comparisons on mean number mites of various predator:prey ratio treatments of *M. basalis* to mixtures of *T. kanzawai* and *P. citri* (Table 3 / Chapter 4)

Statistics	*T. kanzawai*	*P. citri*	Total
n	25	25	25
df	124	124	124
H^*	35.0412	38.9982	47.8361
P	< 0.0001	< 0.0001	< 0.0001

[*] Kruskal-Wallis test.

Table A-19 Statistics of comparisons on age class distribution of *T. kanzawai* 3 days after release of *M. basalis* at predator:prey ratios of 1:30, 1:15, 1:10, and an untreated check (Figure 1 / Chapter 4)

Statistics	Mite age class			
	Egg	Larva	Nymph	Adult
n	24-25	24-25	24-25	24-25
df	98	98	98	98
Test statistic[*]	$H = 2.9810$	$F = 1.15$	$H = 2.7323$	$H = 7.6198$
P	0.3946	0.3329	0.4348	0.0546

[*] *F* for normally distributed data with *F* test; *H* for non-normally distributed data with Kruskal-Wallis test.

Table A-20 Statistics of comparisons on age class distribution of *P. citri* 3 days after release of *M. basalis* at predator:prey ratios of 1:30, 1:15, 1:10, and an untreated check (Figure 2 / Chapter 4)

Statistics	Mite age class			
	Egg	Larva	Nymph	Adult
n	24-25	24-25	24-25	24-25
df	98	98	98	98
H^*	$H = 10.9993$	$H = 3.8175$	$H = 4.3185$	$H = 5.8066$
P	0.0117	0.2819	0.2291	0.1214

[*] Kruskal-Wallis test.

Table A-21 Statistics of comparisons on locality distribution of *P. citri* on papaya leaves 3 days after release of *M. basalis* at predator:prey ratios of 1:30, 1:15, 1:10, and an untreated check (Figure 3 / Chapter 4)

Statistics	Locality distribution of *P. citri*	
	undersurfaces	uppersurfaces
n	24-25	24-25
df	98	98
H [*]	5.0981	1.9676
P	0.1648	0.5792

[*] Kruskal-Wallis test.

Table A-22 Statistics of comparisons on age class distribution of *T. kanzawai* and *P. citri* 3 days after release of *M. basalis* at predator:prey ratios of 1:30, 1:15, 1:10, and an untreated check when the two mites present simultaneously (Figure 4 / Chapter 4)

Mite species	Statistics	Mite age class			
		Egg	Larva	Nymph	Adult
T. kanzawai	n	19-25	19-25	19-25	19-25
	df	90	90	90	90
	Test statistic*	$H = 3.392$	$F = 1.21$	$F = 0.17$	$F = 1.00$
	P	0.3350	0.3097	0.9165	0.3989
P. citri	n	23-25	23-25	23-25	23-25
	df	97	97	97	97
	Test statistic*	$H = 3.3139$	$H = 2.92$	$H = 0.4728$	$F = 0.95$
	P	0.3457	0.4041	0.9248	0.4180

Table A-23 Statistics of comparisons on prey consumption of *M. basalis* to *T. kanzawai* and *P. citri* among various temperatures (Table 1 / Chapter 5)

Statistics	Mite species	
	T. kanzawai	*P. citri*
n	20	20
df	99	99
H^*	47.0471	20.9579
P	< 0.0001	0.0003

* Kruskal-Wallis test.