

Physiological and Behavioral Characteristics of *Chilocorus* spp. (Coleoptera: Coccinellidae) in the Laboratory Relative to Effectiveness in the Field as Biocontrol Agents

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ABSTRACT Differences between six *Chilocorus* spp. in their usefulness as biocontrol agents in southern Africa were reflected in aspects of physiological and behavioral measurements derived from a quality monitoring program in the laboratory. Differences in natural climatic adaptations and distributions of *Chilocorus bipustulatus* (L.), *C. cacti* L., *C. distigma* (Klug), *C. infernalis* (Mulsant), *C. nigritus* (Fabricius), and *C. simoni* Sicard were not as accurately reflected in the relationship between feeding rate and temperature as in mortality as a function of time of exposure to high temperature. The effects of various rearing and handling procedures were evaluated focusing on *C. nigritus*. The vigor of *C. nigritus* was not improved by maintenance under fluctuating temperatures. Feeding rates of this species were lower during the scotophase than during the photophase and increased as a function of duration of starvation. The weights of adult *Chilocorus* spp. at eclosion was a function of larval diet and increased with adult feeding for variable lengths of time depending on species and larval diet before plateauing. These results have implications for the rearing of, experimentation with, and use in biocontrol of these *Chilocorus* spp.

KEY WORDS *Chilocorus* spp., biological control, citrus

Chilocorus is a large, cosmopolitan genus which includes a number of important biocontrol agents of scale insects (Homoptera), particularly on citrus, which is grown over a broad range of climatic regions, including southern Africa. A survey of museum collections in South Africa indicated that there are 10 *Chilocorus* species indigenous to southern Africa. The exotics *Chilocorus bipustulatus* (L.), *C. cacti* L., *C. circumdatus* (Schönherr), and *C. infernalis* (Mulsant) have been introduced as potential biocontrol agents; only *C. cacti* has become established. Accidental introduction of *C. nigritus* (F.) led to establishment (Samways 1989). There is no documented evidence of these introductions having led to reductions in population levels of other coccinellids. However, increasing concern for environmental repercussions of introducing alien insects, even if considered beneficial (Howarth 1983, 1991; Samways 1988), emphasizes the need to improve methods for screening candidate biocontrol agents to improve predictability of importations.

We studied two *Chilocorus* spp. which are indigenous to southern Africa and four exotic species. The species range from being highly valuable as a biocontrol agent to having no economic

importance to citrus. To facilitate more judicious introductions by improving the predictiveness of species translocations, measurements of physiological and behavioral characteristics in the laboratory were evaluated as indicators of climatic adaptation, potential distribution, and biocontrol value. Feeding rates and survival at a range of static temperatures were evaluated as laboratory indicators of differences in climatic adaptation and distribution of the species studied. Biological characteristics used in a quality-monitoring program for insectary cultures of *C. nigritus* were assessed as indicators of the usefulness of the species studied as biocontrol agents. To facilitate such laboratory studies of *Chilocorus* spp. in the future, the appropriateness of various handling and rearing procedures was assessed. Additionally, rearing in fluctuating laboratory temperatures may produce more vigorous insect populations than in constant temperatures (Hagstrum & Hagstrum 1970, Hodek 1973, Scriber & Slansky 1981). It is unclear from previous studies whether improved performance is a behavioral response of individuals or is caused by selection. We examined the vigor of *C. nigritus* individuals within one generation as a behavioral response to fluctuating temperatures.

Samways (1989) demonstrated with *C. nigritus* that the geographical zonobiome classification system of Walter & Leith (1967) can be valuable

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in directing biocontrol projects. We refer to this system in the following discussion.

Chilocorus nigritus originated from the Indian subregion (Samways 1989), which is classified as climatic zonobiome II (tropical with summer rainfall). This species has become established and is economically valuable as a biocontrol agent in numerous zonobiome II regions. In southern Africa, it effectively controls high populations of California red scale, *Aonidiella aurantii* (Maskell) (Homoptera: Diaspididae), on citrus (Samways 1984, 1986a). In southern Africa, its distribution is restricted to humid, low-altitude areas of Zonobiome II regions (Samways 1989).

Chilocorus cacti is indigenous to southern United States, central America, and northern South America (Gordon 1985). Distribution is centered in zonobiome I (equatorial, humid) and II regions, but also encompasses zonobiomes III (hot and arid, subtropical), V (warm, temperate humid), VII (arid, with a cold season) and X (mountainous). *C. cacti* was introduced into South Africa in 1966 from Texas (DeBach & Rosen 1976), where it is useful in controlling various scale insects on citrus (Thomas 1964). In South Africa, despite widespread introduction (E.C.G. Bedford, ITSC, Nelspruit, South Africa, personal communication), this species became established only in southwestern Cape Province, a zonobiome III region, and failed to control scale outbreaks there (unpublished data).

Chilocorus bipustulatus is indigenous to the greater Mediterranean region but has become established in parts of California (Huffaker & Doutt 1965, Rosen & Gerson 1965, Gordon 1985). The Mediterranean climate is classified primarily as zonobiome IV, with regions of zonobiome III. *C. bipustulatus* is effective in controlling various diaspidid scale insects in several countries (Nadel & Biron 1964, Huffaker & Doutt 1965, Rosen & Gerson 1965, Gordon 1985). It was first imported into South Africa in 1963 as a potential biocontrol agent of diaspidid scale insects on citrus (E.C.G. Bedford, ITSC, Nelspruit, South Africa, personal communication), and again in 1987 by M.J.S., but failed to become established (unpublished data).

The distribution of *C. infernalis* is centered in the highlands of northern India and Pakistan, which are classified as zonobiomes X and II(X) (a transitional zone between II and X). This species was imported from the northern highlands of Pakistan (Samways 1986b) but also failed to become established in southern Africa (unpublished data).

Chilocorus distigma (Klug) is widely distributed throughout Africa, south of the Tropic of Cancer (Hattingh 1991), encompassing zonobiomes I, II, III, IV, and V. This species was considered to be of some importance in controlling *A. aurantii* on citrus in earlier years (Bedford 1968) but is now thought to be of minimal value.

C. simoni Sicard is a southern African species occurring in the higher altitude regions of zonobiome II and is not known to be associated with citrus.

Materials and Methods

Origins of Cultures. Specimens studied were obtained from cultures maintained and reared at the University of Natal, Pietermaritzburg, South Africa. These cultures consisted of specimens from numerous overlapping generations, making it impossible to determine accurately how many previous generations had been in laboratory culture for each specimen. However, individuals studied were taken from populations which had not been in laboratory culture at the university for more than 1 yr. A maximum of 8 successive generations of *C. nigritus*, which has the shortest generation time of the species studied, could be cultured in 1 yr.

Cultures of the following species were established with field-collected specimens: *C. cacti* and *C. nigritus*, collected on citrus and giant bamboo, *Dendrocalamus giganteus* Munro; *C. distigma*, collected on *D. giganteus* and feeding on the asterolecaniid *Asterolecanium miliaris* (Boisduval); and *C. simoni*, collected on *Protea roupelliae roupelliae* Meisner and feeding on an unidentified scale insect. The University cultures of *C. bipustulatus* and *C. infernalis* were established with specimens obtained from cultures at Outspan Citrus Centre, Nelspruit, South Africa, 2 yr after importation for field introductions.

Quality Monitoring. Beetles were reared under controlled conditions of 25–26°C, 50–70% RH, and a 14:10 (L:D) h photoperiod. They were fed oleander scale, *Aspidiotus nerii* Bouché, cultured on 'Waltham' butternuts, *Cucurbita moschata* (Turnhalle). Water was provided in the rearing cages by spraying them with an atomizer one to three times per week. Newly hatched larvae were removed daily; time from hatching to adult eclosion was determined, and percentage survival of the immature stages was recorded. Adult beetles older than 14 d were weighed. Development times and weights for the six *Chilocorus* spp. were compared with a Kruskal-Wallis analysis of variance (ANOVA), followed by nonparametric multiple comparison (Siegel & Castellan 1989).

In the laboratory, *C. bipustulatus* laid eggs between strands of frayed linen (Nadel & Biron 1964, Hattingh & Samways 1991) and *C. nigritus* in pads of polyester fiber wadding (Samways & Tate 1986, Hattingh & Samways 1991). To determine percentage of egg hatch, egg pads were removed from rearing cages in which cultures of *C. nigritus* ($n = 7$ egg pads) or *C. bipustulatus* ($n = 8$ egg pads) were maintained and eggs were counted. Pads were held under the same condi-

tions, and the number of neonates were counted and removed daily until no eggs hatched for 5 consecutive days. Percentages of eggs of the two species that hatched were compared with a Mann-Whitney *U* test (Siegel & Castellan 1989).

The sex of *Chilocorus nigritus* was easily determined according to the method described by Samways & Tate (1984). Similarly, we found that *C. infernalis* males had an invagination in the fifth and sixth abdominal sternites which was not present in any of the females identified during copulation. No easily recognizable differences between the sexes of *C. bipustulatus* were found. However, when attached to adhesive tape by their elytra and held upside down, they everted their genitalia, making sex determination possible.

To estimate oviposition rate, pairs of *C. bipustulatus* and *C. nigritus* variably older than 14 d were enclosed individually in circular plastic collars (10 mm high, 35 mm diameter). These were attached to the surfaces of scale-bearing butternuts, and the open ends were covered with fine nylon gauze. Each pair ($n = 9$ for *C. bipustulatus* and $n = 17$ for *C. nigritus*) was provided with an egg pad which was replaced daily to avoid egg cannibalism by adults. Rates of egg laying for the two species were compared with a Mann-Whitney *U* test (Siegel & Castellan 1989).

To estimate the pre-oviposition period, pairs of newly eclosed *C. bipustulatus* ($n = 9$) and *C. nigritus* ($n = 6$) were enclosed individually in plastic collars. The onset of oviposition was recorded.

The numbers of oleander scale consumed per unit time per individual *C. bipustulatus*, *C. infernalis*, and *C. nigritus* were determined. The scales were in approximately equal densities and were equally aged mature females (1 wk before emergence of the first nymphs). Adult and fourth-instar beetles were not starved before individuals were enclosed in circular arenas and allowed to feed for 4 h. The numbers of scales eaten per individual ($n = 20$ or 49 adults per spp; $n = 9, 10,$ or 24 fourth instars per spp.) were determined from feeding damage and compared with Kruskal-Wallis ANOVA, followed by nonparametric multiple comparisons (Siegel & Castellan 1989).

Adult Age-Weight Relationship. Change in weight of *C. nigritus* ($n = 14$), *C. bipustulatus* ($n = 8$), and *C. infernalis* ($n = 16$) with time after eclosion was measured to evaluate the need for taking weight measurements at a fixed time after eclosion. Larvae were reared on oleander scale on butternuts, and newly eclosed adults were fed oleander scale and weighed daily.

In addition, the effect of larval diet on subsequent adult weight of *C. nigritus* was evaluated. Larvae were reared on a suboptimal synthetic diet based on macerated honey bee brood (unpublished data) or on oleander scale on butter-

nuts which was considered an optimal diet. The resulting adults ($n = 8$) were fed oleander scale and weights were determined daily from the time of eclosion.

Feeding Rate: Photophase and Starvation. The importance of photophase on feeding rate of *Chilocorus* spp. was determined. Feeding rates of fourth-instar ($n = 11$) and adult ($n = 20$) *C. nigritus* were measured as described in *Materials and Methods* (Quality Monitoring). Measurements were taken during the middle of the light and dark phases without prior starvation and compared by the Mann-Whitney *U* test (Siegel & Castellan 1989).

The effect of starving for 0, 4, 10, 24, and 48 h on the feeding rates of individual *C. nigritus* adults ($n = 10$ per treatment) on oleander scale was evaluated as described in *Materials and Methods* (Quality Monitoring). These rates were compared with a Kruskal-Wallis ANOVA, followed by a nonparametric multiple comparison (Siegel & Castellan 1989).

Constant Versus Fluctuating Temperature. Two environments were maintained: (1) constant temperature of 25–26°C, 50–70% RH, and a 14:10 (L:D) h photoperiod (photophase from 0500 to 1900 hours); and (2) fluctuating temperature (changing gradually between 15°C at 0200 hours and 28°C at 1300 hours) with fluctuating RH (changing gradually between 70% at 0200 hours and 35% at 1300 hours) and a 14:10 (L:D) h photoperiod (photophase from 0500 to 1900 hours). *C. nigritus* were kept in cubical, wooden-framed cages (8 dm³) covered in fine gauze netting. Each cage contained one butternut encrusted with several generations and mixed ages of oleander scale. Experimental beetles had been maintained on oleander scale at 25–26°C and were 4–6 wk old. They were weighed, and three pairs were enclosed per cage with 10 cages per environment.

The adult beetles were allowed 2 wk to acclimate to the new environment before measurements began. One egg pad (10 by 40 by 200 mm) was wrapped around the butternut in each cage and replaced twice at 3-d intervals. The number of eggs laid per pair per day (in days) and the percentage hatch was recorded.

The feeding rates of the adults were measured 3 wk after they were introduced into the two environments. Six beetles were enclosed per arena (described in *Materials and Methods* (Quality Monitoring) and the number of scales eaten in each arena was divided by six to give a measurement of the number of scales eaten per individual, with 10 replicates per environment. Feeding rates were measured during the first, middle, and last 4 h of the photophase. Each group of six beetles was weighed 4 wk after introduction to these environments and compared with weights at commencement of the trial. Measurements from cultures in the two environ-

Table 1. Mean weights of adults older than 14 d, times from egg hatch to adult eclosion, and percentage survival of immature stages of six *Chilocorus* spp. reared on oleander scale

Species	Adult wt, mean mg \pm SE (n)	Development time, mean d \pm SE (n)	% Survival
<i>C. bipustulatus</i>	9.5 \pm 0.2 (24)a	29.0 \pm 0.4 (33)c	69
<i>C. cacti</i>	20.0 \pm 0.4 (52)c	30.6 \pm 0.7 (21)c	71
<i>C. distigma</i>	37.2 \pm 1.0 (28)d	33.2 \pm 0.4 (40)d	70
<i>C. infernalis</i>	15.5 \pm 0.4 (21)b	26.2 \pm 0.4 (37)b	76
<i>C. nigritus</i>	8.5 \pm 0.2 (40)a	21.9 \pm 0.3 (39)a	78
<i>C. simoni</i>	17.6 \pm 0.6 (37)bc	NA ^a	—

Kruskal-Wallis ANOVA followed by a nonparametric multiple comparison (Siegel & Castellan 1989) ($\alpha = 0.05$); common letter following sample size indicates no significant difference between means in a column.

^a Ten individuals were still alive and had not completed development after 40 d.

ments were compared with Mann-Whitney *U* tests (Siegel & Castellan 1989).

Temperature-Feeding Rate and Temperature-Survival Relationships. The feeding rates and survival of adult *C. bipustulatus*, *C. cacti*, *C. distigma*, *C. infernalis*, *C. nigritus*, and *C. simoni* were determined at constant temperatures and relative humidities of 3°C and 90% RH, 10°C and 80% RH, 17°C and 50% RH, 24°C and 53% RH, 31°C and 48% RH, 38°C and 35% RH, and 41°C and 35% RH. Fifteen to 20 adults (mixed ages) per species were taken from the stock cultures maintained on oleander scale at a constant 25–26°C and 50–70% RH. Twenty four h after commencement of exposure to the test temperature, the feeding rates were determined as described in *Materials and Methods* (Quality Monitoring), with between 6 and 15 replicates. However, the scale insects were not mature, as in the previous trials, but were 3-wk-old males and females. For each species, the feeding rates were compared with a Kruskal-Wallis ANOVA followed by a nonparametric multiple comparison (Siegel & Castellan 1989).

Survival after 48 h of exposure to all temperatures was recorded for between 14 and 21 replicates per species. Survival after 14, 21, 41, and 48 h of exposure to 41°C was also measured for between 14 and 21 replicates per species. Different individuals were used for each temperature trial.

Results

Quality Monitoring. A comparison of adult weight, larval plus pupal development time, and percentage survival of immature stages for the six *Chilocorus* spp. is given in Table 1. The feeding rates of *C. bipustulatus*, *C. infernalis*, and *C. nigritus* are compared in Table 2.

Egg hatch of *C. bipustulatus* was 69 \pm 5.8% (mean \pm SE) ($n = 8$ egg pads). The hatch rate of *C. nigritus* was 74 \pm 2.6% ($n = 7$ egg pads). The hatch rates were not significantly different (Mann-Whitney *U* test) ($U = 29$; $n_1, n_2 = 7, 8$; $\alpha = 0.05$).

The first observation during evaluation of the period between adult eclosion and the com-

mencement of oviposition for *C. bipustulatus* was made 5 d after eclosion; oviposition had already commenced in seven of the nine pairs tested. The remaining two pairs started ovipositing 13 d and 15 d after eclosion. The mean preoviposition period for *C. nigritus* was 14 \pm 0.5 d ($n = 6$ pairs).

The oviposition rate of *C. bipustulatus* was 3.8 \pm 0.9 eggs ($n = 9$ pairs) per d over 25 d. The mean oviposition rate for *C. nigritus* was 2.8 \pm 0.4 eggs ($n = 17$ pairs) per pair per d over 11 d. The oviposition rates were not significantly different (Mann-Whitney *U* test) ($U = 91.5$; $n_1, n_2 = 9, 17$; $\alpha = 0.05$).

Adult Age-Weight Relationship. When fed oleander scale on butternuts, the weight of *C. bipustulatus*, *C. nigritus*, and *C. infernalis* increased for $\approx 6, 9,$ and 11 d after eclosion, at which time they were $\approx 37, 38,$ and 15% heavier than 1 d after eclosion (Fig. 1). *C. nigritus* adults that were undernourished at eclosion (because of a deficient larval diet) were significantly lighter than 1-d-old adults from larvae reared on an adequate diet (Mann-Whitney *U* test) ($U = 97.5$; $n_1, n_2 = 7, 14$; $\alpha = 0.05$). Increase in weight of these undersized adults continued longer than for the adults from adequately fed larvae (Fig. 1). After ≈ 23 d, they were 59% heavier than 1 d after eclosion. This stable end weight was still significantly lower than those of adults from well-fed larvae (Mann-Whitney *U* test) ($U = 98$; $n_1, n_2 = 7, 14$; $\alpha = 0.05$).

Feeding Rate: Photophase and Starvation. The number of mature female oleander scales eaten per adult *C. nigritus* in 4 h was 1.4 \pm 0.4 ($n = 20$)

Table 2. Mean numbers \pm SE (n) of mature female oleander scale consumed per individual *Chilocorus* sp. in 4 h

Species	Stage tested	
	Adult	Fourth instar
<i>C. bipustulatus</i>	2.4 \pm 0.4 (20)a	2.6 \pm 0.5 (10)a
<i>C. nigritus</i>	2.8 \pm 0.4 (49)ab	1.2 \pm 0.2 (24)b
<i>C. infernalis</i>	3.8 \pm 0.4 (20)b	4.6 \pm 0.7 (9)c

Kruskal-Wallis ANOVA followed by a nonparametric multiple comparison (Siegel & Castellan 1989) ($\alpha = 0.05$); common letter following sample size indicates no significant difference between means in a column.

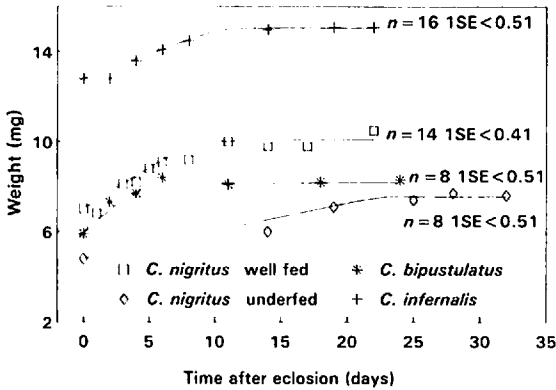


Fig. 1. Mean adult weight as a function of time after eclosion for *C. bipustulatus*, *C. infernalis*, and *C. nigritus* from well-fed larvae and for *C. nigritus* from larvae reared on a suboptimal synthetic diet.

during photophase and 0.4 ± 0.2 ($n = 20$) during scotophase. These feeding rates were significantly different (Mann-Whitney U test) ($U = 274$; $n_1, n_2 = 20, 20$; $\alpha = 0.05$). The feeding rate of fourth instars in the photophase was 1.8 ± 0.1 ($n = 11$) and in the scotophase was 1.0 ± 0.3 ($n = 11$). These feeding rates were significantly different (Mann-Whitney U test) ($U = 93$; $n_1, n_2 = 11, 11$; $\alpha = 0.05$). The feeding rates of *C. nigritus* adults tended to be higher after longer periods of starvation (Fig. 2).

Constant Versus Fluctuating Temperatures. The vigor of *C. nigritus* was not increased by maintenance at fluctuating temperatures (Mann-Whitney U test) ($\alpha = 0.007$ to hold P at 0.05 by Bonferroni's inequalities [Snedecor & Cochran 1980], $n_1 = 10$, $n_2 = 10$) (Table 3). Feeding rates during periods of reduced temperature and oviposition rates were significantly lower in an environment of fluctuating temperature than at a constant temperature. Percentage egg hatch and weights of adults, at the commencement of the experiment and after 40 d of exposure to the different temperature conditions and feeding rates at times of equal temperature, were not significantly different in the two environments.

Temperature-Feeding Rate and Temperature-Survival Relationship. Feeding and survival rates at various temperatures indicate that the species could be ranked in the following order of increasing tolerance of high temperatures: *C. infernalis*, *C. simoni*, *C. nigritus*, *C. bipustulatus*-*C. distigma*, *C. cacti* (Tables 4 and 5, Fig. 3).

Discussion

Biocontrol Predictiveness. Differences in the value of biocontrol agents in the field can be predicted with caution, from measurements of biological parameters used in quality monitoring. Hattingh & Samways (1992) indicated that

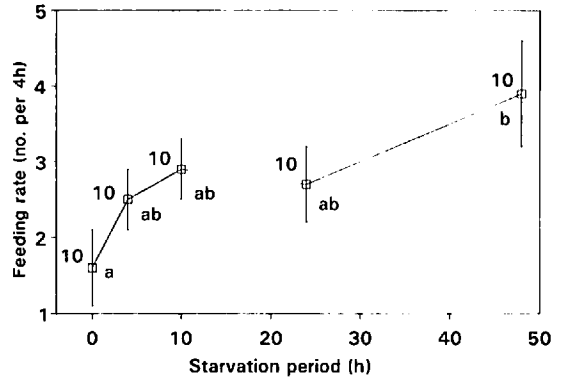


Fig. 2. Mean number (\pm SE) of mature female oleander scale eaten (n at left of SE bars) per *C. nigritus* adult in 4 h after various periods of starvation. A common letter to the right of SE bars indicates no significant difference by Kruskal-Wallis ANOVA followed by a nonparametric multiple comparison (Siegel & Castellan 1989).

there may be a high selective advantage for coccinellids to have rapid larval development, thereby reducing the duration of this highly vulnerable life stage. We have demonstrated (unpublished data) that the ability of *C. nigritus* larvae to detect prey is considerably inferior to that of adults. Larvae are also more susceptible than adults to the deleterious effects of a change-over from one prey species to another (Hattingh & Samways 1992). It follows that it is advantageous for larvae not to deplete the prey patch on which they are feeding; therefore, there is selective pressure for developing a low feeding rate and a short developmental period.

Development time for immatures of *C. nigritus* is significantly shorter than for the other *Chilocorus* spp. we studied (Table 1). The feeding rate of *C. nigritus* larvae is lower than that of *C. bipustulatus* larvae (Table 2), a species of similar size (Table 1), and adult *C. nigritus* are smaller than all the other *Chilocorus* spp. we studied (Table 1). However, adult feeding rate is surprisingly high (Fig. 3), peaking at a level lower than that of *C. distigma* and *C. cacti* only, which are the two largest species studied. This fortuitous combination of a short larval developmental period, low larval feeding rate, and high adult feeding rate in relation to size may explain why *C. nigritus* is such a successful predator.

Unfortunately, factors not measurable in quality monitoring can be of overriding importance. Compared with the highly successful biocontrol agent *C. nigritus*, the less economically important *C. cacti* had a higher adult feeding rate over a broad range of temperatures (Fig. 3) and was more tolerant to heat. There is a good match between the climate in the region of origin of this species and parts of southern Africa. However, field performance in southern Africa is poor

Table 3. Comparison between various measures of vigor of *C. nigritus* cultures maintained at constant and fluctuating temperatures on oleander scale

Measurement	Temperature		U ^a
	Constant	Fluctuating	
Eggs per pair/d	4.3 ± 0.3a	2.2 ± 0.3b	90
% Egg hatch	74 ± 6a	71 ± 9a	50.5
Adult wt at start of trial, mg	8.2 ± 0.2a	8.1 ± 0.1a	57
Adult wt after 40 d exposure to treatment, mg	8.8 ± 0.2a	8.4 ± 0.1a	75.5
No. <i>A. nerii</i> eaten per beetle in first 4 h of light phase	1.1 ± 0.1a	0.6 ± 0.1b	85.5
No. <i>A. nerii</i> eaten in middle 4 h of light phase	1.5 ± 0.2a	1.5 ± 0.2a	53
No. <i>A. nerii</i> eaten in last 4 h of light phase	1.4 ± 0.2a	0.7 ± 0.1b	89

Mean ± SE, $n = 10$, common letter indicates no significant difference, separate comparisons for each row, Mann-Whitney U test ($\alpha = 0.007$ required for P to be held at 0.05 by Bonferroni's inequalities [Snedecor & Cochran 1980]).

^a Value of Mann-Whitney U statistic ($n_1 = 10$, $n_2 = 10$).

(unpublished data). This may be attributed to extensive parasitism of *C. cacti* in South Africa by *Ooencyrtus sinis* Prinsloo (Hymenoptera: Encyrtidae) (V.H., unpublished data), whereas *C. nigritus* is not known to be parasitized in southern Africa (unpublished data). The comparatively high level of performance of *C. cacti* in the laboratory indicates that this species may be a valuable biocontrol agent in other regions where they would not be exposed to such parasitism.

Accurate biogeographical climatic matching can be valuable in directing biocontrol projects (Samways 1989). The major differences in climatic adaptations of the species we examined were not clearly reflected in differences between feeding rate-temperature relations, although they did roughly parallel the survival data. Survival times at excessively high temperatures were more informative than these feeding rate data when comparing the temperature adaptations of these species (Table 5). *C. infernalis*, from a temperate, high-altitude region, was the first species to die, followed by *C. simoni*, from a high-altitude, tropical region. *C. nigritus*, from a low-altitude, tropical region was the next species to experience extensive mortality, followed (at about the same time) by *C. bipustulatus*, from a Mediterranean climate, and *C. distigma*, with a broad distribution including most of sub-Saharan Africa, and finally *C. cacti*, also with a distribution covering a wide range of climate types. In view of these results, *C. infernalis* probably did not become established in southern Africa be-

cause of high summer temperatures, which are often well in excess of 30°C.

Adult Weight. Although this has not been demonstrated for *Chilocorus* spp. specifically, fecundity of individuals within a species is widely accepted to be proportional to adult size (Beddington et al. 1976, Slansky & Rodriguez 1987). The width of the foraging track across which a coccinellid detects individual prey by contact may be determined by measuring the foreleg span (Carter & Dixon 1982). Because size influences fecundity and prey location, it may be used as an indicator of fitness of individuals within a species. However, measuring weight is a more time-efficient and simpler procedure. Our results showed that differences in weight 1 d after eclosion reflect weight differences remaining after adults had reached a stable end weight, although the differences decreased slightly through weight gain with time after eclosion. The nutritional history of coccinellid larvae has been shown to affect adult size (Hodek 1973). This indicates that the simple procedure of measuring weight 1 d after eclosion may be indicative of the effects that larval treatments have on the fitness of subsequent adults.

Feeding Rates. Feeding rates were not the same after various periods of starvation, requiring the use of a standard starvation period when measuring them. Feeding rates of adults and larvae were significantly slower during the scotophase than the photophase, which is valuable information for performing feeding rate trials in

Table 4. Percentage of *Chilocorus* spp. (n) surviving 48 h of exposure to various constant temperatures

Species	Temperature, °C						
	3	10	17	24	31	38	41
<i>C. bipustulatus</i>	85 (20)	94 (17)	100 (20)	100 (20)	100 (20)	100 (16)	0 (21)
<i>C. cacti</i>	100 (20)	95 (15)	95 (20)	95 (18)	100 (20)	100 (20)	0 (20)
<i>C. distigma</i>	100 (20)	100 (16)	100 (18)	100 (20)	100 (20)	100 (20)	0 (21)
<i>C. infernalis</i>	85 (20)	100 (15)	100 (20)	100 (20)	95 (20)	84 (19)	0 (20)
<i>C. nigritus</i>	100 (20)	88 (16)	100 (20)	95 (20)	95 (20)	95 (19)	0 (20)
<i>C. simoni</i>	100 (15)	93 (15)	94 (17)	100 (15)	100 (16)	88 (17)	0 (14)

Table 5. Percentage of *Chilocorus* spp. surviving various periods of exposure to 41°C

Species	n	Duration of exposure to 41°C, h			
		14	21	41	48
<i>C. bipustulatus</i>	21	91	62	5	0
<i>C. cacti</i>	20	100	95	50	0
<i>C. distigma</i>	21	100	57	0	0
<i>C. infernalis</i>	20	0	0	0	0
<i>C. nigritus</i>	20	90	5	0	0
<i>C. simoni</i>	14	43	7	0	0

has been reported to improve with exposure to fluctuating temperatures (Gawande 1966, Hagstrum & Hagstrum 1970, Hodek 1973, Scriber & Slansky 1981). Our study did not demonstrate an improvement in the vigor of *Chilocorus* spp. within one generation with exposure to fluctuating temperatures. Improvement in culture vigor may be based on selection, in which case rearing at fluctuating temperatures for several generations may be required for increased vigor to become evident in the population.

In conclusion, basic biological measurements in the laboratory were of limited value in improving the biocontrol predictiveness of *Chilocorus* spp. However, survival at increasingly high temperatures was valuable in comparing

the laboratory. The selective advantage of such behavior is unclear.

Constant and Fluctuating Temperatures. Culture vigor of many insects including coccinellids

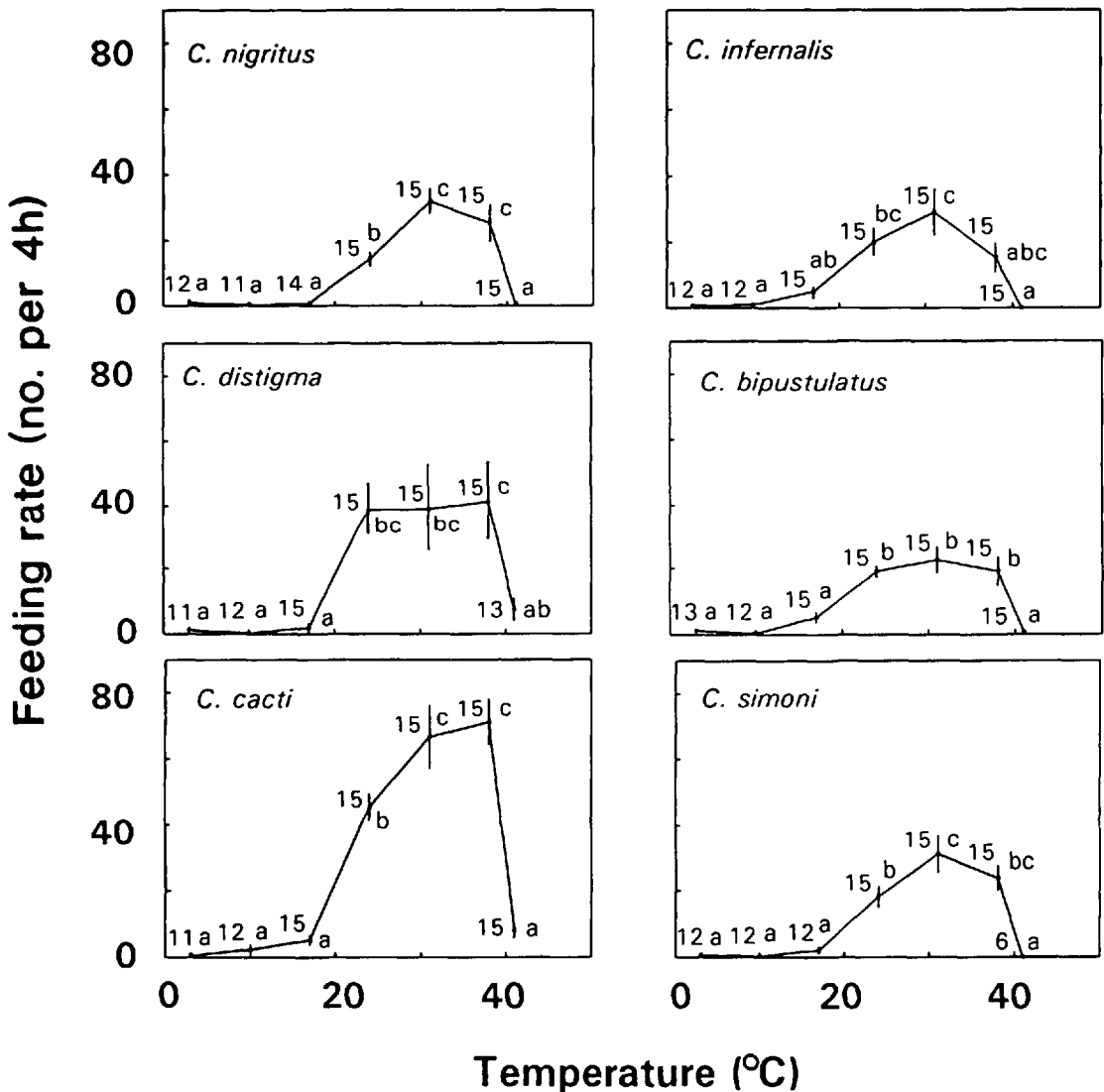


Fig. 3. Mean number (\pm SE) of 3-wk-old male and female oleander scale eaten (*n* at left of SE bars) per adult *Chilocorus* spp. in 4 h at various constant temperatures. A common letter to the right of SE bars indicates no significant difference by Kruskal-Wallis ANOVA followed by a nonparametric multiple comparison (Siegel & Castellan 1989).

the climatic adaptations of the species studied. The use of various handling and rearing procedures for *Chilocorus* spp. identified appropriate procedures for evaluating the effects of larval treatment on the fitness of subsequent adults and conducting feeding rate experiments. Although much of this information may be more a posteriori in value, it may facilitate further work with these and other species to improve our understanding of the factors affecting the outcome of geographical translocations.

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