

Life history, predatory biology, and population ecology of *Lyctocoris campestris* (F.) (Heteroptera: Anthocoridae)

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Abstract

Lyctocoris campestris (F.) has been collected worldwide, but its biology and predatory behaviour have been largely neglected. Our work demonstrates *L. campestris* can be a voracious polyphagous predator of stored-product insects. We describe the general biology and life history characteristics of *L. campestris* and give methods for a laboratory rearing procedure. *L. campestris* requires approximately 4 weeks to complete the life cycle from egg to adult. Females can lay up to 300 eggs, with an average fecundity of approximately 6 eggs per female per day at 30°C. Field studies using probe traps in a flat storage of maize showed that bugs preferred mouldy over drier areas. Sex ratios of field-collected bugs were highly female-biased as opposed to 1:1 in laboratory colonies. Both adults and nymphs of *L. campestris* can utilise eggs and larvae of most stored-product insects. The species can also be reared successfully on nonstored-product insects. However, prey type had a significant effect on development and reproductive biology of *L. campestris*. Both males and females are equally capable of prey utilisation under both laboratory and simulated field conditions. In the three prey species tested (Indianmeal moth, red flour beetle, and sawtoothed grain beetle), both sexes of *L. campestris* showed a curvilinear Type II functional response.

Introduction

There are at least 10 species of heteropteran predators inhabiting the stored-product ecosystems (Arbogast 1979, 1984; Parajulee and Phillips 1992a). Only do a few of those species commonly establish populations in stored grain (e.g. Arbogast 1979; Parajulee and Phillips 1992b). For example, *Xylocoris flavipes* (Reuter) has been studied and reported as a generalist predator of eggs and small, soft-bodied larvae of a variety of insects that occur in storage habitats (e.g. Arbogast 1979, 1983). *L. campestris* (F.) has been collected worldwide (Anderson 1962a; Kelton 1978), but its biology and predatory behaviour have been largely neglected. Parajulee and Phillips (1992a) reported *L. campestris* as a voracious polyphagous predator in the stored-product ecosystems. Historically, the predatory nature of this bug has been indicated in the literature (Essig 1954; Moore 1972; Kinzer 1976; Berisford 1980), but the potential of this species as a predator of stored-product insects has been documented only recently (Parajulee and Phillips 1992b). We have recently described the general biology and life history characteristics of *L. campestris*, and developed an optimal laboratory rearing procedure. Parajulee

and Phillips (1993) and Parajulee et al. (1994) studied the prey suitability for, and the predatory biology of, *L. campestris* in the laboratory. *L. campestris* appears to be a potential biological control agent that could be used in stored-grain pest management in the near future. This paper synthesises some of our recent work from the USDA ARS Stored-Product Insects Research Laboratory in Madison and presents an overview of different projects that have been undertaken to understand the general biology and predatory potential of *L. campestris*.

Prey Range

Previous literature documents an association of *L. campestris* with potential prey species, but does not study predation directly. Moore (1972) and Berisford (1980) found *L. campestris* associated with scolytid beetles under the bark of trees, and Legner et al. (1975) reported that *L. campestris* were known to prey on many species of Diptera. Recently, we conducted an experiment to examine the ability of *L. campestris* to kill different prey species. One-week-old adult *L. campestris* were starved for 48 hours, and then confined with 10 late instars or adults of each prey species ($N = 5$) in a glass jar (118 mL) for 24 hours. After 24 hours, the number of prey killed per jar was recorded. *L. campestris* showed a high degree of prey generality evidenced by feeding on species of Lepidoptera, Coleoptera, and Hymenoptera in no-choice tests (Table 1). In our laboratory study, *L. campestris* also preyed upon both eggs and larvae of the parasitic wasps *Bracon hebetor* Say and *Laelius pedatus* (Say). In Lepidoptera, all pyralids and a noctuid that were offered as prey were fed upon by *L. campestris*. Large prey size alone is apparently not a limiting factor to the bugs, as evidenced by their successful killing of last instar *Galleria mellonella* (L.), a larva that was >20 mm long in our studies. Our data indicate *L. campestris* can prey on 20 different species of Coleoptera belonging to seven different families. Both late instars and adult *L. campestris* could easily kill all stages including adults of Cucujidae and Bostrichidae that were tested, and they could kill all stages except adults of tenebrionids tested. *Xylocoris flavipes* also has been reported to prey on larval stages of Cucujidae, Bostrichidae, and Tenebrionidae (e.g. Jay et al. 1968). Adult Bostrichidae and Cucujidae are vulnerable to predation by *L. campestris* due to their soft body parts such as the cervix or the tip of the abdomen. Larvae of many Dermestidae could be preyed upon by the predator, but these are not easily overpowered because of their high degree of sclerotisation and heavy vestiture of setae. We believe that *L. campestris* might opt for alternate prey in natural settings where multiple prey species exist. Our findings of broad prey range are consistent with what is known about other anthocorids, such as *Anthocoris* spp. (Anderson 1962b), *Orius insidiosus* Say (Kiman and Yeargan 1985; McCaffrey and Horsburgh 1986), *Xylocoris galactinus* (Fieber) (Afifi and Ibrahim 1991), *Cardiastethus nazarens* Reuter (Awadallah et al. 1976), and *X. flavipes* (Jay et al. 1968; Arbogast 1979; Brower and Press 1992).

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Table 1. Suitability of different prey species and life stages as prey for *Lyctocoris campestris* in no-choice tests (Parajulee and Phillips 1993).

Lepidoptera	Stage tested ^a	
	Larva	Adult
Pyrallidae		
<i>Plodia interpunctella</i> (Hübner)	+	NT
<i>Cadra cautella</i> (Walker)	+	NT
<i>Ephestia kuehniella</i> Zeller	+	NT
<i>Galleria mellonella</i> (L.)	+	NT
<i>Amyelois transitella</i> (Walker)	+	NT
Noctuidae^b		
<i>Trichoplusia ni</i> (Hübner)	+	NT
Sphingidae^b		
<i>Manduca sexta</i> (L.)	–	NT
Coleoptera		
Anobiidae		
<i>Lasioderma serricorne</i> (F.)		
Bostrichidae		
<i>Rhyzopertha dominica</i> (F.)	+	+
Bruchidae		
<i>Callosobruchus maculatus</i> (F.)	+	–
<i>Callosobruchus chinensis</i> (L.)	+	–
Cucujidae		
<i>Oryzaephilus surinamensis</i> (L.)	+	+
<i>Oryzaephilus mercator</i> (Fauvel)	+	+
Curculionidae		
<i>Sitophilus zeamais</i> Motschulsky	+	–
<i>Sitophilus oryzae</i> (L.)	+	–
<i>Sitophilus granarius</i> (L.)	+	–
Dermestidae		
<i>Trogoderma variabile</i> Ballion	+	–
<i>Trogoderma glabrum</i> (Herbst)	+	NT
<i>Trogoderma inclusum</i> LeConte	+	NT
<i>Trogoderma simplex</i> Jayne	+	NT
<i>Trogoderma sternale</i> Jayne	+	NT
<i>Trogoderma grassmani</i> Beal	+	NT
<i>Trogoderma granarium</i> Everts	+	NT
Tenebrionidae		
<i>Tribolium castaneum</i> (Herbst)	+	–
<i>Tribolium confusum</i> Jacquelin du Val	+	–
<i>Tribolium brevicornis</i> (LeConte)	+	–
<i>Alphitobius diaperinus</i> (Panzer)	+	–
<i>Tenebrio molitor</i> L.	–	–
Hymenoptera		
Braconidae		
<i>Bracon hebetor</i> Say	+	NT
Bethylidae		
<i>Laelius pedatus</i> (Say)	+	NT

^a NT, not tested; +, successful killing of prey with sustained feeding; –, unsuccessful attempts to kill prey.

^b Nonstored-product insects.

Life History

General biology of *L. campestris*, including immature development, survivorship, mating, oviposition, and fecundity, has been described in a laboratory environment of 30°C, 65±5% r.h., and a photoperiod of 16:8 (L:D) (Parajulee and Phillips 1992b). We recently studied the effect of eight different prey species, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), *Cadra cautella* (Walker) (Lepidoptera: Pyralidae), *Lasioderma serricornis* (F.) (Coleoptera: Anobiidae), *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), *Oryzaephilus surinamensis* (L.) (Coleoptera: Cucujidae), *Trogoderma variabile* Ballion (Coleoptera: Dermestidae), *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae), and *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), on the development and reproduction of *L. campestris* (Parajulee and Phillips 1993). The incubation period of eggs at 30°C ranges between 6 and 8 days with an average of 7.45 (± 0.21) days. New eggs are almost colourless at first, but by the third day two pale orange spots, which represent the embryonic eyes, become obvious at the operculum end of the egg. Eclosion of the nymph takes place via a separation of the operculum from the upper rim of the chorion. Neonate bugs are always oriented head-up, and break through the operculum during eclosion. Newly emerged nymphs are hyaline, but assume a pale brown colour within a few hours. Nymphs are active immediately after eclosion and search for prey. We also have determined that moisture is critical for egg hatch (Parajulee and Phillips 1992b). The rate of egg hatch was ≈89% when oviposition substrates containing eggs were moistened for three days, but it was reduced to ≈74% when no moisture was added in the substrate after oviposition (unpublished data).

L. campestris passes through five nymphal stadia. The first three stadia are fairly short (2–4 days each), the fourth stadium is slightly longer than the first three (3–5 days), and the final stadium is the longest (6–9 days). Adults of both sexes are winged and are capable of flight. The sex ratio of emerging *L. campestris* adults is 1:1. There is no effect of prey species on the sex ratio of emerging adults of the bug. Sexes can be distinguished by the external claspers of the male genitalia and the ovipositor of the female when each are viewed ventrally. Mating is via normal copulation instead of traumatic haemocoelic insemination found in many anthocorids. When a male approaches a female and attempts to mount, he does so very

fast, extending his aedeagus and jumping on top of the female. The mounting male immediately aligns his body longitudinally with the female, curves his abdomen down and inserts his aedeagus into the female. Multiple mating by females with the same or different males is common in this species. Duration of copulation is variable in sexually deprived bugs, and ranges from several seconds up to 35 min.

The preoviposition period in a female that has been paired with a male since emergence ranges from 5–15 days (Parajulee and Phillips 1992b, 1993) when *P. interpunctella* is the prey. However, the preoviposition period varies with the prey species (Table 2). So far, successful oviposition and subsequent embryonic development have been achieved only on a moist substrate, preferably a stack of three filter papers saturated with the water. We are currently examining the possible utilisation of an oviposition substrate that may not require water-saturation. Females spend an average of 82.2 (± 2.4) seconds for each oviposition. This time period includes abdomen bending, touching the substrate with the ovipositor, inserting the egg into the substrate, and elevating the abdomen back to the beginning position. Eggs are generally creamy white or translucent, but the operculum is somewhat brown so that we could easily recognise and count the number of eggs laid in the substrate. Mean lifetime and per day fecundities per female vary with the prey species (Table 2). However, a strong correlation between the length of the oviposition period and the total number of eggs laid per female has been found irrespective of the prey species (Parajulee and Phillips 1993).

Egg production per day by individual females shows an oscillating trend through the course of oviposition for all females (see m_x curves in Fig. 1). Generally, when a female lays more than 10 eggs in one day, the egg production for subsequent days ultimately declines to a point below the mean level, and again increases gradually above the mean for the next few days. The duration of these cycles depends on the type of prey species. This cyclic nature of oviposition in *L. campestris* indicates that vitellogenesis and egg maturation may proceed to a point at which the ovaries are full, followed by an oviposition period when the ovaries are voided, and subsequently followed by another several days of egg regeneration during which no or very few eggs are laid. Cyclic oviposition also suggests that in a natural setting *L. campestris* may lay eggs in clutches, and then move on to other oviposition sites during egg development.

Table 2. Developmental and reproductive statistics (mean ± SEM) for *L. campestris* on different prey regimes (Parajulee and Phillips 1993).

Prey species	Nymphal duration (d)	Preoviposition period (d)	Oviposition period (d)	Fecundity (no. eggs/d)	Maximum ovi. pd.
<i>P. interpunctella</i>	22.63±0.27 ^e	9.08±1.25 ^d	20.25±3.75	4.31±0.25 ^a	51
<i>C. cautella</i>	21.71±0.31 ^f	12.25±1.09 ^{cd}	20.87±2.94	3.53±0.28 ^{ab}	42
<i>T. castaneum</i>	21.85±1.19 ^f	9.44±1.45 ^d	12.78±0.87	3.64±0.44 ^{ab}	17
<i>O. surinamensis</i>	24.81±0.27 ^{cd}	12.64±1.16 ^{bcd}	15.36±2.27	2.23±0.30 ^c	36
<i>T. variabile</i>	25.87±0.30 ^b	16.92±1.20 ^a	23.38±2.45	3.56±0.31 ^{ab}	35
<i>R. dominica</i>	25.29±0.26 ^{bc}	14.31±1.21 ^{abc}	21.69±3.54	2.78±0.27 ^{bc}	44
<i>L. serricornis</i>	24.24±0.26 ^d	12.36±1.31 ^{cd}	23.09±4.50	3.12±0.27 ^b	44
<i>T. ni</i>	27.91±0.31 ^a	16.20±1.94 ^{ab}	12.60±3.18	1.99±0.38 ^c	23
F	56.68	4.42	1.61	6.59	
df	7.256	7.85	7.84	7.284	
P	0.0001	0.0003	0.1436	0.0001	
N	29 to 39	5 to 15	5 to 15	5 to 15	

Means followed by different letters in each column are significantly different (ANOVA with protected LSD test, $P < 0.05$).

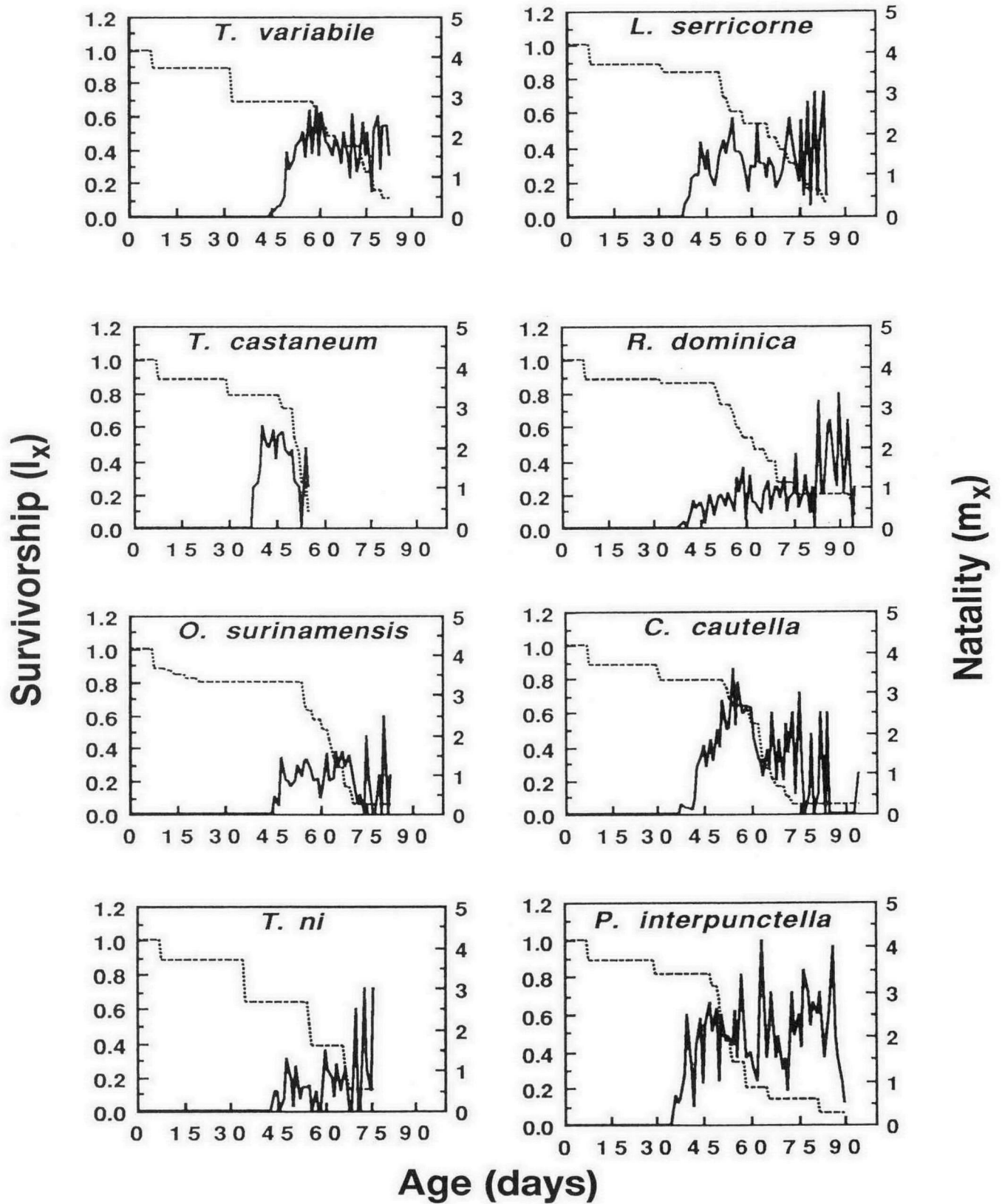


Fig. 1. Survivorship (l_x) and natality (m_x) patterns for *L. campestris* cohorts at different prey regimes. Natality represents the mean number of female eggs produced per female per day. Survivorship represents the proportion of individuals surviving to a given day. Day 1 on x axis is the first day of immature stage, and the last day where the graph terminates represents the death of the last female in the cohort. -----, survivorship; —, natality.

Population Dynamics

Survivorship and natality patterns of *L. campestris* under eight prey regimes are shown in Figure 1 (Parajulee and Phillips 1993). It is apparent that prey species has a pronounced effect on both survivorship and daily oviposition patterns. However, the mean egg production per female per day shows an oscillating trend through the course of oviposition irrespective of the prey. The survivorship of immature stages of the predator was significantly reduced when feeding on *T. variabile* and *T. ni* (Fig. 1). Oviposition began around 45 days after the birth of the parent and ceased within 85 days on *T. variabile*, *T. ni*, and *O. surinamensis*. Both the prolonged developmental period and the preoviposition period contributed to delayed reproduction in the females reared on the above three prey species. In contrast, predator reproduction began much earlier (35 days) than in the case of the above three prey species when *P. interpunctella*, *C. cautella*, *T. castaneum*, and *L. serricorne* were used as prey. Adult longevity was relatively short when *T. castaneum* was the prey, which gave rise to a lower total fecundity (Table 3) despite a considerably high rate of reproduction on a daily basis (Table 2). Hence, both the oviposition period and the rate of oviposition determine the total reproductive potential of the predator on a prey.

We have demonstrated that the variation on the availability of prey species has a pronounced effect on the resulting population dynamics in *L. campestris* (Table 3). Natality and survivorship curves (Fig. 1) reflect the highest gross reproductive rate (total lifetime production of female offspring per female, denoted by *GRR*) of *L. campestris* on *P. interpunctella* and the lowest on *T. ni*. The *GRR* of *L. campestris* is substantially higher than any other stored-product anthocorids studied to date (Arbogast 1975, 1984; Arbogast et al. 1983; Parajulee and Phillips 1993). The net reproductive rate (a population multiplication rate per generation, denoted by *R_o*) of *L. campestris* also varied like *GRR*, with maximum values on pyralids and the minimum on *T. ni*. In contrast to *GRR*, the *R_o* of *L. campestris* is similar to those of *X. flavipes* and *X. sordidus*, but much higher than that of *D. ater* (e.g. Arbogast 1984). The intrinsic rate of increase (*r*) is an

instantaneous growth rate of a population under a given condition. Hence, the interpretation of this statistic could be better made by its discrete analog, the finite rate of increase λ . The finite rate of increase is the capacity for population growth per unit time. Although variability exists on the finite rate of increase, *L. campestris* is capable of population increase ($\lambda > 1$) for all prey species tested (Table 3). The highest rates of population increase have been found on *P. interpunctella*, *T. castaneum*, *C. cautella*, and *L. serricorne*, while *T. ni* has been responsible for the lowest rate of population increase. Although the total fecundity of *L. campestris* is very low on *T. castaneum*, this has been compensated for by a short generation time on this prey, which has resulted in a finite rate of increase similar to that on *P. interpunctella*. Mean generation time (*T*) is also influenced by prey (Table 3). For example, *L. campestris* took almost two months to produce 50% of its total progeny when feeding on *T. variabile*, but the same proportion was produced within 44 days on *T. castaneum*.

Predatory Response

Quantitative predatory response of natural enemies is referred to as functional and/or numerical response. A functional response of the predator can be defined as the relationship between the number of prey consumed per predator and prey density (Solomon 1949; Holling 1959) which is a basic component of all predator-prey interactions (Murdoch and Oaten 1975; Hassell 1978). Parajulee et al. (1994) presents a detailed account of basic information on predatory behaviour of *L. campestris* by manipulating three attributes (predator sex, experimental habitat and prey type) influencing the predatory response (see Parajulee et al. 1994 for details on experimental methodology and data analyses). *L. campestris* has been shown to display a Type II functional response on all 12 treatment combinations where two experimental habitats (no-maize and maize habitats) and three prey species (*P. interpunctella*, *O. surinamensis*, *T. castaneum*) were tested for each sex of the predator. Most adult *L. campestris* consume all

Table 3. Life table statistics (mean \pm SEM) for *L. campestris* on different prey regimes (Parajulee and Phillips 1993).

Prey species	<i>GRR</i>	<i>R_o</i>	<i>r</i>	λ	<i>T</i>
<i>P. interpunctella</i>	106.98 ^a (1.41)	34.35 ^a (0.41)	0.0729 ^a (0.0037)	1.0757 ^a (0.0039)	48.60 ^e (0.20)
<i>T. castaneum</i>	29.78 ^f (1.60)	20.58 ^d (0.47)	0.0691 ^a (0.0042)	1.0715 ^a (0.0044)	43.94 ^f (0.23)
<i>C. cautella</i>	77.18 ^b (1.27)	33.75 ^a (0.36)	0.0675 ^a (0.0033)	1.0699 ^a (0.0035)	52.19 ^c (0.20)
<i>L. serricorne</i>	62.13 ^c (1.46)	30.38 ^b (0.43)	0.0652 ^{ab} (0.0038)	1.0673 ^{ab} (0.0041)	52.70 ^c (0.23)
<i>T. variabile</i>	61.68 ^c (1.36)	27.80 ^c (0.39)	0.0561 ^{bc} (0.0035)	1.0577 ^{bc} (0.0038)	59.42 ^a (0.21)
<i>O. surinamensis</i>	35.44 ^e (1.36)	15.21 ^e (0.39)	0.0527 ^c (0.0035)	1.0541 ^c (0.0038)	50.80 ^d (0.21)
<i>R. dominica</i>	55.77 ^d (1.36)	19.38 ^d (0.39)	0.0510 ^c (0.0035)	1.0523 ^c (0.0038)	58.96 ^a (0.21)
<i>T. ni</i>	22.72 ^g (2.07)	8.51 ^f (0.60)	0.0373 ^d (0.0054)	1.0380 ^d (0.0058)	55.72 ^b (0.33)
F	331.22	421.41	7.45	7.48	505.48

Means followed by different letters in each column are significantly different (ANOVA with protected LSD test, *df* = 7, 91; *P* < 0.0001). *GRR*, gross reproductive rate; *R_o*, net reproductive rate; *r*, instantaneous growth rate; λ finite rate of increase; *T*, mean generation time.

or most prey at lower prey densities (e.g. 2, 4, 8 prey per predator), and show a deceleration in rate of predation with greater variation at higher prey densities (e.g. 12, 16, 24, 30, 40) in a 24-hour experiment. Predatory response of *L. campestris* varies with the prey species. For example, both sexes of *L. campestris* showed the highest responses on *P. interpunctella* in both habitats, which was significantly different from responses on other prey in the no-maize habitat (Figs 2 and 3, Parajulee et al. 1994). However, the degree of response was reversed on the other two prey species for males and females. Males showed higher responses on *O. surinamensis* than on *T. castaneum* in both maize and no-maize treatments. In

contrast, females exhibited a higher response on *T. castaneum* than on *O. surinamensis* in the no-maize treatment only (Figs 2 and 3). When responses of the sexes on the same prey within habitats were compared, females killed more *P. interpunctella* ($P = 0.02$) and *T. castaneum* ($P = 0.02$) than males, and males killed more *O. surinamensis* than females ($P = 0.01$) in no-maize habitats. In a maize habitat, however, both sexes showed a similar response on *P. interpunctella* and *O. surinamensis*, but males killed more *T. castaneum* than females ($P = 0.004$). Similarly, habitat structure has a tremendous effect on predatory response of this species. A marked reduction in the functional response of *L. campestris* has been observed in an

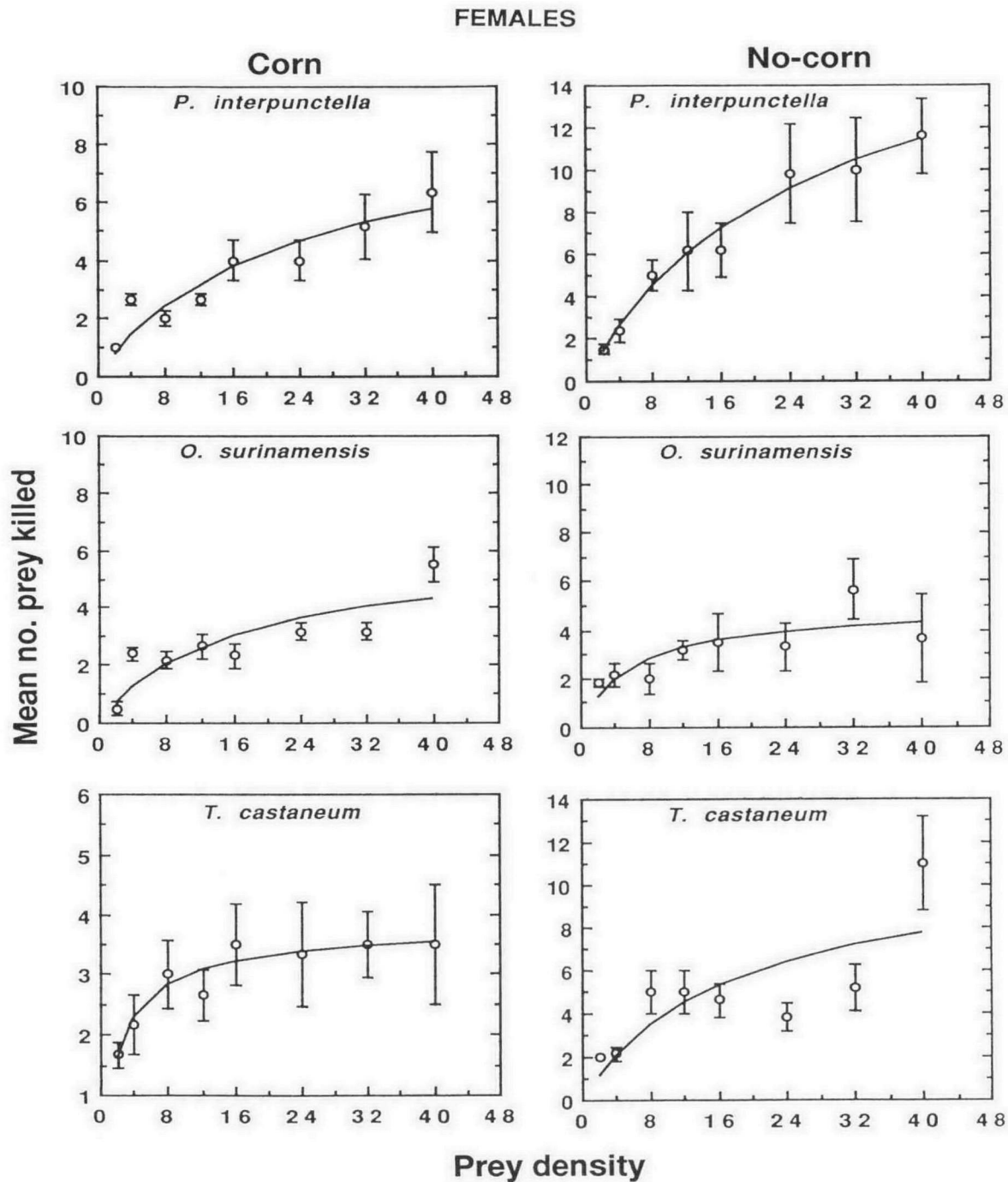


Fig. 2. Mean attack rate (number of fully-grown larvae of a given prey killed by *L. campestris* female per 24 hours \pm SEM) as a function of prey density in maize and no-maize arenas. Superimposed curves show the attack rate predicted by the disk equation. Note different scales on y-axis while comparing responses across habitats or prey types. Responses in maize and no-maize habitats are not significantly different in *O. surinamensis*.

experimental maize habitat compared to a no-maize habitat. From the study by Parajulee et al. (1994), it is clear that we must note that the effects of predator sex, prey species and habitat structure are also interactive among themselves. Habitat biomass and structure change continuously throughout the growing season in agricultural (field crop) systems, which can force predators to change search strategies (O'Neil 1990; Wiedenmann and O'Neil 1992). On the other hand, stored-product habitats are presumably more stable than conventional cropping systems and predators can employ the same search strategy throughout the storage period. The

response of *L. campestris* in an actual stored grain habitat may vary as a function of grain species, kernel size, grain moisture content, or spatial dimensions of the storage container. Because of size variations among different stored grains that affect the movement of both predators and prey (Press et al. 1978), we might expect a differential response of a predator to prey in different grain commodities. We feel that all three factors, prey species, habitat, and predator sex, including many other biotic and abiotic factors are important in determining predator-prey interactions in stored grain ecosystems.

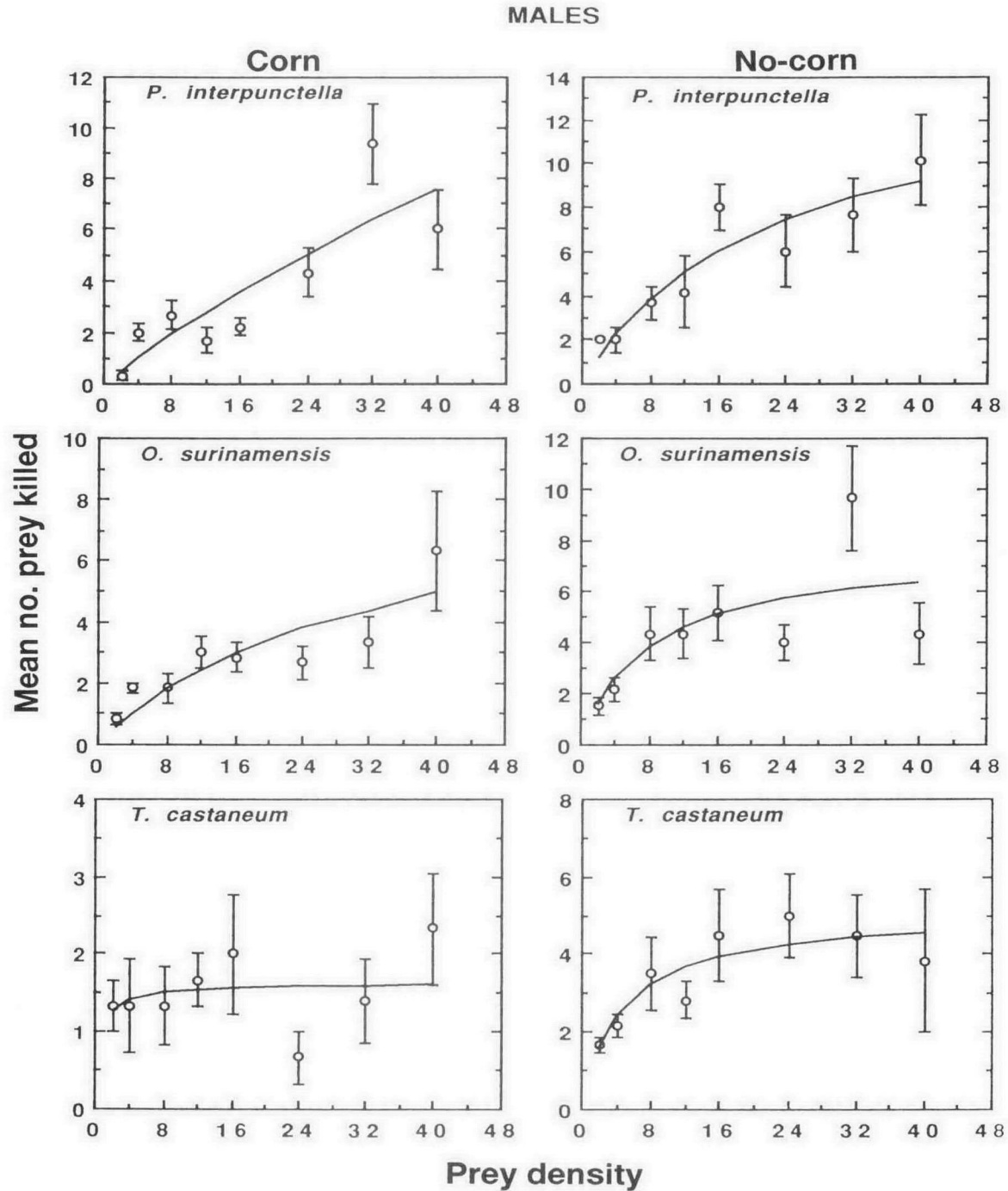


Fig. 3. Mean attack rate (number of fully-grown larvae of a given prey killed by *L. campestris* male per 24 hours \pm SEM) as a function of prey density in maize and no-maize arenas. Superimposed curves show the attack rate predicted by the disk equation. Note different scales on y-axis while comparing responses across habitats or prey types. Responses in corn and no-corn habitats are significantly different for all three prey species.

Many population biologists argue that a Type II response is inversely density dependent in changes in prey density and thus cannot by itself affect prey population regulation (e.g. van den Bosch et al. 1982). However, a numerical response via predator reproduction, movement or human intervention (e.g., augmentation) can exhibit positive density dependence and provide regulation of the prey population. *Lyctocoris campestris* does kill more prey at a higher density than it actually consumes. A similar behaviour has been reported for other species of predaceous arthropods (e.g. Mansour and Heimbach 1993). Hence, the efficiency of the bug depends more on its ability to find and subdue prey than on its satiation. In fact, *L. campestris* can survive for many days without food or water (unpublished data), resulting in a type of self-provisioning that might enable it to survive until prey populations rebound in a stored grain environment. The range in prey density tested in the experiments of Parajulee et al. (1994) includes and exceeds the density that we find in bins during the storage season. If the low density experiments in Parajulee et al. (1994) reflect a normal storage situation, *L. campestris* should be able to suppress populations of all three of the species they have tested. Quantitative information on the response of *L. campestris* to different prey species can be used to build predator-prey interaction models. Since a functional response is a fundamental component of predator-prey interactions, understanding this component on a range of prey species and habitats will help in designing an effective biological control program in stored-product ecosystems.

Field Biology

The natural history of *L. campestris* in field situations is poorly known. We found that these bugs prefer mouldy, moist areas over dry areas in the field. Of the 974 *L. campestris* trapped during our 4-week study in 1991–92 in a flat storage of maize, 874 of these, or ~90%, were trapped in mouldy areas (Parajulee and Phillips 1992b). Nearly all *L. campestris* trapped were adults, with fewer than 10 late instar nymphs trapped during the entire study. Low counts of nymphs in our study during 1991–92 posed a question regarding their habitat. To understand the habitat of nymphs in the grain storage, we collected nine samples of a 1140 mL volume of decayed and matted maize from moist areas around the wall and floor surfaces on September 5, 1992. Similarly, we used a 1140 mL cup sampler and collected samples from the grain mass over an 18-week sampling period (June 24 1992 to August 26 1992). Each sample was sifted and bugs were sorted by stages, nymphs versus adults. Our results showed that nymphs were predominant in these moist areas around the wall and floor surfaces. Our samples from those areas showed a nymph to adult ratio of 0.88: 0.12 (Fig. 4a). In contrast, we found a nymph to adult ratio of 0.37: 0.63 in absolute grain samples in the grain mass (Fig. 4b). Moreover, there were no nymphs in our grain mass samples until August, and we collected nymphs from August to October when the grain moisture was rising in the grain mass. This result is in agreement with our earlier finding that eggs require moisture for development. Thus, females may lay eggs in moist areas such as areas adjacent to walls near storage entrance doors and floor surfaces, and nymphs develop in such areas. When nymphs emerge as adults, they presumably disperse to the grain mass. Similarly, females may lay eggs in the grain mass late in the season when the grain moisture rises. More intensive sampling is underway to further investigate the distribution of nymphs and adults in the grain. The sex ratio of *L. campestris* adults trapped in grain masses has been found to be significantly biased toward females (Fig. 5). However, since other sampling methods yielded different sex ratios, probe

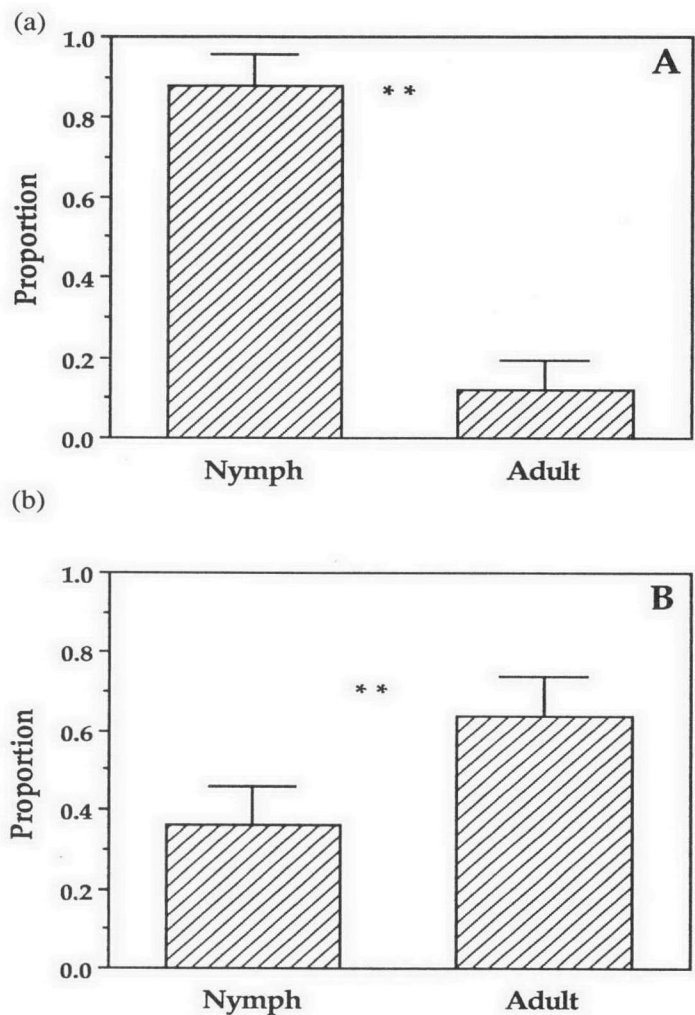


Fig. 4. Proportion of nymphs and adults collected by absolute sampling of 1140 mL of (a) thickly matted grain debris from the floor and wall surfaces in a flat storage of maize, September 5, 1992 and (b) samples from the grain mass (N = 342) in a flat storage of maize, 24 June–21 October 1992. Nymph to adult ratios were significantly different ($P < 0.005$; G - test) in both cases.

traps appeared to be a biased estimator of sex ratio in field populations (Parajulee and Phillips, these proceedings).

Conclusions

Developmental stages and oviposition behaviour of *L. campestris* are not unlike other Anthocoridae that have been studied (e.g. Anderson 1962a), and preference by *L. campestris* for mouldy areas of stored grain has been noted earlier (Kelton 1978), but not experimentally documented. Our finding that moist filter paper serves as a good oviposition substrate is similar to that for other bugs that oviposit into moist plant material or decaying vegetation (Anderson 1962a; Arbogast et al. 1983; Arbogast 1984). The importance of moisture for egg laying and egg survival that we found in the laboratory is reflected in field activity patterns. The majority of *L. campestris* were found in moist and mouldy areas, and this reflects their need for such areas as oviposition sites. The significant female-biased sex ratios of field-trapped *L. campestris* depicted by probe traps were merely due to differential mobility of females and males in the grain (Parajulee and Phillips, these proceedings). The paucity of nymphs of *L.*

References

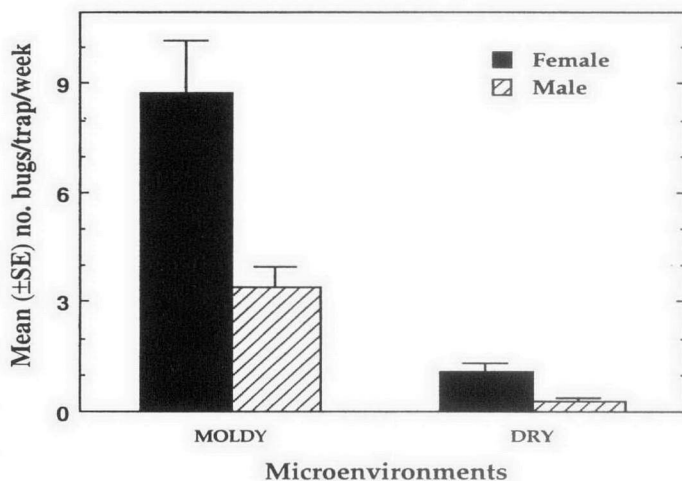


Fig. 5. Mean numbers of female and male *L. campestris* caught by using pitfall probe traps at two microenvironments in a flat storage of shelled maize in Madison, Wisconsin from 14 August to 4 September 1991. Sex ratios were female biased in both microenvironments ($P < 0.05$; G - test).

campestris in our field collections was due to different habitat preferences of nymphs compared with adults.

The use of natural enemies for the suppression of stored-product insects is a promising pest management tactic (e.g. Arbogast 1983). Most of the parasitoid species available as biocontrol agents of stored-product pests, as in other systems, are host and stage specific. The predator *X. flavipes* has been well studied and is commercially available for use in stored products, but it too may be limited because of its inability to subdue larger prey (Brower and Press 1992). However, *L. campestris* can use larvae of different sizes from among stored-product insect pests, ranging from the small *O. surinamensis* (≈ 3 mm) to the large *Galleria mellonella* (L.) (>20 mm). The ability to exploit a wide range of prey species and size is a useful attribute for a biological control agent, but is not sufficient to determine whether this predator could regulate prey populations in nature. Our results indicate that all prey are not equal in their quality for individual reproductive fitness and ultimate population increases in *L. campestris* (Parajulee and Phillips 1993). Life table studies revealed that *P. interpunctella*, *T. castaneum*, *C. cautella* and *L. serricornis* were the most suitable prey for development and reproduction of *L. campestris*, followed by *T. variable*, *O. surinamensis*, and *R. dominica*, with *T. ni* least suitable. Hence, one must also consider quality of prey when undertaking mass production of *L. campestris*. Because of its adaptability to mass rearing conditions, predatory ability (Figs. 2 and 3), and its apparent broad range in prey species and prey size (Table 1), we feel that *L. campestris* has potential for development as a biological control agent in stored products, and more research on its field ecology, predatory efficacy and pest suppression abilities should be undertaken.

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