Effects of Millet, Wheat, Rice, and Sorghum Diets on Development of *Corcyra cephalonica* (Stainton) (Lepidoptera: Galleriidae) and Its Suitability as a Host for *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae)

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ABSTRACT Emergence and survival of adults for 24 h was compared for *Trichogramma chilonis* Ishii reared on eggs of *Corcyra cephalonica* (Stainton) adults whose larval growth and development had been monitored on broken grains of four different cereals: finger millet (*Eleusine coracana* L. Gaertn), soft white wheat (*Triticum aestivum* L.), short-grained white rice (*Oryza sativa* L.), and durra sorghum (*Sorghum bicolor* L. Moench). For *C. cephalonica*, the percentage adult emergence and several fifth-instar food use indices (consumption index, relative growth rate, and efficiencies of conversion of ingested and digested food) were significantly higher for millet-reared than for sorghum-reared larvae. The nutritional indices for wheat- and rice-reared *C. cephalonica* larvae were intermediate between the indices for larvae reared on millet and sorghum. The percentage adult emergence and percentage 24-h survival of *T. chilonis* were significantly higher on eggs of *C. cephalonica* hosts reared on millet than on eggs of those reared on sorghum. These results suggest that the rearing of *C. cephalonica* larvae on a high-quality nutritional source resulted in high-quality eggs, which ultimately resulted in high-quality *T. chilonis* reared on those eggs. Such an effect has been modeled in ecological theory as a "bottom up cascade." Improved knowledge of the nutritional ecology of parasitoids and hosts can lead to improved understanding of the ecological mechanisms affecting host plant, host, and parasitoid abundance, as well as to improved efficiency and quality of *Trichogramma* production in mass rearing programs.

KEY WORDS nutritional ecology, plant–herbivore–parasitoid interaction, biological control

Trichogramma species are used worldwide in biological control against insect pests (Li 1994, Kuske et al. 2003). Approximately 15 million ha of agricultural crops and forests are treated with *Trichogramma* annually (van Lenteren 2000). Many *Trichogramma* species are generalist egg parasitoids with a broad host range, including Lepidoptera, Diptera, Coleoptera, Hymenoptera, Neuroptera, and Megaloptera (Thomson and Stinner 1989, Li et al. 1994, Hoffmann et al. 1995, McGregor et al. 1998, Orr et al. 2000, Wright et al. 2002, Mansfield and Mills 2004). *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammidae) are widely used against cereal pests. Commercial facilities produce large numbers of *T. chilonis* from parasitized eggs of the rice moth, *Corcyra cephalonica* (Stainton)

(Lepidoptera: Pyralidae), and other stored product moths (Bernardi et al. 2000).

The rearing host diet is potentially of importance to the nutritional quality of host eggs and the survival of *Trichogramma* and other egg parasitoids released into the environment as biological control agents (Hunter 2003). It has been reported that *C. cephalonica* have a shorter development time on millet than on sorghum (Russell et al. 1980) and a shorter development time on maize than on cocoa (Mbata 1989). In this report, we considered the hypothesis that the quality of *T. chilonis* obtained from *C. cephalonica* eggs is affected by the type of cereal used to feed the host larvae. Such a result would be an example of a "bottom-up cascade" of ecological effects (Hunter and Price 1992). High-quality plants may support development of herbivores with high nutritional quality that ultimately support high-quality parasitoids (van Huis and de Rooy 1998) or predators (Shahayaraj and Sathiamoorthi 2002).

Materials and Methods

Corcyra cephalonica eggs were obtained from naturally infested grain stored in a local warehouse (Food

Corp. of India, Peelamedu, Coimbatore, Tamil Nadu, India). The *C. cephalonica* were mass cultured at 28 ± 2°C, 65% RH, with a 14:10 light:dark cycle in 45 by 45-cm plastic troughs on broken seeds of finger millet, *Eleusine coracana* L. Gaertn.; soft white wheat, *Triticum aestivum* L.; short-grained white rice, *Oryza sativa* L., and *Sorghum bicolor* L. Moench, purchased from a local market.

To obtain eggs for developmental experiments, adult *C. cephalonica* were transferred to 24 by 10-cm-diameter glass jars and fed with 10% sucrose solution ad libitum. After 3 d, the eggs deposited in the jars were brushed out and counted. Individual eggs were placed in 500 by 356 by 200-mm perspex containers (Displaysense, Bishop's Stortford, UK) so that development could be followed on a daily basis until hatch of the first instars. On hatching, each larva was transferred to a 10 by 4-cm-diameter glass jar with two broken seeds of one of the four different cereals. After successful tunneling, the uninfested seed was removed. Additional seeds were added when the infested seed was consumed, usually three to five seeds during the course of development. All experiments were carried out at 28 ± 2°C, 65% RH, with a 14:10 light:dark cycle. Thirty jars of larvae feeding on each cereal were examined daily (120 jars) in three separately conducted tests (90 larvae total for each cereal) to monitor developmental durations and adult longevity.

The nutritional indices of consumption index (CI), relative growth rate (RGR), efficiency of consumption of ingested food (ECI), and efficiency of consumption of digested food (ECD) were calculated for 10 individual fifth instars on each cereal using equations 1–4, respectively, listed in Fig. 1 (see Waldbauer 1968). The procedures used to determine the indices were similar to those described in Waldbauer (1968) and Bowers et al. (1991). All indices were calculated using measured or estimated dry weights. To estimate initial dry weight, a freshly molted fifth instar and a broken seed of its rearing cereal were weighed and placed in a glass jar with 100% RH. After 1 d, larval and seed weights were measured separately. The larva and seed were dried at 60°C for 36 h and weighed to determine dry weight. Twenty newly molted fifth instars and 20 seeds of each cereal were used in calculating a mean dry-to-fresh-weight ratio for instars and the mean dry-to-fresh-weight ratio for seeds of each cereal. The instar-weight ratio was used in calculation of Wt_{instar} and Wt_{gained}, and the seed-weight ratio was used in calculation of $Wt_{food\ ingested}$. Dry weight of frass, Wt_{frass}, was determined after drying the fresh frass at 60°C for 36 h.

The *T. chilonis* used for parasitization studies were initially obtained as adults from an existing colony at the Biocontrol Laboratory, Vadavalli, Coimbatore, Tamil Nadu. To mass culture *T. chilonis* for these experiments, fresh *C. cephalonica* eggs from adults reared on each host cereal were sterilized under an UV lamp (UVP, Upland, CA) for 0.5 h and attached to paper cards coated with locally obtained 10% *Acacia arabica* (Lam.) Willd. gum. The egg cards were cut

into 1-cm squares, and the numbers of eggs were recorded in each card. Egg cards were placed in loose-fitting, 15 by 7-cm polyvinyl bags and maintained at 27 ± 1°C, 70–80% RH, and a L 16:D 8 photoperiod. Male and female adult parasitoids emerged within the bags and mated within the first day after emergence began (Singh et al. 1994).

For the parasitization experiments, five *T. chilonis* females that had emerged from eggs of *C. cephalonica* reared on a particular host cereal and allowed to mate for 24 h were released for 4 h onto 250 eggs of *C. cephalonica*, reared on the same host cereal, on cards that had been placed in a 10-mm-diameter by 8-mm perspex container (Displaysense). Percentage emergence (Fig. 1, equation 5) was calculated by individual observation of five replicates of 30 parasitized eggs from each host cereal. Parasitized eggs were identified by color, turning from white to tan by the third day and to black by the fifth day after parasitism. Eggs that did not go through a color change were considered unparasitized. Percentage survival for 24 h after emergence (Fig. 1, equation 6) was monitored. Five replicates of 30 adults picked at random from those that emerged in the perspex containers were monitored in the percentage survival trials for each cereal.

Data from all experiments were subjected to analysis of variance (ANOVA; Proc ANOVA), with cereal type as a main factor, and means were separated using Tukey's honestly significant difference (HSD) test (SAS Institute 1988). Percentages were transformed by arcsine square root before ANOVA.

Results and Discussion

Food Use Measurements. The *C. cephalonica* larvae survived well on all four cereals and, as in Tauthong (1989), there were no significant differences in mean time from egg to adult for males and females across different cereals. The mean generation time ranged from 37.9 ± 2.7 d for males reared on *E. coracana* to 44.3 ± 3.3 d for females reared on *S. bicolor.* However, four indices of food use by fifth instars were significantly higher for fifth instars reared on *E. coracana* than for those reared on *S. bicolor* (Table 1): the CI ($F = 8.87$; df = 3,36; $P < 0.01$), RGR ($F = 15.37$; df = 3,36; $P < 0.01$), ECI ($F = 5.54$; df = 3,36; $P < 0.01$), and ECD ($F = 7.99$; df = 3,36; $P < 0.01$). The index CI is a measure of the rate of intake relative to the mean larval weight during the feeding period, RGR is a measure of the rate of growth relative to the mean larval weight during the feeding period, ECI is a measure the ability of a larva to incorporate ingested food into growth, and ECD is a measure of the efficiency of conversion of digested food into growth. In addition, *C. cephalonica* reared on *E. coracana* had a significantly higher percentage adult emergence than those reared on other cereals ($F = 16.07$; df = 3,36; $P < 0.01$). These results, which suggest that *E. coracana* has more nutritive value for *C. cephalonica* larvae than *S. bicolor*, are consistent with the findings of Russell et al. (1980) that overall performance of *C. cephalonica* was better

Consumption index $\qquad CI = \dfrac{Wt_{food\ ingested} - Wt_{frass}}{\text{Mean } Wt_{instar} \times \text{feeding period}}$ (1)

Relative growth rate $\qquad RGR = \dfrac{Wt_{gained}}{\text{Mean } Wt_{instar} \times \text{feeding period}}$ (2)

Efficiency of conversion of ingested food $\qquad ECI = \dfrac{Wt_{gained}}{Wt_{food\ ingested}} \times 100$ (3)

Efficiency of conversion of digested food $\qquad ECD = \dfrac{Wt_{gained}}{Wt_{food\ ingested} - Wt_{frass}} \times 100$ (4)

Percentage emergence $\qquad EM = \dfrac{\text{No. } T.\ chilonis \text{ emerged}}{\text{No. parasitized eggs}} \times 100$ (5)

Percentage survival $\qquad S_{24h} = \dfrac{\text{No. } T.\ chilonis \text{ surviving 24 h}}{\text{No. } T.\ chilonis \text{ emerged}} \times 100$ (6)

Fig. 1. Equations used for calculation of consumption index, relative growth rate, efficiency of conversion of ingested food, and efficiency of conversion of digested food of fifth-instar *C. cephalonica* (equations 1–4), and percentage emergence and 24-h survival of *T. chilonis* parasitoids (equations 5 and 6). $Wt_{food\ ingested}$, dry weight of food eaten during feeding period; Wt_{frass}, dry weight of feces, mean Wt_{instar}, mean dry weight of instar during feeding period; Wt_{gained}, dry weight gain of instar during feeding period.

on *E. coracana* than on *S. bicolor*. In general, the values for RGR, ECI, and ECD in this report lie within the ranges reported for other Lepidopteran species (Slansky and Scriber 1985, Bowers et al. 1991).

Some of the observed differences in the development and emergence of *C. cephalonica* on different cereals, as well as similar findings by Kumar et al. (1998), Kalaivani et al. (1999), and Bernardi et al.

Table 1. Food use of fifth instars and percentage adult emergence of *C. cephalonica* fed on different cereal diets

Diet	CI (mg/mg/d)	RGR (mg/mg/d)	ECI (%)	ECD (%)	Adult emergence (%)
E. coracana	0.693 ± 0.039a	0.100 ± 0.01a	14.5 ± 1.2a	55.6 ± 3.4a	92.5 ± 3.5a
T. aestivum	0.571 ± 0.034ab	0.067 ± 0.005ab	11.8 ± 0.9ab	47.3 ± 2.7ab	70.4 ± 5.2b
O. sativa	0.501 ± 0.031b	0.053 ± 0.004b	10.7 ± 0.9ab	43.6 ± 2.9ab	70.4 ± 5.4b
S. bicolor	0.476 ± 0.025b	0.044 ± 0.004b	9.3 ± 0.7b	38.7 ± 2.4b	68.0 ± 6.1b

Means ± SEM within the same column followed by the same letters are not significantly different ($P < 0.05$; Tukey test).

Table 2. Nutrient profiles of cereals used for *C. cephalonica* diets

Cereal	Nutrient (mean ± SEM in mg/g)			
	Carbohydrate	Protein	Lipid	Water
E. coracana[a]	728.4	110.2 ± 6.8	42.2 ± 0.31	86.7 ± 5.84
T. aestivum[b]	753.6	106.9 ± 10.8	19.9 ± 0.14	104.2 ± 10.6
O. sativa[b]	719.5	65.0 ± 5.1	5.2 ± 0.12	132.9 ± 6.7
S. bicolor[b]	746.3	113.04 ± 10.3	33.0 ± 0.18	92.0 ± 5.84

[a] Sripriya et al. 1997.
[b] USDA–ARS 2004.

(2000), could be caused by the relatively high lipid content of *E. coracana* (Table 2). Growth, development, and reproduction of insects are strongly dependent on the quality and quantity of food ingested (Scriber and Slansky 1981). However, a possible reason for the lower ranking of *S. bicolor* on measures of *C. cephalonica* development and adult emergence is that it contains the cyanogenic glycoside, dhurrin, which may function as a defense against insect herbivory (Celenza 2001).

Plant Quality and Parasitoid Performance. A significantly greater percentage of *T. chilonis* emerged from eggs produced by *E. coracana*–fed *C. cephalonica* ($F = 33.8$; $df = 3,596$; $P < 0.01$) than from eggs produced by *S. bicolor*–fed, *O. sativa*-fed, or *T. aestivum*–fed *C. cephalonica* (Table 3). The sex ratio was not measured, but previous studies of *T. chilonis* reared on eggs of *Sitotroga cerealella* Olivier have found the proportion of females to be 0.55–0.6 at these temperatures at ratios of 150 host eggs per female (Haile et al. 2002), and the proportion would not be expected to decrease unless the ratio of females to host eggs increased to levels >1:10 (Smith 1996). There were no significant differences in the percentages parasitized, which ranged from 93.7 ± 4.1 for eggs produced by *E. coracana*--fed *C. cephalonica* to 79.7 ± 6.9 for eggs produced by *S. bicolor*–fed *C. cephalonica.* A significantly greater percentage of *T. chilonis* survived 24 h after emerging from eggs produced by *C. cephalonica* that were fed *E. coracana* ($F = 16.4$; $df = 3,596$; $P < 0.01$) than from eggs of adults fed *S. bicolor* as larvae (Table 2). Other examples where plant quality affected parasitoid performance on different hosts include *Uscana lariophaga* Steffan performance on *Callosobruchus maculatus* (Fabricius) fed on cowpea, chickpea, and pigeonpea (van Huis and de Rooy 1998) and *Cotesia congregata* (Say) performance on

Table 3. Percentage adult emergence and percentage 24-h survival of *T. chilonis* from *C. cephalonica* eggs of adults that were fed different cereals as larvae

Diet	Percentage emergence	Percentage 24-h survival
E. coracana	96.9 ± 2.5a	94.4 ± 2.1a
T. aestivum	84.2 ± 3.2b	85.2 ± 3.2ab
O. sativa	81.7 ± 3.5b	82.0 ± 4.1b
S. bicolor	76.7 ± 4.1c	79.1 ± 4.2b

Means ± SEM within the same column followed by the same letters are not significantly different ($P < 0.05$; Tukey test).

Manduca sexta L that were fed artificial diets with different amounts of casein and sucrose (Thompson et al. 2004).

These effects of host cereal quality on parasitoid performance are possible examples of a "bottom up cascade" of ecological effects driven by nutrient availability (Hunter and Price 1992) or other trophic interactions (Knight et al. 2005). High nutritional quality plants may support development of herbivores with high nutritional quality that ultimately support high performance parasitoids. However, the "bottom up cascade" and the possible effects of allelochemicals passed through a herbivore host to a parasitoid are just two of many possible factors that can affect the survival of parasitoids (Turlings and Benrey 1998, Hunter 2003, Davies et al. 2004). Consequently, it is difficult to predict beforehand whether the use of a particular plant for nutrition by a host will have a positive or negative effect on the quality of parasitoids reared on the host eggs, and it is necessary to determine the effect experimentally.

Acknowledgments

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