

COMMENTARY

Sex Ratios of Commercially Reared Biological Control Agents

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We purchased samples of 27 parasitoids, six coccinellid beetles, and the predatory midge *Aphidoletes aphidimyza* (Rondani) from commercial insectaries and scored the sex ratios from groups of approximately 200 individuals from each of these samples. Parasitoid sex ratios ranged from all female to 0.77 (proportion males), and none of the predator sex ratios differed significantly from 0.5. Among the parasitoids, we found no significant effect of taxonomic affiliation (family, superfamily) or life history (gregarious vs solitary development) on the sex ratio. The pteromalid parasitoids *Muscidifurax raptorellus* (Kogan and Legner), *M. zaraptor* (Kogan and Legner), and *Nasonia vitripennis* (Walker) and the eulophid *Diglyphus isaea* (Walker) all had significantly male-biased sex ratios, and an additional five species that did not have male-biased sex ratios had sex ratios that had a higher proportion of males than reported in the literature. These were *Cotesia plutellae* Kurdjumov (Braconidae), *Dacnusa sibirica* Telenga (Braconidae), *Eretmocerus* nr. *californicus* Howard (Aphelinidae), *Trichogramma brassicae* Bezdenko (Trichogrammatidae), and *Pediobius foveolatus* (Crawford) (Eulophidae). This suggests that it may be possible to increase the proportion of females produced by these species under conditions of commercial rearing. In the rest of the species studied (74% of species purchased), sex ratios either conformed to most published reports or had a higher proportion of females. We discuss the sex ratios of each species or group of species separately and review potential explanations for the sex ratios that we found, as well as implications of the results for mass rearing. © 2000 Academic Press

Key Words: biological control; sex ratio; parasitoids; insectary; Coccinellidae.

1993; Sabelis and Nagelkerke, 1993). In principle, this variability in sex ratios can either benefit or hinder the practice of biological control. Consistently female-biased sex ratios are expected to benefit biological control because of increased population growth rates and, in the case of parasitoids, because males do not contribute to pest mortality (Waage, 1982a; Hassell *et al.*, 1983; Comins and Wellings, 1985; Hall, 1993). On the other hand, male-biased sex ratios can without question be a hindrance to successful biological control. Indeed, the failure of numerous biological control projects involving parasitoid wasps have been tentatively attributed to male-biased sex ratios and related phenomena (Stouthamer *et al.*, 1992), and the literature is filled with cases of male-biased sex ratios of parasitic wasps under conditions of laboratory and mass rearing (Table 1).

Approximately 150 species of biological control agents are available commercially from over 100 retail and wholesale suppliers in North America (Hunter, 1997) and more species and suppliers are available in Europe (van Lenteren *et al.*, 1997). A substantial subset of these natural enemies—parasitoid wasps (King, 1987, 1993; Luck *et al.*, 1993; Godfray, 1994; Quicke, 1997), predatory mites (Sabelis and Nagelkerke, 1993; Nagelkerke and Sabelis, 1996), coccinellid beetles (Hurst *et al.*, 1997; Majerus and Hurst, 1997), and predatory midges (Snell, 1976; Gilkeson and Hill, 1986)—are known to contain species with variable sex ratios. Here we document the sex ratios of 34 species of biological control agents after purchasing them from commercial insectaries. The main objectives of the study were to determine whether unexpected male or female biases in sex ratio are present in commercially available stocks of biological control agents and to review the mechanisms affecting the sex ratios of these species under mass rearing.

INTRODUCTION

Sex ratio variation is widespread among biological control agents and can be attributed to a wide range of causes (Ebbert, 1993; King, 1987, 1993; Luck *et al.*,

MATERIALS AND METHODS

We purchased 27 species of parasitoid wasps, 6 species of coccinellid beetles, and the predatory midge

TABLE 1

Parasitoid Wasps Reported to Produce Male-Biased Sex Ratios under Conditions of Laboratory or Mass Rearing

Species	Proportion male	Explanation given	References
Ichneumonidae			
<i>Aenoplex</i> (= <i>Mastra</i>) <i>carpocapsae</i> (Cush.)	0.61–0.87	?	Simmonds (1947)
<i>Angitia punctoria</i> Rom.	“Very male-biased”	?	Wilkes (1947)
<i>Campoletis perdistinctus</i> (Viereck)	0.56–0.92	Photoperiod effects	Hoelscher and Vinson (1971)
<i>C. sonorensis</i> (Cameron)	0.84	?	J. Harvey, pers. comm.
<i>Campoplex haywardi</i> Blanchard	0.67 ^a	?	Platner and Oatman (1972)
<i>Cremastus flovoorbitalis</i> Cameron	Unspecified but very male-biased	?	Wilkes (1947)
<i>Diadegma eucerophaga</i> (Cush.)	0.67	Inbreeding	Waage (1982)
<i>D. stellenbochense</i> (Cameron)	0.83 ^a	?, but member of related genus has single-locus CSD (see text)	Platner and Oatman (1972)
<i>Glypta fumiferanae</i> Viereck	0.67–0.98	Virginity	Rappaport and Page (1985)
<i>Harogenes punctorius</i> (Roman)	0.66	?	Baker <i>et al.</i> (1949)
<i>Mallochia pyralidis</i> Viereck	0.70–0.91	Virginity and other unknown factor(s)	Smith <i>et al.</i> (1990)
<i>Nythobia</i> sp.	0.75 ^a	?	Platner and Oatman (1972)
<i>Pimpla</i> (= <i>Coccygomimus</i>) <i>parnarae</i> Viereck	0.44–0.85	Host size effects	Ueno (1999)
<i>P. luctuosa</i> Smith	0.62–0.79	Host size, in part	Ueno and Tanaka (1994)
<i>Temelucha</i> sp.	0.83 ^a	?	Platner and Oatman (1972)
Braconidae			
<i>Agathis gibosa</i> Say	0.67 ^a	?	Platner and Oatman (1972)
<i>A. unicolorata</i> Shenefelt	0.80 ^a	?	Platner and Oatman (1972)
<i>Apanteles scutellaris</i> Muesebeck	0.75 ^a	?	Platner and Oatman (1972)
<i>A. subandinus</i> Blanchard	0.75 ^a	?	Platner and Oatman (1972)
<i>Chelonus curvimaculatus</i> Cameron	0.67 ^a	?	Platner and Oatman (1972)
<i>Cotesia melanoscela</i> Ratzeburg	0.40–1.0	?	Kolodny-Hirsch (1988); Kruse and Raffa (1997)
<i>Eubazus crassigaster</i> (Provancher)	0.58	“Rearing conditions”	Kenis <i>et al.</i> (1996)
<i>E. robustus</i> (Ratzeburg)	0.80	“Rearing conditions”	Kenis <i>et al.</i> (1996)
<i>E. semirugosus</i> (Nees)	0.62	“Rearing conditions”	Kenis <i>et al.</i> (1996)
<i>Eubazus</i> sp.	0.60	“Rearing conditions”	Kenis <i>et al.</i> (1996)
<i>Fopius</i> (= <i>Biosteres</i>) <i>arisanus</i> (Sonan)	0.45–0.84	Unmatedness	Bautista <i>et al.</i> (1999)
<i>Glyptapanteles militaris</i> (Walsh)	0.81–0.88	Unmatedness	Oliveria <i>et al.</i> (1999)
<i>Habrobracon</i> (= <i>Bracon</i>) <i>hebetor</i>	0.39–0.80	Sperm depletion, sex specific differences in developmental mortality (CSD not mentioned)	Rotary and Gerling (1973)
<i>H. sp. nr. hebetor</i>	0.80	Single-locus CSD	Heimpel <i>et al.</i> (1997), Holloway <i>et al.</i> (1999)
<i>Macrocentrus ancylivorus</i> Roh.	0.49–0.70	?, overmating	Garman and Schread (1931), Flanders (1945)

TABLE 1—Continued

Species	Proportion male	Explanation given	References
<i>M. grandii</i> (= <i>gifuensis</i> = <i>cingulum</i>) (Ashmead)	Highly variable; can approach 1	?	G. E. H., unpublished data, K. R. Hopper, pers. comm., D. Ragsdale, pers. comm.
<i>Microctonus aethioides</i> (= <i>aethiops</i>) (Nees)	0.65–0.75	Possibly related to <i>Nosema</i> infection	Fusco and Hower (1973)
<i>Microplitis croceipes</i> (Cresson)	0.74–0.81	Inbreeding under probable CSD	Steiner and Teig (1989)
<i>M. croceipes</i>	0.67	?	K. Kadash, pers. comm.
<i>M. demolitor</i> Wilkinson	0.6–0.7 ^a	?	M. R. Strand, pers. comm.
<i>M. mediator</i> (Haliday)	0.68	?	K. Kadash, pers. comm.
<i>Opius pallipes</i> Wesmael	>0.9	?	Minkenbergh and van Lenteren (1986)
<i>Orgilus lepidus</i> Muesebeck	0.67 ^a	?	Platner and Oatman (1972)
<i>O. parvus</i> Turner	0.75 ^a	?	Platner and Oatman (1972)
<i>Praon pequodorum</i> Viereck	“Extremely male-biased”	?	N. Schellhorn, pers. comm.
<i>Rogas lymantriae</i> Watanabe	0.70–0.80	Virgin reproduction	Grinberg and Wallner (1991)
Pteromalidae			
<i>Muscidifurax raptor</i> G. & S. (long-term culture)	0.40–0.55	Microsporidian infection	Geden <i>et al.</i> (1992), Zchori-Fein <i>et al.</i> (1992b)
<i>Psychophagus</i> (= <i>Diglochus</i>) <i>omnivorosus</i> Walker	0.77–0.87	?	Mosson <i>et al.</i> (1997)
Eulophidae			
<i>Diglyphus begini</i> (Ashmead)	0.6–0.72	?, but sex-specific differences in mortality, and superparasitism ruled out	Heinz and Parrella (1990a,b)
<i>D. intermedius</i> (Girault)	0.69	Host quality effect	Hendrickson and Barth (1978)
<i>D. isaea</i> (Girault)	0.6–0.7 ^a	Host quality effect	Hendrickson and Barth (1978), P. J. Ode and K. M. Heinz, unpublished data
<i>Microplectron fuscipennis</i> Zett.	0.15–0.85	Inbreeding effect	Wilkes (1947)
Trichogrammatidae			
<i>Trichogramma minutum</i> Riley	0.75	Refrigeration	Garman and Schread (1931)
Eupelmidae			
<i>Anastatus disparis</i> Ruschka	0.91 ^a	Host stage effect	Clausen (1978)
Encyrtidae			
<i>Anarhopus sydneyensis</i> Timb.	0.95 ^a	?	Compere and Flanders (1934)
<i>Metaphycus helvolus</i> (Compere)	0.63	Low parasitoid/host ratio	Ibrahim (1986)

^a Approximate.

Aphidoletes aphidimyza (Rondani) from various United States insectaries (Table 2). To maintain anonymity of the insectaries used, we do not list them here. Single shipments containing at least 200 individuals were used. While sex ratios of different shipments of mass-reared natural enemies have been relatively consistent in some studies (Losey and Calvin, 1995; Fernandez and Nentwig, 1997; O'Neil *et al.*, 1998), we recognize that variability among shipments may be high (e.g., Cerruti and Bigler, 1995). By using a single shipment for each species, we are reporting data for representative samples only.

Species that were shipped as live adults were killed by freezing before being sexed. Some species were shipped as immatures within host eggs, mummies, or puparia. In these cases, the potential for sex-specific differences in emergence times introduces a potential experimental bias into the scored sex ratio. For these species, we waited until all individuals had emerged before killing them by freezing and scoring sex ratios. In cases in which natural enemies were shipped within loose substrate that allowed disproportionate settling of contents by weight (i.e., fly puparia containing immature stages of the four pteromalid parasitoids used in the study), we removed all of the puparia from each shipment into plastic dishes prior to parasitoid emergence. In the one case in which we failed to take this precaution (*Muscidifurax raptorellus* (Kogan and Legner); see Table 2), we scored each emerged individual in the shipment bag.

Various characters were used to score sex. For some parasitoids, females are easily recognizable by ovipositors that are either extruded or otherwise clearly visible at magnification levels of 50 \times or less using a dissecting microscope. These included *Goniozus legneri* Gordh, *Cotesia plutellae* Kurdjumov, *Dacnusa siberica* Telenga, *Habrobracon* (= *Bracon*) *hebetor* (Say), *Opius pallipes* Wesmael, and all of the encyrtids and pteromalids. For *Diglyphus isaea* (Walker), sexual dimorphism of hind tibial markings (Gordh and Hendrickson, 1979) was used in conjunction with externally visible reproductive structures. All *Aphidius* spp., aphelinids, eulophids, trichogrammatids, and the mymarid *Anaphes iole* (Girault) were slide mounted in distilled water and viewed at 100 \times and/or 400 \times and reproductive and antennal characters were used to score sex. The terminal abdominal segment of many coccinellid species is sexually dimorphic and this character was used in most cases for the coccinellids in the study (at a magnification of $\geq 20\times$). In ambiguous cases, individuals were dissected and internal reproductive structures were used to identify sex. Individuals of the cecidomyiid *Aphidoletes aphidimyza* were slide-mounted and viewed at 100 \times and 400 \times and sex was scored using genital and antennal characteristics described by Harris (1973).

We used log-likelihood goodness-of-fit tests to evaluate the hypothesis that observed sex ratios for each

species differed from 0.5 (proportion males) (Sokal and Rohlf, 1981):

$$G = \frac{2 \left(M \ln \frac{M}{0.5N} + F \ln \frac{F}{0.5N} \right)}{1 + \frac{1}{2N}},$$

where M is the number of males in the sample, F is the number of females in the sample, N is $M + F$, and the denominator is Williams' correction factor (Sokal and Rohlf, 1981). Significance levels were determined using the χ^2 distribution at one degree of freedom. We tested for effects of natural enemy taxon and whether parasitoids had solitary or gregarious development on sex ratio using single-classification Kruskal–Wallace tests (SAS Institute, 1995).

RESULTS AND DISCUSSION

Significantly female-biased sex ratios were found in 17 species of parasitoids (including 2 species that included only females) and significantly male-biased sex ratios were found in 4 species of parasitoids (Table 2). The remaining 6 parasitoid species and all of the predators had sex ratios that were not significantly different from 0.50. Overall, sex ratios of parasitoids were more female-biased than those of predators, but this difference was not significant (0.34 ± 0.04 [SE], $n = 27$ spp. vs 0.50 ± 0.01 [SE], $n = 7$ spp.; Kruskal–Wallace test $\chi^2 = 3.1$, $P = 0.077$). The only parasitoid family that had a higher average sex ratio than that of the predators was the Pteromalidae (Fig. 1). Within the parasitoids, neither family, superfamily, nor whether species were solitary or gregarious had a significant effect on sex ratio (single-classification Kruskal–Wallace test for all analyses: $P > 0.25$).

The sex ratios of most parasitoid species from our samples were significantly female biased (63%) and only a minority had male-biased sex ratios (15%). This prevalence of female-biased sex ratios is consistent with favorable rearing conditions under mass rearing. Conditions that can lead to male-biased sex ratios in parasitoids under conditions of mass rearing include poor host quality and/or a high parasitoid/host ratio (Waage *et al.*, 1985) and, for some species, inbreeding (Stouthamer *et al.*, 1992; Cook, 1993b). While these conditions can also lead to less female-biased sex ratios than may be optimal from an economic standpoint (Heinz, 1998), conditions for most parasitoids in this study are at least adequate to prevent male biases. The lack of female-biased sex ratios in the coccinellids sampled here is consistent with the absence of male-killing endosymbionts in these populations (Hurst *et al.*, 1997; Majerus and Hurst, 1997).

TABLE 2

Sex Ratios (Proportion Males), Sample Sizes (Total Numbers of Adults Scored), and Results of Goodness-of-Fit Tests for Biological Control Agents Purchased from Commercial Insectaries

Species	Proportion males	Total <i>N</i>	<i>G</i>
Parasitoids			
Bethylidae			
<i>Goniozus legneri</i>	0.18	236	105.91***
Braconidae			
<i>Aphidius colemani</i>	0.52	202	0.49
<i>A. ervi</i>	0.15	205	113.23***
<i>A. matricariae</i>	0.32	206	28.64***
<i>Cotesia plutellae</i>	0.51	209	0.12
<i>Dacnusa sibirica</i>	0.40	212	8.36***
<i>Habrobracon</i> (= <i>Bracon</i>) <i>hebetor</i>	0.32	204	27.40***
<i>Opius pallipes</i>	0.52	166	0.22
Aphelinidae			
<i>Aphelinus abdominalis</i>	0.22	103	33.23***
<i>Aphytis melinus</i>	0.38	207	12.66***
<i>Encarsia formosa</i>	0.00	35	N/A
<i>Eretmocerus</i> nr. <i>californicus</i>	0.56	142	2.28
Encyrtidae			
<i>Leptomastix dactylopii</i>	0.23	147	44.63***
<i>Metaphycus helvolus</i>	0.08	204	170.22***
Eulophidae			
<i>Diglyphus isaea</i>	0.77	241	75.05***
<i>Pediobius foveolatus</i>	0.51	37	0.03
<i>Thripobeus semiluteus</i>	0.00	173	N/A
Mymaridae			
<i>Anaphes iole</i>	0.17	200	94.67***
Pteromalidae			
<i>Muscidifurax raptorellus</i>	0.65	1,569	138.64***
<i>M. zaraptor</i>	0.62	207	12.66***
<i>Nasonia vitripennis</i>	0.61	200	8.86***
<i>Spalangia endius</i>	0.37	221	14.84***
Trichogrammatidae			
<i>Trichogramma brassicae</i>	0.44	228	2.96
<i>T. minutum</i>	0.07	194	167.94***
<i>T. platneri</i>	0.08	199	164.12***
<i>T. pretiosum</i>	0.13	196	121.77***
<i>Trichogrammatoidea bactrae</i>	0.44	318	5.04*
Predators			
Coccinellidae			
<i>Cryptolaemus montrouzieri</i>	0.47	206	0.70
<i>Delphastus pusillus</i>	0.48	203	0.40
<i>Harmonia axyridis</i>	0.52	210	0.30
<i>Hippodamia convergens</i>	0.52	207	0.39
<i>Lindorus lophanthae</i>	0.48	206	0.31
<i>Stethorus punctillum</i>	0.50	209	0.00
Cecidomyiidae			
<i>Aphidoletes aphidimyza</i>	0.55	198	2.02

* $P < 0.05$.** $P < 0.01$.*** $P < 0.005$.

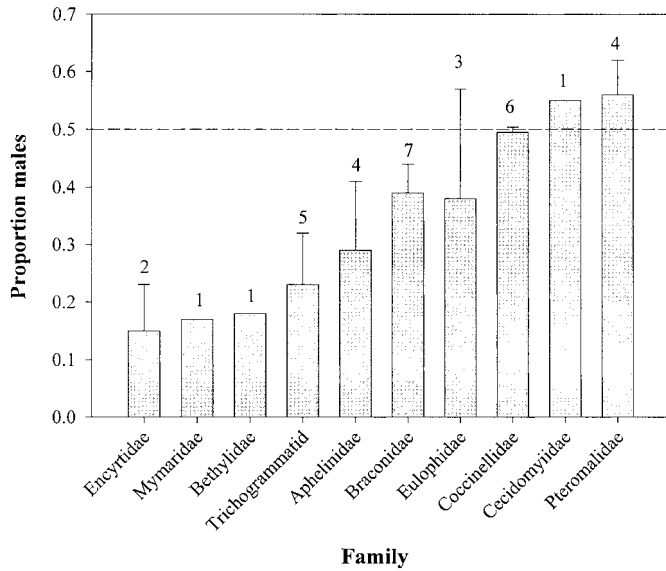


FIG. 1. Mean proportion of males from the natural enemy families surveyed. Bars are SE and numbers above columns are the numbers of species per family. Sample sizes for each species are given in Table 2.

The relative paucity of male-biased sex ratios in these samples of mass-reared parasitoids that are currently available commercially stands in contrast to a relatively long list of parasitoids that are known to exhibit male-biased sex ratios under conditions of mass and laboratory rearing (Table 1). Very few of the species listed in Table 1 are available commercially and one of the reasons for this may be their susceptibility to male-biased sex ratios. Thus, it appears that sex ratio may be a factor limiting the number of species that are being successfully mass reared.

Male-biased sex ratios from Table 1 are clearly most prevalent in the superfamily Ichneumonoidea (families Ichneumonidae and Braconidae). Currently, the best explanation for this apparent trend lies in the genetics of sex determination. The Ichneumonoidea is the only parasitoid superfamily that includes species in which sex is known to be determined at a single genetic locus by a process known as "complementary sex determination" (CSD) (Cook, 1993c; Godfray and Cook, 1997). Under single-locus CSD, females develop from fertilized eggs that are heterozygous at a single "sex locus," and males develop either from unfertilized haploid eggs or from fertilized (diploid) eggs that are homozygous at the sex locus. These diploid males are either developmentally inviable or sterile if they reach adulthood and their production constitutes a genetic load that can have drastic consequences for sex ratio and population growth (Stouthamer *et al.*, 1992; Werren, 1993; Cook and Crozier, 1995). One of the important consequences of CSD is that sex ratio (proportion male) and developmental mortality can increase under conditions of inbreeding (Stouthamer *et al.*, 1992). To date,

single-locus CSD has been unambiguously identified in three species of *Habrobracon* (= *Bracon*), including *H. hebetor* (Whiting, 1943; Whiting, 1961; Holloway *et al.*, 1999, 2000) and the ichneumonid *Diadromus pulchellus* Wesmael (Periquet *et al.*, 1993). In addition, strong circumstantial evidence exists for CSD in the braconids *Cotesia rubecula* Marshall (Stouthamer *et al.*, 1992) and *Microplitis croceipes* (Steiner and Teig, 1989). Single-locus CSD has been ruled out in two alysiine braconids (Beukeboom *et al.*, 2000). Similarly, Quicke (1997) asserted that the braconid *Heterospilus prosopidis* Viereck does not exhibit CSD based on the observation that multiple rounds of inbreeding did not increase the proportion of males produced. It is possible, however, that the initial stock used to initiate this inbreeding study contained only two sex alleles and thus single-locus CSD cannot yet be ruled out in this species (J. M. Cook, personal communication). If CSD is present in a substantial fraction of species in the Ichneumonoidea, then this superfamily may be especially susceptible to male-biased sex ratios, especially under conditions that favor inbreeding.

The lack of a significant effect of parasitoid family or superfamily on sex ratio is perhaps unexpected, given the differences in genetic modes of sex determination discussed above. Our finding that members of the Ichneumonoidea (in our case only braconids) did not have more male-biased sex ratios than Chalcidoidea suggests either that inbreeding is not common in mass rearing operations and/or that single-locus CSD is not ubiquitous among commercially reared ichneumonoids. The lack of a significant effect of gregarious development on the sex ratio was also unexpected. Gregarious development in the parasitoid Hymenoptera is often associated with inbreeding and local mate competition (LMC; Hamilton, 1967), conditions which are known to lead to selection for female-biased sex allocation patterns (Hamilton, 1967; Godfray, 1994; Antolin, 1999). Outbreeding may be selected for in gregarious members of the Ichneumonoidea for reasons discussed above (e.g., see Ode *et al.*, 1995), but the lack of a significant effect of gregariousness on sex ratio was maintained when ichneumonoids were excluded from the data set (Kruskal-Wallis test: $P > 0.50$).

In the remainder of this section, we consider the sex ratios of each species or group of species separately and discuss potential explanations for the sex ratios that we report as well as implications of the results for mass rearing and augmentative biological control. We discuss parasitoids first and then predators, and the order in which species are discussed follows that of Table 2.

Parasitoids

Goniozus legneri (Bethylinidae). Females of gregarious bethylinid species typically produce sex ratios that are highly female-biased (Griffiths and Godfray, 1988;

Hardy and Mayhew, 1998). Mating is thought to occur primarily or exclusively among brood-mates, which are likely to be siblings (Hardy and Blackburn, 1991; Peterson and Hardy, 1996; Hardy *et al.*, 1999), so that many of the conditions of local mate competition appear to be satisfied. Cook (1993a) showed that inbreeding had no effect on the sex ratio or developmental mortality of *G. nephantidis*; so, there would seem to be no genetic barrier to inbreeding in this species.

The clutch size of *G. legneri* varies between approximately 5 and 20 on host species that have been studied (Gordh *et al.*, 1983; Butler and Schmidt, 1985; Gothilf and Mazar, 1987; Legner and Warkentin, 1988; Hardy *et al.*, 1998). The number of males per brood tends to be one for brood sizes of less than 10 and two or three for larger clutches (Gordh *et al.*, 1983). These patterns resulted in an average sex ratio of 0.19 for broods that contained both males and females when the host was the navel orange worm, *Amyelois transitella* (Walker) (Gordh *et al.*, 1983), although substantially more female-biased sex ratios were obtained on this same host by Legner and Warkentin (1988). Hardy *et al.* (1998) reported a sex ratio of 0.18 from single broods of *G. legneri* parasitizing *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). In the study by Gordh *et al.* (1983), broods laid late in the female's lives contained only males (presumably due to sperm limitation), so that the average lifetime sex ratio produced was 0.45. Our finding of a population-level sex ratio of 0.18 from the mass-reared sample is consistent with no sperm depletion or virgin oviposition and suggests either that females are ovipositing only early in their life or that they are remating late in life.

A small to moderate fraction of bethylid broods also often contains only females due to developmental mortality of males (Green *et al.*, 1982; Gordh *et al.*, 1983; Morgan and Cook, 1994; Hardy and Cook, 1995; Hardy *et al.*, 1998, 1999; Perez-Lauchaud and Hardy, 1999). Depending on whether males from other broods are present, the females that develop from these broods may be constrained to oviposit as virgins (and therefore produce only males) (Godfray and Hardy, 1993) and this would inevitably affect the population sex ratio (Heimpel, 1994). Our finding of a population sex ratio similar to that of brood sex ratios of mated females reported by other researchers is consistent with little or no virgin oviposition by *G. legneri* under conditions of mass rearing.

Aphidius spp. (Braconidae). All members of this genus are solitary endoparasitoids of aphids. Female-biased population sex ratios have been found in field and laboratory populations of various *Aphidius* spp. (van den Bosch *et al.*, 1966, 1967; Stary, 1970; Mackauer, 1976; Giri *et al.*, 1982; Reed *et al.*, 1992; Sequiera and Mackauer, 1993; Elliot *et al.*, 1994; Mackauer and Lardner, 1995), but the underlying mechanistic or evo-

lutionary reasons for these biases are not well understood. Many *Aphidius* spp. produce disproportionately more males from small hosts and more females from large hosts (Hagvar and Hofsvang, 1991), a pattern that may be due to increased male survivorship on small hosts rather than facultative sex allocation (Wellings *et al.*, 1986). It is possible that female-biased sex ratios are simply a reflection of disproportionate numbers of encounters with large vs small hosts, but this hypothesis was disproved in a field study on *A. ervi* Haliday by Sequiera and Mackauer (1993). Mackauer and Lardner (1995) also rejected the hypothesis that size or sex-selective hyperparasitism is responsible for biased sex ratios in *A. ervi*. Another possibility is that sex ratio is related to mating structure in this genus. Because aphids in general, and parasitized aphids in particular, show an aggregated distribution (Mackauer and Völkl, 1993), partial local mating and some degree of inbreeding can be expected, and this can select for female-biased sex ratios (Hardy, 1994). Whether or not this scenario can explain biased sex ratios in *Aphidius* will depend in part on whether members of this genus exhibit complementary sex determination. If so, the associated inbreeding depression will potentially select for mating away from the natal site (Godfray and Cook, 1997). Finally, female-biased sex ratios in *Aphidius* spp. may be linked to sex-specific dispersal. Data provided by van den Bosch *et al.* (1966, 1967) is consistent with females of *A. smithi* dispersing farther from the natal site than males (but see Stary (1970) for a dissenting interpretation of these data). This pattern can lead to selection for female-biased sex ratios because of elevated levels of competition between males for mates (Ode *et al.*, 1998).

Of the three *Aphidius* species that we surveyed, *A. ervi* and *A. matricariae* Haliday had significantly female-biased sex ratios and *A. colemani* Viereck had an even sex ratio (Table 2). These results mirror other studies, although the female bias for *A. ervi* is stronger than has been previously reported (Mackauer, 1976; Sequiera and Mackauer, 1993; Mackauer and Lardner, 1995). *Aphidius colemani* sex ratios sampled from commercial insectaries by Fernandez and Nentwig (1997) were consistently even, despite the fact that partial thelytoky may be present in some populations of this species (Tardieux and Rabasse, 1988).

Cotesia plutellae (Braconidae). The genus *Cotesia* (= *Apanteles* in part) contains at least one species that exhibits male-biased sex ratios in the laboratory (Table 1). Diploid males have been discovered in *C. rubecula* (Stouthamer *et al.*, 1992), and CSD probably operates in this species. *Cotesia plutellae* is a solitary parasitoid of the diamondback moth, *Xylostea plutellae* (L.) (Mitchell *et al.*, 1997), and laboratory sex ratios of this species were slightly female-biased in a study by Okine *et al.* (1998). Our finding of an even sex ratio in this

species (Table 2) suggests that there is some potential for increasing the female bias of this species in commercial settings.

Dacnusa sibirica and *Opius pallipes* (*Braconidae*). These species are solitary endoparasitoids of agromyzid leafminer larvae and are used most commonly in greenhouse settings (Minkenberg and van Lenteren, 1986). *Dacnusa sibirica* produces female-biased sex ratios from *Chromatomyia syngenesiae* Hardy, with the proportion of females increasing with the larval instar of the host (Croft and Copland, 1995). Male proportions were 0.36, 0.28, and 0.13 for first, second, and third instars, respectively, in Croft and Copland's study. Our finding of a male proportion of 0.4 therefore suggests that sex ratios under commercial mass rearing may be less female biased than is potentially achievable. As in two of the *Aphidius* species discussed above, the female bias of *D. sibirica* is difficult to explain. Larger hosts produce larger parasitoids and larger females are more fecund than smaller females (Croft and Copland, 1995). Thus, a high proportion of large hosts may result in female-biased sex ratios (Werren and Simboloti, 1989). However, female biases were found from all host sizes (Croft and Copland, 1995). Although mating and population structures have not been studied in *D. sibirica* to our knowledge, this species is solitary and presumably outbreeds. Although *D. sibirica* belongs to the superfamily Ichneumonoidea and may therefore be subject to complementary sex determination, it is also a member to the braconid subfamily Alysiinae, which contains at least two members that do not exhibit single-locus complementary sex determination (Beukeboom *et al.*, 2000).

The sex ratio of *O. pallipes* increased from 0.5 (proportion males) to over 0.9 in at least one study, limiting the capability of researchers to rear this insect (Minkenberg and van Lenteren, 1986; Table 1). No reasons were given for this extreme male bias, but our finding of no male bias (Table 2) shows that even sex ratios can be maintained under mass rearing of *O. pallipes*.

Habrobracon (= *Bracon*) *hebetor* (*Braconidae*). This species was the first hymenopteran in which sex was shown to be determined at a single locus by complementary sex determination (Whiting, 1943), and sex ratios of at least some laboratory cultures have shown male biases (Rotary and Gerling, 1973; Table 1). Invi-able diploid males are produced when sex alleles are shared between mates (Petters and Mettus, 1980; Heimpel *et al.*, 1999). The implications of this mode of sex determination for sex ratio under mass rearing have been discussed above: inbreeding and/or restricted population sizes are expected to lead to an increase in the proportion of males (Stouthamer *et al.*, 1992). A corollary of CSD is also that outcrossing is expected to evolve because of the inbreeding depression associated

with CSD (Werren, 1993). This, in turn, should lead to equal production of males and females (Godfray, 1994). However, females of *H. hebetor* typically produce approximately twice as many females as males (Whiting, 1961; Antolin *et al.*, 1995; Heimpel *et al.*, 1997, 1999; Ode *et al.*, 1997) despite evidence of outcrossing (Antolin and Strand, 1992; Ode *et al.*, 1995).

Two evolutionary explanations support the allocation of female-biased sex ratios in *H. hebetor*. First, Ode *et al.* (1997) showed that a substantial fraction of field-caught *H. hebetor* females are sperm depleted (or virgins) and therefore constrained to producing only male offspring. This is expected to lead to increased production of daughters by unconstrained females (Godfray, 1990). Ode *et al.* (1997) were able to explain approximately 60% of the female bias in sex allocation patterns of mated females as a response to constrained oviposition (Heimpel, 1997). The second explanation involves sex-dependent dispersal. Ode *et al.* (1998) found that female *H. hebetor* dispersed more readily from laboratory cages than did males. As was discussed above for *Aphidius* spp., this can lead to selection for female-biased sex allocation, and Ode *et al.* (1998) concluded that both responses to constrained oviposition and sex-specific dispersal combined to select for female-biased sex allocation in *H. hebetor*.

The population sex ratios of *H. hebetor* in the field have remained unstudied because of the difficulties of sampling the sexes in a nonbiased fashion (Antolin and Strand, 1992; Guertin *et al.*, 1996; Ode *et al.*, 1997). Our finding of a significantly female-biased sex ratio under conditions of mass rearing could be regarded as an estimate of a population-level sex ratio for this species. However, it is possible that sex ratio biases result from collection procedures in mass-rearing operations since females disperse more readily than males and may be disproportionately collected from the sides or tops of rearing cages (Ode *et al.*, 1998). In any case, the female bias that we found is consistent with female-biased sex allocation under conditions of mass rearing. Perhaps more importantly, our finding of a female-biased sex ratio under conditions of mass rearing is consistent with the presence of multiple sex alleles within the mass-rearing cultures. This conclusion supports a study by Heimpel *et al.*, (1999), which showed that a commercial culture of *H. hebetor* harbored between 5 and 18 sex alleles, a range that is sufficient to avoid the worst effects of CSD on sex ratio and population growth (Stouthamer *et al.*, 1992).

Aphelinus abdominalis Dalman (*Aphelinidae*). *Aphelinus* spp. are solitary endoparasitoids of aphids. In the species that have been studied, females are disproportionately produced from large hosts and female-biased sex ratios are produced when sufficient large hosts are available (Raney *et al.*, 1971; Asante and Danthanarayana, 1993; Yokomi and Tang, 1995;

Honek *et al.*, 1998a). Honek *et al.* (1998b) also showed that larger parasitized aphids dispersed farther from drought-stressed plants than did smaller parasitized aphids. These larger aphids harbored a higher proportion of female *A. abdominalis*, and such sex-specific dispersal patterns can lead to selection for female-biased parasitoid sex ratios (Ode *et al.*, 1998). Higher proportions of males are also produced in *A. semiflavus* and *A. asychis* when temperatures exceed 30°C (Schlinger and Hall, 1959; Force and Messenger, 1964; Raney *et al.*, 1971). Our finding of a female-biased sex ratio for *A. abdominalis* (Table 2) is therefore consistent with favorable host size distributions and temperatures under commercial mass rearing.

Aphytis melinus (DeBach) (Aphelinidae). The genus *Aphytis* includes solitary and facultatively gregarious ectoparasitoids of armored scale insects (Rosen and DeBach, 1979; Rosen, 1994). As in the *Aphelinus* species discussed above, female-biased sex ratios are typical in *A. melinus* when sufficient numbers of large hosts are available (Abdelrahman, 1974a; Luck *et al.*, 1982; Luck and Podoler, 1985; Reeve, 1987) and when temperatures are below 30°C throughout development (Kfir and Luck, 1979; Abdelrahman, 1974b). Our finding of a female-biased sex ratio in *A. melinus* is consistent with favorable mass-rearing conditions for this species.

Eretmocerus sp. nr. californicus Howard (Aphelinidae). *Eretmocerus* spp. are solitary parasitoids of whitefly nymphs (Gerling, 1966; Vet and van Lenteren, 1981). Populations designated as *E. sp. nr. californicus* originate from various sites in California, Arizona, and Texas (Powell and Bellows, 1992; Hunter *et al.*, 1996) and include both sexual and asexual (thelytokous) strains. Sex ratios of sexual strains range from approximately 0.50 (Powell and Bellows, 1992; Headrick *et al.*, 1995; Hunter *et al.*, 1996) to highly female-biased (Powell and Bellows, 1992; McAuslane *et al.*, 1995) and host plants can influence sex ratios in this species (Powell and Bellows, 1992). Powell and Bellows also discovered that longevity, fecundity, and developmental time did not differ between a sexually reproducing and a thelytokous strain of *E. sp. nr. californicus*. This led to a higher rate of increase for the thelytokous strain than for the sexual strain. Thelytokous strains of this species may therefore be better biological control agents than sexual strains (Aeschlimann, 1990; Stouthamer, 1993). However, our finding of a sex ratio not significantly different from 0.5 (Table 2) indicates sexual reproduction in this sample of *E. sp. nr. californicus*.

Encarsia formosa Gahan (Aphelinidae) and *Thripobius semiluteus* Boucek (Eulophidae). These were the only two samples that consisted entirely of females. Thelytoky in *E. formosa* is caused by infection by *Wolbachia* bacteria and, although it can be "cured" by

antibiotic treatment (Zchori-Fein *et al.*, 1992a; Stouthamer *et al.*, 1994), no sexually reproducing strains are available commercially (Stouthamer, 1997; Hoddle *et al.*, 1998; O'Neill *et al.*, 1998). Males are unknown for *T. semiluteus* (Boucek, 1976), but to our knowledge no studies have been done to determine the cause of thelytoky in this species or in any other eulophid.

Leptomastix dactylopii (Howard) (Encyrtidae). This is a solitary endoparasitoid of mealybugs that produces proportionately more females from larger hosts (de Jong and van Alphen, 1989; Yang and Sadof, 1997). The proportion of *L. dactylopii* males from our sample (0.23; Table 2) was similar to that reported from fourth instar citrus mealybugs, *Planococcus citri* (Risso), raised on sprouted potatoes and transferred to oleander leaves (de Jong and van Alphen, 1989), but more female-biased than those produced from fourth instar *P. citri* growing on ornamental *Coleus blumei* (Benthham) (Yang and Sadof, 1997). This suggests that rearing conditions are acceptable for optimum sex allocation in *L. dactylopii*.

Metaphycus helvolus (Compere) (Encyrtidae). This is a facultatively gregarious endoparasitoid of soft scale insects that produces a greater proportion of females from larger hosts (Lampson *et al.*, 1996). Mass rearing of *M. helvolus* is relatively labor intensive and smaller rearing operations have typically produced higher proportions of females than have large-scale production procedures (Ibrahim, 1986; Lampson *et al.*, 1996). However, the sex ratio of our sample (0.08; Table 2) was substantially more female biased than any reported in the literature.

Diglyphus isaea (Eulophidae). *Diglyphus* spp. are ectoparasitoids of agromyzid leafminer larvae, and *D. isaea* has been used with some success against leafmining agromyzids in greenhouses and field crops (Minkenberg and van Lenteren, 1986; Minkenberg, 1989). Like the better-studied *D. begini* (Ashmead) (Heinz and Parrella, 1990a,b), sex ratios produced by *D. isaea* females are highly dependent on host size, with relatively smaller hosts producing disproportionately more male offspring (P. J. Ode and K. M. Heinz, unpublished data). Population-level sex ratios of both of these species can be male biased under conditions of mass and laboratory rearing, presumably due in part to the effects of host size (Heinz and Parrella, 1990a,b; P. J. Ode and K. M. Heinz, unpublished data), and P. J. Ode and K. M. Heinz have shown that female-biased sex ratios can be obtained by host size manipulation. Heinz (1998) developed a host-size manipulation technique for the pteromalid *Catolaccus grandis* (Burks) and demonstrated how plasticity in sex allocation behavior can be used to increase the female bias of parasitoids under mass rearing. The sex ratio of our sample of *D. isaea* was significantly male biased (Table 2), as

were other samples of this species obtained from commercial insectaries (P. J. Ode, personal communication). *Diglyphus isaea* should be seen as a prime candidate for sex ratio improvement under mass-rearing conditions.

Pediobius foveolatus (Crawford) (Eulophidae). This is a gregarious endoparasitoid that was introduced from India to the eastern United States to control the Mexican bean beetle, *Epilachna varivestris* Mulsant (Stevens *et al.*, 1975b). In *P. foveolatus*, mating can apparently take place within the host prior to emergence, but postemergence mating has been observed also (Stevens *et al.*, 1975a). Presumably, some level of LMC is possible within this species. It has also been suggested that female *P. foveolatus* may disperse more actively than males (Coll and Bottrell, 1996). As we have discussed above, both LMC and sex-specific dispersal can lead to selection for female-biased sex allocation patterns. In one study, the average proportion males produced under laboratory rearing conditions was 0.13, whereas field samples had a less pronounced female bias of 0.43 proportion males (Stevens *et al.*, 1975a). In a study of augmentative biological control, Coll and Bottrell (1996) released mass-reared *P. foveolatus* with a sex ratio of approximately 0.28. Our finding of an even sex ratio in this species (Table 2) is clearly more male biased than that achievable under mass-rearing conditions.

Anaphes iole (Girault) (Mymaridae). *Anaphes* spp. are egg parasitoids of a number of insect species. At least one thelytokous species is known (Aeschlimann, 1986, 1990) and the sex ratios of sexually reproducing species are typically even or slightly female-biased (Stoner and Surber, 1971; Boivin, 1988; DeGrandi-Hoffman *et al.*, 1994; van Baaren *et al.*, 1995). *Anaphes iole* is a solitary parasitoid of *Lygus* bugs, and whereas our finding of an extremely female-biased sex ratio (Table 2) is consistent with favorable rearing conditions, it may also reflect differences in the ease with which male and female individuals are collected from mass-rearing containers. Female *A. iole* are more positively phototrophic than males and therefore are collected in disproportionately higher numbers near light sources within rearing cages than are males (S. Udayagiri, personal communication).

Muscidifurax spp. (Pteromalidae). The genus *Muscidifurax* contains five species (Kogan and Legner, 1970), several of which are commercially available for use against muscoid flies. Previous laboratory and field studies of this species complex have documented female-biased population sex ratios (Coats, 1976; Legner, 1979; Wylie, 1979; Antolin, 1992a,b). Recently, however, male biases have been recorded from studies of mass rearing that are consistent with our results of 0.65 for *M. raptorellus* and 0.62 for *M. zaraptor* (Table 2) (Geden *et al.*, 1992).

A number of factors can influence *Muscidifurax* sex ratios. One factor that may play a significant role in the sex ratio of laboratory cultures is infection with microsporidian parasites (Antolin, 1992; Geden *et al.*, 1992; Zchori-Fein *et al.*, 1992b; Dry *et al.*, 1999). Infection by microsporidians has been reported in *M. raptor* and *M. zaraptor*, but not in *M. raptorellus* (Zchori-Fein *et al.*, 1992b). Reduced longevity, fecundity, and searching behavior accompany infection (Antolin, 1992b; Geden *et al.*, 1992; Zchori-Fein *et al.*, 1992b), and these traits are correlated with sex ratio in a way that increases the proportion of males produced (Antolin, 1989, 1992a,b). Part of this correlation can be explained by the order in which male and female offspring are produced: males are laid earlier than females in an oviposition bout (with the exception of the first egg, which tends to be a female) so that decreased age-specific fecundity results in a proportionate increase in the production of males (Antolin, 1989). The effects of inbreeding on the sex ratios of mass reared colonies are unclear. Legner (1979) found the sex ratio of *M. zaraptor* to be unaffected by short-term, severe inbreeding, whereas Antolin (1992b) found that outcrossing led to the production of a significantly higher proportion of females and hypothesized that inbreeding depression in *M. raptor* may result in increases in the proportion of males. Geden *et al.* (1992) proposed that deterioration of colonies is too rapid for inbreeding of *M. raptor* to be operating alone and that microsporidian infection is largely responsible for colony decay. Legner (1985) found that *M. uniraptor* Kogan and Legner went from being thelytokous to producing mainly males over 16 years in culture, suggesting a different mechanism for increasing male biases than Geden *et al.* (1992).

Intraspecific differences in oviposition behavior may also affect the sex ratios of laboratory cultures (Legner, 1988). Gregarious and solitary strains of *M. raptorellus* have been identified (Legner, 1988; Antolin *et al.*, 1996), and these strains produce different sex ratios. Crosses between these strains show intermediate oviposition behaviors and related changes in sex ratio of the offspring (Legner, 1988). Whereas thelytoky occurs in some strains of *M. uniraptor* and *M. raptor* (Legner, 1987, 1988; Stouthamer *et al.*, 1993, 1994), it has not been reported in the species used in our study.

Rearing procedures may also play a role in the production of male-biased sex ratios. *Muscidifurax zaraptor* tend to produce males on older hosts, which are of lower quality than are younger hosts. Increased female age also leads to a higher proportion of male offspring in *M. zaraptor* (Coats, 1976). *Muscidifurax zaraptor* is monandrous (Coats, 1976), suggesting that sperm limitation may play a role in this species. Superparasitism does not distort sex ratios in *M. zaraptor*, though overcrowding of wasps in culture can lead to sex ratio distortions through interference between females (Rivers, 1996; Wylie, 1979). In addition, crowding may

facilitate the horizontal transmission of microsporidian pathogens and increase the rapidity of colony deterioration (Zchori-Fein, 1992b).

The sex ratios that we report also may simply be due to a biased collection procedure at the insectary. Sex allocation can fluctuate over the life of *M. zaraptor* females (Coats, 1976); if collection occurs during one of the periods of low female allocation, the sample may not be representative of the lifetime sex ratio of the females.

Nasonia vitripennis (Walker) (Pteromalidae). *Nasonia vitripennis* is a gregarious parasitoid of muscoid flies, with up to 25 larvae developing per host (Wylie, 1966). Under suitable conditions, the proportion of males is typically less than 0.35 (Wylie, 1966, 1976), though many factors can affect the sex ratio to produce the male proportion of 0.61 observed in our study (Table 1). High female/host ratios result in higher rates of superparasitism and a higher proportion of males. Differential larval mortality under crowded conditions favors male larvae, which are more competitive on lower quality hosts (Wylie, 1966). The fertilization rate may be reduced as a result of physical contact between females during oviposition (Wylie, 1976) and/or by detection of cues emitted by parasitized pupae (Wylie, 1966; King and Skinner, 1991).

Sex allocation behavior in gregarious parasitoids that results in an increased proportion of males under high female/host densities can be explained by LMC models, and *N. vitripennis* has been used successfully to test these models (Werren, 1980; King and Skinner, 1991). Sex allocation behavior in *N. vitripennis* is also under partial genetic control (Orzack and Gladstone, 1994). Rivers (1996) has demonstrated that *Sarcophaga bullata* produces a more female-biased sex ratio of *N. vitripennis* than *Musca domestica*. The widespread use of *M. domestica* as the rearing host for this parasitoid may therefore reduce the effectiveness of this parasitoid in the field.

Spalangia endius Walker (Pteromalidae). *Spalangia endius* is a solitary parasitoid of muscoid flies with typical male proportions of 0.35 in culture (Morgan *et al.*, 1978; Donaldson and Walter, 1984), which is similar to what we found in our survey (Table 1). Several factors seem to be operating in sex allocation by *S. endius*, though these factors are different from those reported in other pteromalid species. Host size and superparasitism do not affect sex allocation in *S. endius* (King, 1991). Field populations of *S. endius* are more male biased than laboratory colonies, possibly as a result of delayed mating (Donaldson and Walter, 1984). Sons are produced earlier in the female's lifetime than daughters are, so reduced longevity could in principle lead to male-biased sex ratios (Donaldson and Walter, 1984).

Trichogramma spp. (Trichogrammatidae). The sex

ratios of arrhenotokous strains of *Trichogramma* spp. are commonly female biased, and a mechanistic model for this phenomenon based on considerations of LMC was simultaneously developed by Suzuki *et al.* (1984) and Waage and Ming (1984) and has been confirmed for a number of *Trichogramma* species (van Dijken and Waage, 1987; Wajnberg, 1993; Olson and Andow, 1997). In this model, females deposit single males early in oviposition bouts (generally as the second egg laid) and up to eight females thereafter before another male is deposited. Waage (1982a,b) and Waage and Ming (1984) have argued that this mechanism, along with the avoidance of superparasitism, results in increasingly male-biased sex ratios as the ratio of parasitoids to hosts increases. This is one of the bases for the general recommendation that parasitoid crowding be avoided in mass-rearing situations (Waage *et al.*, 1985).

A number of *Trichogramma* species contain both arrhenotokous and thelytokous strains (Stouthamer *et al.*, 1990; Wang and Smith, 1996) and thelytoky in most of these cases has been linked to bacteria in the genus *Wolbachia* (Stouthamer, 1997). Thelytoky has been reported from three of the four *Trichogramma* species that we surveyed here. These are *T. minutum* Riley, *T. pretiosum* Riley, and *T. platneri* Nagarkatti (Wang and Smith, 1996; Stouthamer, 1997). To our knowledge, no thelytokous strains of *T. brassicae* (= *T. maidis*) have been found. The sex ratios of all three species in which thelytoky is known were significantly female biased, whereas the sex ratio of *T. brassicae* was not significantly different from 0.50 (Table 1). This is consistent with the presence of thelytokous strains within mass-reared cultures of *T. pretiosum*, *T. platneri*, and *T. minutum*, but as was discussed above, female-biased sex ratios can be expected even from purely arrhenotokous cultures when the parasitoid/host ratio is relatively high. Still, *Wolbachia*-induced thelytoky often becomes prevalent in mass-rearing cultures even though thelytokous forms often make up less than 5% of affected field populations (Pinto and Stouthamer, 1994; but see Wang and Smith, 1996). Other reports of sex ratios of commercially reared *T. pretiosum*, *T. minutum*, and *T. platneri* cite even sex ratios (Losey and Calvin, 1995; O'Neil *et al.*, 1998) for all three species. The difference between these values and those that we report indicates that conditions differ among or within insectary operations and/or that thelytokous strains are present in some, but not all, insectary cultures. We feel that thelytoky is likely in these cultures, given the extremely female-biased sex ratios (Table 2).

Thelytokous lines of *T. pretiosum* and *T. minutum* produce fewer daughters than do arrhenotokous lines when given unlimited access to hosts (Stouthamer and Luck, 1993; Wang and Smith, 1996). Under conditions of host limitation, however, thelytokous females may

lay the same number of eggs as arrhenotokous females, but since they do not produce males, thelytokous females may produce more female offspring than arrhenotokous females (Stouthamer and Luck, 1993). Thus, *Wolbachia* infections may be beneficial in biological control programs despite their detrimental effects on potential fecundity. Also, Wang and Smith (1996) have shown that cold tolerance is higher in a thelytokous strain of *T. minutum* than in an arrhenotokous strain and argued that this may explain the high prevalence of the thelytokous strain of this species in the field.

The sex ratio for *T. brassicae* Bezdenko reported here has a considerably higher proportion of males than that observed in some previous research (Wajnberg, 1993; Cerutti and Bigler, 1995). Potential explanations for the higher male proportion include suboptimal female/host ratios, poor fertilization levels of females, or genetic differences in sex allocation behavior between our insectary strains and other documented strains (Wajnberg, 1993, 1994).

Trichogrammatoidea bactrae Nagaraja (*Trichogrammatidae*). *Trichogrammatoidea* is closely related to *Trichogramma*, but no thelytokous populations are known from this genus. As is the case with many parasitoids, a larger proportion of females is allocated earlier in life in *T. bactrae*, possibly due to sperm limitation. One result of this phenomenon is that the proportion males produced by long-lived (e.g., fed) females is higher than that of short-lived (e.g., starved) females (Lim, 1986; Naranjo, 1993). Male proportions reported in the literature for this species are consistently between 0.3 and 0.5 (Lim, 1986; Hutchison *et al.*, 1990; Naranjo, 1993), which is consistent with our estimate of 0.44 (Table 2).

Predators

Coccinellid beetles. At least five species of primarily aphidophagous coccinellid beetles contain populations that harbor male-killing bacteria (Hurst, 1997; Majerus and Hurst, 1997). One of these, *Harmonia axyridis* (Pallas), was part of our survey, but we found no evidence of female-biased sex ratios in this species (Table 1). *Harmonia axyridis* is native to eastern Asia and surveys of two populations in Russia have revealed infection rates of 0.00 and 0.02, whereas one Japanese population had an infection rate of 0.49 (Majerus *et al.*, 1998). *Harmonia axyridis* has been introduced into North America numerous times throughout the 20th century and has become established following a series of releases of Japanese populations in the southeastern United States in the late 1970's and early 1980's (Tedders and Schaeffer, 1994; Krafur *et al.*, 1997; but see Day *et al.*, 1994, for a conflicting view of this scenario). However, no male-killers have been recovered from North American populations of *H. axyridis* (M. E. N. Majerus, personal communication). None of the other

coccinellids that we surveyed had sex ratios that differed significantly from 0.5 (Table 1).

Aphidoletes aphidimyza (*Cecidomyiidae*). *Aphidoletes aphidimyza* is known as a "monogenic" species, meaning that individual females produce either only males or only females (Snell, 1976). Sex ratios of this species are typically female biased in the laboratory but can show slight male biases (Gilkeson and Hill, 1986 and references therein) and the establishment of wild strains in the laboratory can be prevented by the production of extreme (presumably male-biased) sex ratios (Gilkeson and Hill, 1986). The sex ratio of *A. aphidimyza* in our survey was not significantly different from 0.5 (Table 1) and is consistent with an equal number of male- and female-producing females.

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