

Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality

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Summary. We studied interactions among collards, *Brassica oleracea* var. *acephala*, the diamondback moth (DBM), *Plutella xylostella* (Lepidoptera: Yponomeutidae) and its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae) by manipulating plant nitrogen (N) concentrations in field and laboratory experiments. Parasitoid abundance strongly reflected DBM abundance and was related to total leaf N. Parasitism rates were high (70.7%) and density-independent. Wasp sex ratios varied markedly (3–93% female) in response to the herbivores, the plants, or both. Higher proportions of female wasps emerged from DBM larvae on plants with high leaf N than on unfertilized plants. More female wasps also emerged from larvae parasitized as larger instars. We suggest that wasps have the potential to control DBM populations through long-term numerical responses mediated by variable sex ratios.

Key words: Sex ratio – Host-parasitoid interactions – Nitrogen – *Plutella xylostella* – *Diadegma insulare* – *Brassica oleracea* var. *acephala*

Dynamics of parasitoid-host interactions often emphasize density relationships between the species (Southwood and Comins 1976; Anderson and May 1978; Hassell 1978, 1986; May and Anderson 1978; Fishlin and Baltensweiler 1979; Murdoch 1979; Murdoch et al. 1984, 1985; Strong 1984, 1986; Hassell and Waage 1984; Reeve and Murdoch 1985; Walde and Murdoch 1988; Murdoch and Stewart-Oaten 1989). Two recent models also considered variation in parasitoid sex ratios in the context of dynamic interactions (Hassell et al. 1983; Comins and Wellings 1985). Parasitoid-host interactions are affected by sex ratios because only females forage for hosts (functional response), and the sexual allocation of their progeny directly affects the numerical response.

Proximal factors influencing biased sex ratios of both parasitoids and their hosts have received particular attention. Several factors, both intrinsic (e.g., meiotic drive of Y chromosomes, inherited microorganisms) and extrinsic (e.g., local resource competition, mate competition, host size, physical environment) differentially affect the production or the survival of one of the sexes (Hamilton 1967; Bouletreau 1976; Kfir and Luck 1979; Charnov 1979, 1982; Charnov et al. 1981; Waage 1982a, b, 1986; Werren 1984; Charnov and Skinner 1984, 1985; Clarke 1984; Porter 1984; Walker 1984; Luck and Podoler 1985; Werren et al. 1986; Nunney and Luck 1988; King 1989).

Nutritional or allelochemical variation in hosts or their food plants may modify the dynamics of parasitoid-host interactions by influencing growth and survivorship of immature parasitoids (e.g., Campbell and Duffey 1979, 1981; Barbosa and Saunders 1985; Barbosa 1988) and oviposition choices of adults (Vinson 1981; Williams et al. 1988). We show that plant and herbivore quality also affect the sex ratio of the parasitoids and therefore the dynamics of parasitoid-host interactions. We describe a three-trophic level system in which sex ratios of a solitary ichneumonid wasp, *Diadegma insulare* Cress. were influenced by the quality of their hosts, larvae of the diamondback moth (DBM) *Plutella xylostella* (L.), and apparently also by differences in the quality of the plants, collards (*Brassica oleracea* var. *acephala* L.) eaten by the DBM larvae. In field and laboratory experiments, female-biased sex ratios of the wasps were correlated with higher nitrogen (N) concentrations in the foliage consumed by DBM.

Methods

Field experiments were conducted adjacent to the farm on the University of California, Santa Cruz campus. The 1.5 ha site has shallow, relatively infertile, marine bench soils. Both field and laboratory experiments were conducted with an open-pollinated variety

of collards, Champion®. Collards were grown initially in Speedling® trays; after the cotyledon stage, they were fertilized daily with dilute fish emulsion until they were transplanted either into the field or into 7.6 l pots for field experiments. Details of the site and general soil amendments are given in Letourneau & Fox 1989.

Main field experiment

We monitored the development of insect communities on collards planted in 16 plots (4.8 m × 4.8 m) of 81 plants (9 × 9 grid) from July to September 1986. Plants were 60 cm apart within a plot, and there was 8 m between plots. We used four treatments of nitrogen (N) fertilizer, added as a 3:1 ratio of ammonium sulfate and ammonium nitrate. Treatment 1 was unfertilized soil, with a basal N level of 67 kg/ha in preliminary soil analyses. We added sufficient N fertilizer to obtain 90, 112 and 336 kg/ha of soil N in treatments 2, 3, and 4. The soil N recommended by UC Agricultural Extension is 112 kg N/ha (N. Welch, pers. comm.). The experiment was set up as a randomized complete block design, with four blocks of the four N treatments. Eight weeks after transplanting, we collected all DBM larvae and pupae from the central grid of 25 plants in each plot and reared them to pupation on collard leaves in the laboratory.

Small-scale field experiments

During August and September 1986, we ran two small-scale experiments using collards grown in pots with field soil. Two fertilizer treatments were used: no fertilizer (Low N plants; ~67 kg N/ha in soil) and fertilized (High N plants; ~224 kg N/ha in soil); plants in pots could not tolerate the highest level (~336 kg N/ha) used in the main field experiment.

The first small-scale experiment compared the effect of plant heterogeneity on insect choice. We set up three groups of 16 potted plants (4 × 4 grid) with plants 1 m apart. Groups consisted of all High N, all Low N, or alternating High N and Low N plants in the grid. Groups were 3 m apart. We collected all DBM on each plant after 4 weeks and reared larvae to pupation on collards.

The second small-scale experiment tested the effects of herbivore properties vs plant properties on parasitism rates and sex ratios. We reared DBM on High N and Low N plants in the laboratory until they were 3rd instar larvae, then placed them on High N or Low N plants in 6 experimental plots. Plots were grouped into 3 blocks of one high N and one low N plot. Each plot contained 49 collards in pots, set 60 cm apart in a 7 × 7 grid. We placed 2 larvae on each of 8 experimental plants, randomly selected from the inner 5 × 5 grid. Half the DBM larvae were placed on plants in plots of the same N level as that on which they had been reared, and half on plants in plots of the alternate N level. After 4 days, all DBM were collected and reared to pupation on collard leaves. The experiment was repeated (with different plants) three times in two blocks and twice in the third, for a total of 8 replications and 64 DBM larvae in each of the 4 treatments. Because the recovery of DBM varied with treatment and because the number of emerging wasps was low in some replicates, we combined data from all replicates for the analyses.

Laboratory choice experiments

We reared DBM on High N and Low N collards in the laboratory and offered them as 3rd instar larvae to ovipositing wasps. In each cage (0.5 × 0.5 × 0.5 m), 10 High N larvae were placed in a bowl with one High N leaf, while 10 Low N larvae of similar size were put in an adjacent bowl with one Low N leaf. We let 3 female wasps oviposit on these larvae for 2 h, and then reared the larvae to pupation on high N collards. There were 13 replicates. Plants were grown in 0.1 l pots in potting soil. High N plants

were fertilized with 25 ml of Peters Fertilizer® 3 times per week. Low N plants were fertilized once a week.

Parasitoid responses to DBM age-classes

We ran three laboratory experiments in which different combinations of DBM instars were available as oviposition sites for recently emerged and mated *D. insulare* females: 1) all four larval DBM instars were available for oviposition by wasps at the same time (7 replicates); 2) 2nd and 3rd instar larvae were offered together (12 replicates); 3) 2nd instars and 3rd instars were offered separately (9 replicates). In each replicate, 8 DBM larvae of each instar were exposed to 2 female wasps for 3 hours on collard leaves kept turgid in Aqua Pics®. Since some larvae were lost in handling, parasitism rates and wasp sex ratios were calculated from the net numbers of DBM larvae that pupated.

Plant nitrogen

We assessed four aspects of plant quality. In all treatments of the main experiment we estimated leaf N as total Kjeldahl N (Allen 1974) and NO₃ (using a specific ion electrode and an ion suppresser solution to reduce interference; Orion 1986). We also estimated total N in potted collard leaves. At the highest and lowest N fertilizer treatments of the main experiment we also estimated leaf protein by the Bradford test (with BSA as the standard protein; Compton and Jones 1985). In the main experiment, we sampled leaves for total N on August 28, and for total N, NO₃ and protein on September 11, when the experiment ended. We sampled leaves from the small-scale field experiments at the end of those experiments in mid-September. Leaves or leaf discs (~1 cm diam) collected for N analyses were dried at 60° C for 48 h.

Insect size

We assessed DBM and wasp size primarily as total adult body length, using a Nikon measuring microscope (ShopScope®) to measure from the vertex of the head to the distal end of the abdomen. Wet weights of unparasitized DBM pupae from the experiment on herbivore vs. plant quality were also used as an estimate of herbivore size.

Statistics

We used SAS (SAS 1988) for correlations, regressions, ANOVAs (2 way randomized complete block designs for the main experiment) and t-tests. We used BIOM (Sokal and Rohlf 1981) for G-tests (Goodness of Fit Tests) for sex ratios and survival in the smaller experiments; all G-values have been adjusted with Williams' correction (Sokal and Rohlf 1981).

Results

Density and parasitism rates

The number of parasitoids that emerged from DBM in the main field experiment was strongly related to the number of their hosts in each plot (Fig. 1A; $r=0.97$, $P<0.0001$, $n=16$ plots). As the number of DBM rose from 15 to over 45 per plot, the number of *Diadegma* also tripled, from about 10 to over 30 per plot. Therefore, parasitism rates over all the plots were uniformly high ($\bar{x}=70.7\% \pm 1.7$ SE), and were independent of DBM abundance (Fig. 1B; $r=-0.13$, $P=0.62$).

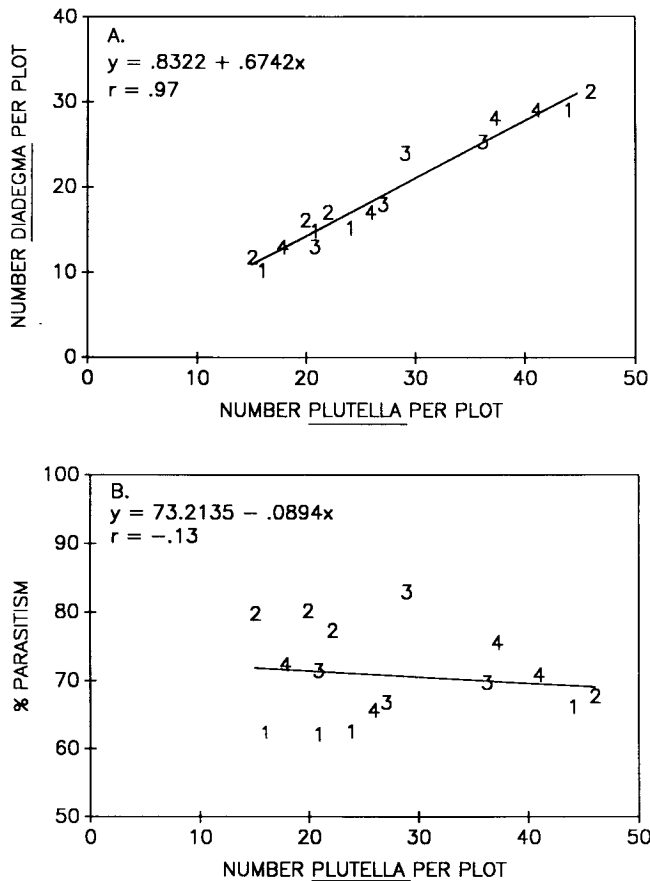


Fig. 1. A Numbers of parasitoids (*Diadegma insulare*) and B % parasitism, both plotted against DBM (*Plutella xylostella*) abundance in each of the 16 plots of the main field experiment. Numbers on the graph are treatment levels from 1 (no additional fertilizer) through 4 (highest fertilizer addition). Lines were fitted by least-squares regression

Variation in insect abundance was associated with leaf properties related to nitrogen (Table 1). DBM abundance was marginally correlated with total leaf N ($r = 0.39$, $P = 0.07$), while the number of wasps was strongly correlated with total leaf N ($r = 0.57$, $P = 0.02$). The % parasitism was lowest in plots without additional fertilizer inputs (level 1, Fig. 1B); but the statistical relationships between parasitism rate and foliar N ($r = 0.47$, $P = 0.07$) and protein ($r = 0.65$, $P = 0.08$), were marginal. Neither DBM nor wasp abundance was related at all to leaf NO_3 .

DBM abundance was also higher on High N plants in the first small-scale experiment, in which the moths colonized homogeneous and mixed plots of potted collards for four weeks (Table 2; 1-way ANOVA, $F = 4.06$, $P = 0.0125$; High N plants had significantly more DBM [Duncan's Multiple Range Test]). DBM density was particularly low on the Low N plants in mixtures. Differential larval survival may explain part of the trend relating DBM abundance to leaf N, because in the second small-scale field experiment we recovered only 35% of the original 128 3rd instar larvae on Low N plants after

Table 1. Correlations between insect abundance and leaf chemistry in the main field experiment. Only correlation coefficients $> |0.4|$ are given. Leaf N and NO_3 were assessed for plants in all 16 plots. Protein was estimated only in the 8 plots with the lowest and highest fertilizer inputs. Values are Pearson r , and P-values (in parentheses)

	# DBM	# <i>Diadegma</i>	% Parasitism	% Female <i>Diadegma</i>
Total Nitrogen	0.46 (0.07)	0.57 (0.02)	0.47 (0.07)	0.41 (0.11)
NO_3	—	—	—	0.44 (0.08)
Protein	—	—	0.65 (0.08)	—

Table 2. Total numbers and % parasitism of DBM (*Plutella xylostella*) and total numbers and % of female wasps (*D. insulare*) collected from plots of homogeneous vs. heterogeneous plants

Plantings	Homogeneous		Mixture		Homogeneous	
	High N	Low N	High N	Low N	High N	Low N
Fertilizer (# plants)	(16)		(8)		(16)	
<i>Plutella xylostella</i>						
# collected	41	32	6	23		
% parasitized	41	56	50	61		
<i>Diadegma insulare</i>						
# adults	15	15	3	14		
% female	53	60	67	29		

Table 3. Total number of DBM collected (from 64 exposed), % of DBM hosts parasitized, and total number and % female wasps emerging from DBM raised on High N or Low N plants and exposed for 4 days to parasitism in the field on High N or Low N plants

			DBM hosts raised on:	
			High N	Low N
Experimental Diet	High N	# DBM	39	42
		% parasitized	38	48
	Low N	# wasps	15	20
		% female wasps	93	70
Low N	High N	# DBM	23	27
		% parasitized	61	44
	Low N	# wasps	14	12
		% female wasps	79	58

4 days, while we found 63% of those on the High N plants (Table 3; $G = 15.11$, 1 df, $P < 0.001$).

In both of these small-scale field experiments, parasitism rates varied from 38% to 61% (Tables 2 and 3) but, as in the main field experiment, these rates were independent of DBM density.

Wasp sex ratios

Parasitoid sex ratios varied from 23% to 68% female in the main experiment. The mean percentage of female wasps increased with fertilizer level from 39%–53%; this variation was marginally associated with leaf N and NO₃ concentrations (Table 1). Parasitoid sex ratios responded more clearly to treatment in both small-scale field experiments. In the first experiment, fewer female wasps emerged from hosts feeding on Low N plants than from those on High N plants in the homogeneous arrays (29% vs. 53%); in the heterogeneous plots, too few wasps emerged from hosts on Low N plants to interpret the data.

The second small-scale experiment, in which we varied insect feeding history and plant N, was designed to test whether parasitoids respond to host or to plant cues (Table 3). While 93% of parasitoids emerging from high quality DBM feeding on High N plants were females, only 58% of the wasps emerging from low quality DBM on Low N plants were female ($G=4.96$, 1 df, $P<0.05$); intermediate percentages of females (70–79%) emerged from larvae in the crossed treatments. These results suggest that parasitoid sex ratios were sensitive to both herbivore and plant quality. However, it is possible that DBM larvae responded to the changes in their diets in the crossed treatments, and that wasps may have been able to detect these differences rather than plant quality itself.

In each field experiment, the range in the percentage of female wasps spanned approximately 40% among plots, although the absolute percentages varied among the experiments. While the strongest relation between wasp sex bias and fertilizer level was in the experiment in which we set out 3rd instar DBM larvae for 4 days, all three field experiments showed the same overall trend: fewer female wasps in the low fertilizer regimes.

The sex ratio biases in laboratory experiments, which excluded any extraneous factors that might have influenced wasp behavior, were even greater than in the field. In these choice experiments, more of the Low N larvae (on Low N leaves) were parasitized than High N larvae on High N leaves (61 vs 25), but 76% of the wasps emerging from the High N larvae were female; in contrast only 3% of the wasps from the Low N plants were female ($G=50.4$, 1 df, $P\leq 0.001$).

DBM instar

Female wasps had clear oviposition preferences among DBM instars. No parasitoids emerged from DBM that were offered to ovipositing wasps as 1st instars, but 26–36% of the larger instars were parasitized.

Wasp sex ratios were affected by DBM instar at parasitization (Table 4). Wasps emerging from DBM parasitized as 2nd instars were more likely to be males (20–45% female; 30% of 2nd instars in all 3 experiments), while those emerging from DBM parasitized as 3rd and 4th instars were mainly females (65–80% female; 70%

Table 4. The total number and % of female wasps *D. insulare* emerging from laboratory experiments with different combinations of DBM instars available to be parasitized

Host Stages Available		Host instar parasitized:			
		1	2	3	4
1+2+3+4	# wasps	0	11	17	14
	% female	–	45	71	71
2+3 together	# wasps		11	10	
	% female		27	80	
2+3 separately	# wasps		15	20	
	% female		20	65	

of 3rd instars in all 3 experiments). When all instars were available, sex ratios of emerging wasps were significantly skewed with instar ($G=6.87$, $P<0.05$, 2 df). More female wasps emerged from 3rd instars than from 2nds, both when wasps were offered several size classes ($G=8.42$, $P<0.005$) and when there was no choice ($G=7.04$, $P<0.01$).

DBM body size

Wasp sex ratios could not be explained by differences in size of DBM larvae from the different fertilizer treatments. Neither female nor male DBM body length varied significantly with treatment in the main field experiment (2 way ANOVAs, $F=0.93$ and 1.05 , both $P>0.4$; females were 4.16 ± 0.13 mm in length, vs. males 4.21 ± 0.08 mm). Female and male sizes among plots were only weakly correlated ($r=0.45$, $P=0.08$), and wasp sex ratios were not correlated with DBM size ($r<0.2$ for both sexes).

In the first (4 week) small-scale field experiment, male DBM were significantly longer on the High N plants than on the Low N plants (t-test, df=20, $P=0.0175$), although weights of DBM pupae from the High N and Low N plants were not significantly different (7.47 ± 0.16 mg vs. 7.09 ± 0.20 mg; t-test, $P=0.15$). Therefore, differences in wasp sex ratios among plots were not based on differences in DBM body length.

Wasp body size

Wasp body size was not consistently related to fertilizer treatment. In the main field experiment, male wasp length was nearly significant among treatments (2-way ANOVA, $F=2.48$, $P=0.056$) and it was correlated significantly with leaf N ($r=0.52$, $P<0.05$); but female wasp sizes did not vary with treatment (2-way ANOVA, $P=0.59$). However, in the first small-scale experiment with potted collards, female wasps were significantly larger in the High N treatment than those in the Low N treatment (t-test, df=21, $P=0.0254$).

Discussion

Properties of food plants affected several components of the collard-DBM-*Diadegma* system. Parasitoid abundance was directly related to DBM numbers, and both were correlated with total N in collard foliage. However, the mean percentage of DBM parasitized (70.7%) was independent of DBM density. Waage (1983) found that parasitism rates by *Diadegma eucero-phaga* on DBM in England also were constant at around 70%. However, parasitism rates were more variable in other studies of DBM: 41–57% by *D. cerophaga* and *D. rapi* (combined) in southern Australia (Goodwin 1979), and 0–80% (\bar{x} ~ 33%) and 9–23% by *D. insulare* in Canada (Harcourt 1963) and Ohio (Horn 1987), respectively.

Wasps from high quality hosts on high quality plants had high female-biased sex ratios in all experiments. Relatively few female wasps emerged from herbivores feeding on lower quality collards. Over all the field experiments, sex ratios of the parasitoids varied from 93% to 23% females on High N vs. Low N plants. Short-term laboratory experiments gave similar ranges, 76% vs. 3% female. Our experiments cannot distinguish whether the parasitoids responded to characteristics of DBM larvae that were influenced by plant quality, to properties of the food plants themselves, or to both.

Diadegma spp. are known to have variable sex ratios. For example, strongly male-biased sex ratios (25% female) was one factor preventing *D. eucero-phaga* from regulating populations of DBM in Malaysia (Chua and Ooi 1986). Sex ratios varied from 24–68% female in Waage's (1982b) laboratory work. From an extensive k-factor analysis of long-term data spanning many generations, Harcourt (1986) concluded that *D. insulare* caused density-dependent mortality of DBM, in direct contrast to findings of short-term studies within single generations (e.g., Waage 1983 and this study). Harcourt's k-factor analysis included numerical responses of parasitoids and hosts *between* generations. We propose that changes in sex ratios provide the mechanism for altering the numerical response between generations and that this mechanism gives *Diadegma* the ability to control the density of DBM.

Skewed sex ratios are observed in many species, especially haplo-diploid Hymenoptera (Bull 1983). These ratios have been linked, at least in theoretical studies, to the spatial structure of populations and to differential distribution of resources with respect to the sexes (Hamilton 1967; Charnov 1982; Werren 1984; Comins and Wellings 1985), and more recently to synchrony of brood maturation and male dispersal (Nunney and Luck 1988). Many studies have also shown that more females emerge from larger hosts, including larval parasites (reviewed in King 1989), as we found in our study. In this paper we have proposed additional mechanisms for producing sex ratio biases: namely, that sex ratios are strongly influenced by differences not only in host quality, but in plant quality as well.

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References

- Allen SE (ed) (1974) *Chemical Analysis of Ecological Materials*. Wiley, New York
- Anderson RM, May RM (1978) Regulation and stability of host-parasite interactions. I. Regulatory processes. *J Anim Ecol* 47:219–247
- Barbosa P (1988) Natural enemies and herbivore-plant interactions: influence of plant allelochemicals and host specificity. In: Barbosa P, Letourneau DK (eds) *Novel Aspects of Insect-Plant Interactions*. Wiley, NY, pp 201–229
- Barbosa P, Saunders JA (1985) Plant allelochemicals: linkages between herbivores and their natural enemies. In: Cooper-Driver GA, Swain T, Conn EE (eds) *Chemically Mediated Interactions between Plants and other Organisms*, Plenum, NY, pp 107–137
- Bouletreau M (1976) Influence de la photoperiode subie par les adultes sur la sex ratio de la descendance chez *Pteromalus puparum* (Hymenoptera; Chalcididae). *Entomol Exp Appl* 19:197–204
- Bull JJ (1983) *Evolution of Sex Determining Mechanisms*. Benjamin-Cummings, Menlo Park CA
- Campbell BC, Duffey SF (1979) Tomatine and parasitic wasps: potential incompatibility of plant antibiosis with biological control. *Science* 20:700–702
- Campbell BC, Duffey SF (1981) Alleviation of tomatine induced toxicity to the parasitoid, *Hyposoter exiguae* by phytosterols in the diet of the host, *Heliothis zea*. *J Chem Ecol* 7:927–946
- Charnov EL (1979) The genetical evolution of patterns of sexuality: Darwinian fitness. *Am Nat* 113:465–480
- Charnov EL (1982) *The Theory of Sex Allocation*. Princeton University Press, Princeton NJ
- Charnov EL, Skinner SW (1984) Evolution of host selection and clutch size in parasitoid wasps. *Florida Entomol* 67:5–21
- Charnov EL, Hartogh RL, Jones WT, Assem J van den (1981) Sex ratio evolution in a variable environment. *Nature* 289:27–33
- Chua TH, Ooi PAC (1986) Evaluation of three parasites in the biological control of diamondback moth in the Cameron Highlands, Malaysia. In: Talekar NS (ed), *Diamondback Moth Management*. Proc. First Intl Workshop, Asian Vegetable Research and Development Center. Shan-hua, Taiwan, pp 173–184
- Clarke C (1984) Upsets in the sex-ratio of some Lepidoptera. In: Vane-Wright RI, Ackery PR (eds) *The Biology of Butterflies*. Academic Press, Orlando FL, pp 255–258
- Comins HN, Wellings PW (1985) Density-related parasitoid sex-ratio: influence on host-parasitoid dynamics. *J Anim Ecol* 54:583–594
- Compton SJ, Jones CG (1985) Mechanism of dye response and interface in the Bradford protein assay. *Anal Biochem* 151:369–374
- Fischlin A, Baltensweiler W (1979) Systems analysis of the larch bud moth system. Part I: The larch-larch bud moth relationship. *Mitt Schweiz Entomol Ges* 52:273–289
- Goodwin S (1979) Changes in numbers in the parasitoid complex associated with the diamond-back moth, *Plutella xylostella* (L.) (Lepidoptera). *Aust J Zool* 27:981–989
- Hamilton WD (1967) Extraordinary sex ratios. *Science* 156:477–488
- Harcourt DG (1963) Mortality factors in the population dynamics

- of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). Mem Entomol Soc Canada 32:55-66
- Harcourt DG (1986) Population dynamics of the diamondback moth in southern Ontario. In: Talekar NS (ed), Diamondback Moth Management. Proc. First Intl Workshop, Asian Vegetable Research and Development Center, Shan-hua, Taiwan, pp 1-15
- Hassell MP (1978) The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton, NJ
- Hassell MP (1986) Parasitoids and population regulation. In: Waage J, Greathead D (eds). Insect Parasitoids. Academic Press, Orlando FL, pp 201-224
- Hassell MP, Waage JK (1984) Host-parasitoid population interactions. Ann Rev Entomol 29:89-114
- Hassell MP, Waage JK, May RM (1983) Variable parasitoid sex ratios and their effect on host-parasitoid dynamics. J Anim Ecol 52:889-904
- Horn DJ (1987) Vegetational background and parasitism of larval diamond-back moths on collards. Ent Exp Appl 43:300-303
- Kfir R, Luck RF (1979) Effects of constant and variable temperature extremes on sex ratio and progeny production by *Aphytis melinus* and *A. lingnanensis* (Hymenoptera: Aphelinidae). Ecol Entomol 4:335-344
- King BH (1989) Host-size-dependent sex ratios among parasitoid wasps: does host growth matter? Oecologia 78:420-426
- Letourneau DK, Fox LR (1989) Effects of nitrogen and parasitism of lepidopterous larvae on cabbage butterflies. Oecologia 80:211-214
- Luck RF, Podoler H (1985) Competitive exclusion of *Aphytis lingnanensis* by *A. melinus*: potential role of host size. Ecology 66:904-913
- May RM, Anderson RM (1978) Regulation and stability of host-parasite interactions. II. Destabilizing processes. J Anim Ecol 47:249-267
- Murdoch WW (1979) Predation and the dynamics of prey populations. Fortschr Zool 25:295-310
- Murdoch WW, Stewart-Oaten A (1989) Aggregation by parasitoids and predators: effects on equilibrium and stability. Am Nat 134:288-310
- Murdoch WW, Reeve JD, Huffaker CB, Kennett CE (1984) Biological control of scale insects and ecological theory. Am Nat 123:377-392
- Murdoch WW, Chesson J, Chesson P (1985) Biological control in theory and practice. Am Nat 125:344-366
- Nunney L, Luck RF (1988) Factors influencing the optimum sex ratio in a structured population. Theor Pop Bio 33:1-30
- Orion (1986) Model 93-07. Nitrate Electrode Instruction Manual. Orion Research, Inc.
- Porter K (1984) Sunshine, sex ratio and behaviour of *Euphydryas aurinia* larvae. In: Vane-Wright RI, Ackery PR (eds), The Biology of Butterflies. Academic Press, Orlando FL, pp 309-311
- Reeve JD, Murdoch WW (1985) Aggregation by parasitoids in the successful control of the California red scale: a test of theory. J Anim Ecol 54:797-816
- SAS (1988) SAS/STAT Guide for Personal Computers. Version 6 edition
- Sokal RR, Rohlf FJ (1981) Biometry. 2nd edition, Freeman & Co. San Francisco CA
- Southwood TR, Comins HN (1976) A synoptic population model. J Anim Ecol 45:949-965
- Strong DR (1984) Density-vague ecology and liberal population regulation in insects. In: Price PW, Slobodchikoff CN, Gaud WS (eds), A New Ecology: Novel Approaches to Interactive Systems. Wiley, New York, pp 313-327
- Strong DR (1986) Density vagueness: abiding the variance in the demography of real populations. In: Diamond J, Case TJ (eds), Community Biology. Harper & Row, New York, pp 257-268
- Vinson SB (1981) Habitat location. In: Nordlund DA, Jones RL, Lewis WJ (eds) Semiochemicals: Their Role in Pest Control, Wiley, New York, pp 51-77
- Vinson SB, Iwantsch GF (1980) Host suitability for insect parasitoids. Ann Rev Entomol 25:397-419
- Waage JK (1982a) Sib-mating and sex ratio strategies in scelionid wasps. Ecol Entomol 7:103-112
- Waage JK (1982b) Sex ratio and population dynamics of natural enemies - some possible interactions. Ann Appl Biol 101:159-164
- Waage JK (1983) Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera, Ichneumonidae). Ecol Entomol 8:447-453
- Waage JK (1986) Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: Waage J, Greathead D (eds), Insect Parasitoids. Academic Press, Orlando, FL, pp 63-95
- Walde SJ, Murdoch WW (1988) Spatial density dependence in parasitoids. Ann Rev Entomol 33:441-466
- Walker TJ (1984) Do populations self-regulate? In: Huffaker B, Rabb RL (eds), Ecological Entomology, Wiley, New York, pp 531-558
- Werren JH (1984) A model for sex ratio selection in parasitic wasps: local mate competition and host quality effects. Neth J Zool 34:81-96
- Werren JH, Skinner SW, Huger AH (1986) Male-killing bacteria in a parasitic wasp. Science 231:990-992
- Williams HJ, Elzen GH, Vinson SB (1988) Parasitoid-host plant interactions emphasizing cotton (*Gossypium*). In: Barbosa P, Letourneau DK (eds) Novel Aspects of Insect-Plant Interactions. Wiley, NY, pp 171-200