

## DENSITY-DEPENDENT PARASITOID RECRUITMENT PER PARASITIZED HOST: EFFECTS ON PARASITOID-HOST DYNAMICS

ANDREW D. TAYLOR\*

Department of Pure and Applied Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, United Kingdom, and Department of Zoology, University of Hawai'i at Mānoa, 2538 the Mall, Edmondson 152, Honolulu, Hawaii 96822

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*Abstract.*—Models of parasitoid-host dynamics are analyzed that include direct density dependence in the host population and either parasitoid- or host-density-dependent variation in parasitoid recruitment per parasitized host (parasitoid "yield"). The principal question addressed is how these forms of density dependence in parasitoid dynamics combine with aggregated parasitism to affect the stability of the models, in relation to suppression of host abundance. When parasitoid yield is an overcompensating function of either parasitoid or host density, stability is enhanced for systems with host equilibria suppressed far below the host carrying capacity. Substantially less aggregation of parasitism is required for stability in this situation than in previous models assuming parasitoid yield is constant. However, this density dependence in parasitoid yield also reduces stability when the host equilibrium is suppressed only moderately below carrying capacity; this is especially true when parasitoid yield is more strongly decreased by high host density than is host per capita reproduction. At present there is little empirical evidence concerning the relationships of parasitoid recruitment to parasitoid and host densities. The substantial effects shown in these models suggest that these relationships should be considered in empirical studies.

Over the last several decades, considerable effort has gone into understanding the dynamics of parasitoid-host interactions. One line of theoretical research has been a search for mechanisms that could allow such interactions to be stable despite the host being reduced far below its single-species equilibrium, as might be the case in a successful biological pest control program (Beddington et al. 1978). This has led to the analysis of a variety of models in which the coupled parasitoid-host interaction has been combined with direct density dependence in the host population (Beddington et al. 1975, 1976, 1978; May et al. 1981; Bernstein 1986; Hochberg and Lawton 1990; Ives 1992).

Most of these models examining direct host density dependence have assumed that the number of parasitoid progeny produced per parasitized host (parasitoid yield) is independent of host and parasitoid densities. Currently, only indirect evidence exists concerning this assumption, since there have been no studies directly relating parasitoid yield to parasitoid and host densities. The available indirect evidence suggests that this assumption is probably valid for

\* Present address: Department of Zoology, University of Hawai'i at Mānoa, 2538 the Mall, Edmondson 152, Honolulu, Hawaii 96822; E-mail: ataylor@lala.zoo.hawaii.edu.

many, perhaps most, parasitoids but not for all: processes have been shown that seem likely to lead to density-dependent yield.

The most common cause of parasitoid-density dependence in yield probably is superparasitism (parasitism of already-parasitized hosts). Superparasitism occurs to at least some extent in virtually all parasitoids (Taylor 1988*b*; van Alphen and Visser 1990; Godfray 1994) and generally will be more frequent at high parasitoid densities. For gregarious parasitoids (in which a single host typically supports development of more than one parasitoid larva), it is generally the case that yield per host varies with the number of eggs laid on the host (Taylor 1988*a*, 1988*b*; Godfray 1994) and thus with superparasitism and parasitoid density. In solitary species, in contrast, supernumerary larvae typically are eliminated (Salt 1961; Godfray 1994). In at least some cases, however, this process is not exact, so that superparasitized hosts may produce either more or fewer parasitoid progeny on average than do singly parasitized hosts (Taylor 1988*b*; see Godfray 1994 for a discussion of mechanisms).

Dependence of parasitoid yield on host density probably is most commonly mediated via host size. Negative effects of high density on size have been described for many insect species (Peters and Barbosa 1977; Clancy and Price 1989; Weaver and McFarlane 1990). Host size in turn often affects parasitoid yield, via effects on clutch size and/or sex ratio (King 1993; Godfray 1994) or larval growth (and thus adult size, fecundity, and longevity) and survival (Salt 1941; Taylor 1988*a*; Tillman and Cate 1993).

Previous theoretical studies (Hassell et al. 1983; Comins and Wellings 1985; Taylor 1988*b*) have shown that density-dependent parasitoid yield can have important dynamic effects. In this article, I extend these results by examining the effects of parasitoid- and host-density-dependent parasitoid yield when combined with direct host density dependence and with aggregation of parasitism. My principal aim is to relate this theory of density-dependent yield to the larger body of theory concerning the relationships between the stability of the parasitoid-host interaction, the suppression of host abundance, and aggregation of parasitism (aggregation of risk) (May 1978; Chesson and Murdoch 1986).

#### MODELS

The models analyzed here are based on the standard discrete-time structure derived from the Nicholson-Bailey (1935) model. This admittedly overly simple formulation is used not only because it is easy to use but also because it allows direct comparison with previous results. There is no obvious reason, however, that the effects of the phenomena of interest here would depend on this choice of model structure.

An assumption in all the models considered here is that both host density dependence and parasitoid reproduction are functions of the host density at the beginning of a generation,  $H_t$ . Although in many natural systems one of these processes will depend on the outcome of the other (May et al. 1981), the assumption made here can be interpreted as representing host competition that precedes parasitism but does not kill hosts until after parasitoid development is

complete or perhaps does not kill hosts at all. In particular, it would be appropriate for systems involving parasitism of host larvae and delayed or sublethal effects of competition among host larvae (e.g., pupal mortality or size reduction).

The models analyzed in this article use a host equation that combines overcompensating (scramble) density dependence among hosts with the negative-binomial model of parasitism (Griffiths and Holling 1969; May 1978; Hochberg and Lawton 1990):

$$H_{t+1} = H_t e^{r(1-H_t/K)} (1 + aP_t/k)^{-k}. \quad (1)$$

Here  $H_t$  and  $P_t$  are, respectively, host and parasitoid densities in generation  $t$ . The parameter  $r$  is the host intrinsic rate of increase (the host population growth rate in the absence of parasitoids and at low host density),  $K$  is the host equilibrium in the absence of parasitoids (the carrying capacity),  $a$  is the Nicholsonian area of discovery, and  $k$  determines the degree of aggregation of the risk of parasitism over hosts (smaller  $k$  representing greater aggregation).

This host equation (and the parasitoid equations below) assume a Type I functional response, in which the fraction of the host population parasitized per parasitoid female does not vary with host density. A Type II functional response, with attack rate decreasing with increasing host density because of handling time and similar factors, would be more realistic. It also quite possibly would produce interesting effects, as it would constitute a destabilizing dependence on host density counteracting the stabilizing factors included in the present models. In the current work, however, host density dependence in the attack rate has been omitted to allow a clear focus on the effects of density dependence in parasitoid recruitment.

The first model analyzed here combines the preceding host equation with a parasitoid equation in which parasitoid recruitment per parasitized host varies with the number of female parasitoids encountering the host. Specifically, there is overcompensating parasitoid competition, with less parasitoid recruitment from hosts encountered many times than from hosts encountered only once. The model (the scramble model of Taylor 1988*b*) is

$$P_{t+1} = caP_t H_t (1 + yaP_t/k)^{-(k+1)}, \quad (2)$$

with  $H_t$ ,  $P_t$ ,  $a$ , and  $k$  defined as in equation (1). The parameter  $c$  scales the density-independent parasitoid recruitment per parasitized host: it is the number of adult female parasitoid progeny produced from a host encountered by one foraging parasitoid female. The parameter  $y$  determines the intensity of parasitoid competition (i.e., the reduction in parasitoid recruitment per encounter as a function of the number of times the host was encountered).

The second model uses a parasitoid equation in which, as in most parasitoid-host models, the number of parasitoid progeny produced per parasitized host is independent of parasitoid density. In this model, however, parasitoid reproduction per parasitized host is inversely dependent on host density:

$$P_{t+1} = c_0 e^{-c_1 P_t H_t / K} H_t [1 - (1 + aP_t/k)^{-k}]. \quad (3)$$

Here the parameter  $c_0$  is the parasitoid reproduction (adult female parasitoids produced per parasitized host) at very low host density, and  $c_1$  determines the dependence of this parasitoid reproductive rate on host density. The host reproductive rate,  $r$ , is included with  $c_1$  in the exponent so that the latter can be interpreted as scaling the effect of host density on parasitoids relative to its effect on hosts, since host reproduction is reduced by the term  $\exp(-rH_t/K)$  and parasitoid reproduction is reduced in the same way but with the exponent scaled by  $c_1$ .

#### RESULTS

The analysis of these models will focus on the qualitative form of their dynamics, as shown by local stability analysis of equilibria. Following authors of previous studies (Beddington et al. 1975, 1976, 1978; May et al. 1981), I will describe stability as a function of  $r$  (the host intrinsic rate of increase) and a parameter  $q$  measuring the host equilibrium relative to what it would be in the absence of the parasitoids (i.e., an inverse measure of host suppression):  $q = N^*/K$ , where  $N^*$  and  $K$  are, respectively, the host equilibria with and without parasitoids.

##### *Scramble Parasitoid Competition with Direct Host Density Dependence*

For the model combining scramble parasitoid competition and scramble host competition (eqq. [1] and [2]), the stability boundaries with strongly aggregated parasitism (small  $k$ ) (fig. 1A) are not greatly different than those previously reported for perfectly compensatory parasitoid competition and scramble host competition (Beddington et al. 1975, 1976, 1978; May et al. 1981; Bernstein 1986; Hochberg and Lawton 1990). In common with those previous results, equilibria generally are stable except when both  $q$  and  $r$  are large; this region of instability is due to strongly overcompensating competition in host populations that are not greatly depressed by parasitism. With scramble parasitoid dynamics, however, stability is lost at very low  $q$  and  $r$  when parasitoid competition is weak (small  $y$ ). Another difference from previous results is that the stability boundary is slightly expanded and more complicated with  $r$  near 4 and  $q$  between roughly 0.5 and 0.7; in this region, stronger parasitoid competition (larger  $y$ ) tends to reduce stability, in contrast to its stabilizing effect at small  $r$  and  $q$ .

When  $k$  is somewhat larger than 1, however, the stability region with scramble parasitoid competition (fig. 1B–D) is very different than in previous models with perfectly compensatory parasitoid dynamics, and the effect of the strength of the competition ( $y$ ) is complex. The most striking difference is that stability is possible with very low  $q$  (extreme host suppression) even with only modest aggregation of parasitism. Figure 1B–D illustrates the situation with  $k = 2$ , but with sufficiently strong parasitoid competition (large  $y$ ), stability at the lowest levels of  $q$  is possible with arbitrarily large (but finite)  $k$ . When the parasitoid scramble competition is weak ( $y = 0.25$ ; fig. 1B), this region of stability at very low  $q$  (and high  $r$ ) is “disjunct” from the main stable region, which is much like that for previous models with constant-yield parasitoid dynamics. With

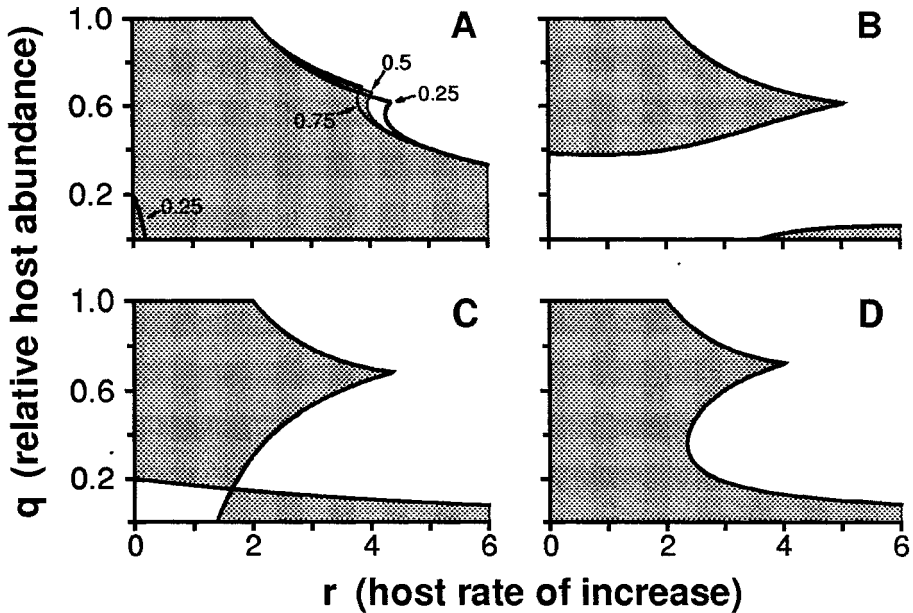


FIG. 1.—Stability diagrams for scramble parasitoid competition with direct host density dependence (eqq. [1] and [2]). The X-axis is the host rate of increase; the Y-axis is the host equilibrium relative to that in the absence of parasitism ( $q = N^*/K$ ). A, Strongly aggregated parasitism ( $k = 0.5$ ). Thick line,  $y = 0.25$  (weak parasitoid competition); shaded area,  $y = 0.5$  (moderate competition); thin line,  $y = 0.75$  (strong competition). Parameter combinations below and to the left of the boundaries give locally stable equilibria, except that the lower-left corner is unstable for  $y = 0.25$ . B–D, Weak aggregation ( $k = 2$ ). Shaded areas represent parameter values giving locally stable equilibria. B,  $y = 0.25$ ; C,  $y = 0.5$ ; and D,  $y = 0.75$ .

stronger scramble competition, the low- $q$  region of stability is larger and merges with the region of stability at larger  $q$ , until with strong scramble competition ( $y = 0.75$ ; fig. 1D) stability is possible with very small  $q$  over the entire range of  $r$  and for any  $q$  whenever  $r$  is relatively small ( $<2$ , roughly).

In contrast to the enhancement of stability at low  $q$  (strong host suppression), stronger scramble parasitoid competition somewhat reduces stability with moderate degrees of host suppression ( $q$  between roughly 0.4 and 0.7, with  $r$  between roughly 2 and 4); this effect is similar to that seen in this region of the diagram with small  $k$  (fig. 1A).

The example trajectories in figure 2 illustrate the stabilizing effect of strong parasitoid competition at very low  $q$ . When both populations start below their equilibrium levels, the host abundance initially increases. With weak parasitoid competition (fig. 2A), the parasitoid abundance, although below equilibrium, increases only slowly because of the low abundance of hosts to parasitize. This increase is insufficient to keep up with the host population, which continues to increase rapidly in the second generation. The high host abundances then allow the weakly regulated parasitoid population to increase greatly. The resulting in-

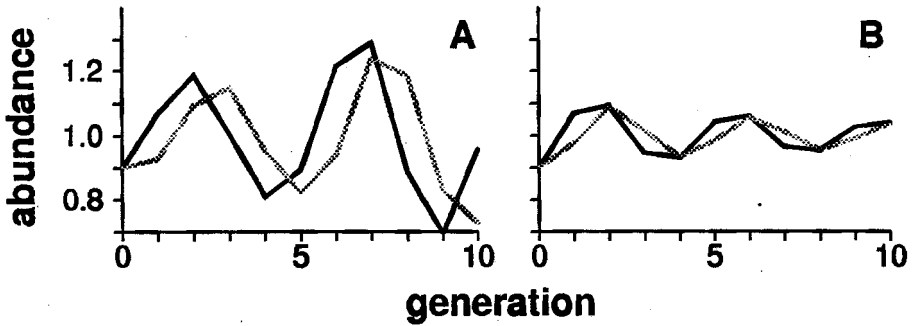


FIG. 2.—Example trajectories for scramble parasitoid competition with direct host density dependence (eqq. [1] and [2]), showing the effects of differing strengths of parasitoid competition. In both cases,  $r = 3$ ,  $q = 0.05$ , and  $k = 2$ . Host trajectories are shown by solid black lines, parasitoids by gray lines; abundances are shown as proportions of equilibrium values. Initial abundances were  $0.9 \times$  equilibria. A, Weak competition ( $y = 0.25$ ); and B, stronger competition ( $y = 0.5$ ).

tense parasitism causes the host population to crash, leading in turn to a parasitoid crash, which then allows the host population to rebound excessively; these overshoots result in increasing oscillations away from the equilibrium.

With strong parasitoid competition (fig. 2B), in contrast, an initially low parasitoid population increases more rapidly, because it is released from the effects of competition. This allows it to control the host population before the latter becomes very large. This more moderate host peak, combined with the regulating effect of the parasitoid competition, prevent an excessive buildup of parasitoids, thus avoiding the crashes in host and subsequently parasitoid populations. By restraining the parasitoid population from overshooting the host peaks and troughs, the parasitoid competition produces gradually decreasing oscillations returning toward the equilibrium point.

Models in which host and/or parasitoid density dependence was undercompensating (contest) rather than the overcompensating competition in equations (1) and (2) produced results consistent with those described above and in previous studies. With contest competition in the host population, the only significant difference from the results shown here is that the region of instability at large  $q$  and large  $r$  is not present. Replacing scramble parasitoid competition by contest competition, however, produces substantially different results: the model is stable in a region of parameter space similar to but smaller than the stable region for the standard model with constant parasitoid yield per host (see below). Stabilization at low  $q$  with  $k > 1$  occurs only with overcompensating competition (eq. [2]), not with undercompensating or perfectly compensating competition.

#### *Host-Density-Dependent Parasitoid Recruitment per Host*

As shown in numerous previous analyses (e.g., Beddington et al. 1978; Hassell 1978), when within-host parasitoid competition is exactly compensatory and parasitoid recruitment per parasitized host is not dependent on host density, sta-

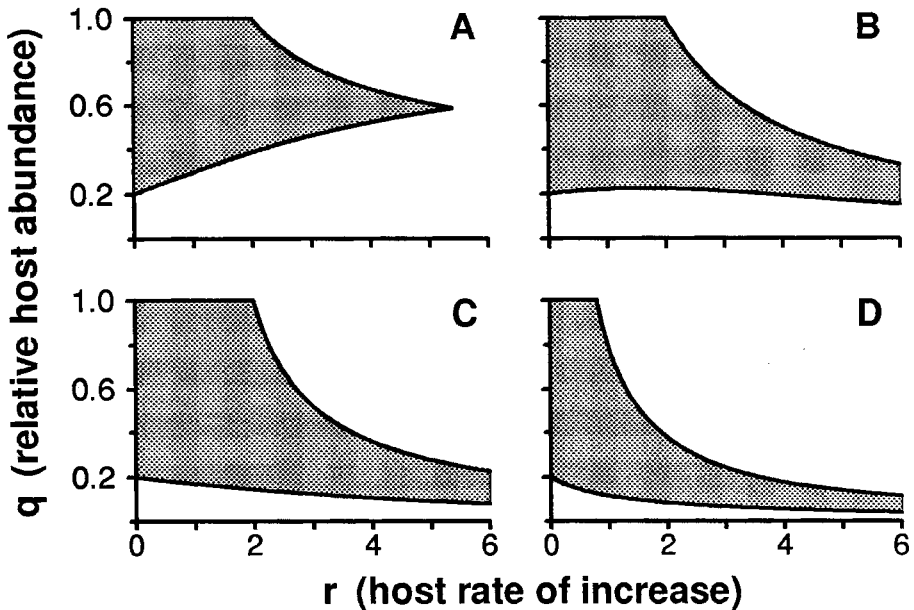


FIG. 3.—Stability diagrams for host-density-dependent parasitoid yield (eqq. [1] and [3]), with  $k = 2$ . Shaded areas represent parameter values giving locally stable equilibria. A,  $c_1 = 0$  (no host-density dependence of parasitoid yield); B,  $c_1 = 0.5$  (moderate dependence); C,  $c_1 = 1$  (strong dependence: host density affects parasitoid recruitment as much as it does host recruitment); and D,  $c_1 = 2$  (very strong dependence).

bility is quite dependent on the degree of aggregation of parasitism: systems with strong host suppression (low  $q$ ) can be stable only with strong aggregation ( $k < 1$ ). With less aggregation (e.g.,  $k = 2$ ; fig. 3A), stability is possible only with moderate to large  $q$ ; as  $r$  increases, the minimum stable  $q$  also increases, and (as with scramble parasitoid competition) there is a region of instability because of host overcompensation at high  $r$  and  $q$ .

If parasitoid recruitment per parasitized host is dependent on host density, however, the stability boundaries can differ markedly. When this dependence is relatively weak—that is, host density has less effect on parasitoids than on hosts ( $c_1 = 0.5$ ; fig. 3B)—the effect is to shift the stability boundaries downward: the minimum stable  $q$  is lower, especially at larger  $r$ , but also the region of instability at large  $r$  and  $q$  is expanded. When parasitoid recruitment is somewhat more strongly host density dependent ( $c_1 = 1$ ; fig. 3C), these effects are even greater. With very strong dependence of parasitoid recruitment on host density—that is, host density affecting parasitoids more than hosts ( $c_1 = 2$ ; fig. 3D)—the downward shift in the stability region for  $r > 2$  is yet greater, but a new phenomenon also occurs: stability is lost at moderate to large  $q$  and  $r < 2$ , with this effect increasing—moving the stability boundary to the left (lower values of  $r$ )—as  $c_1$  increases.

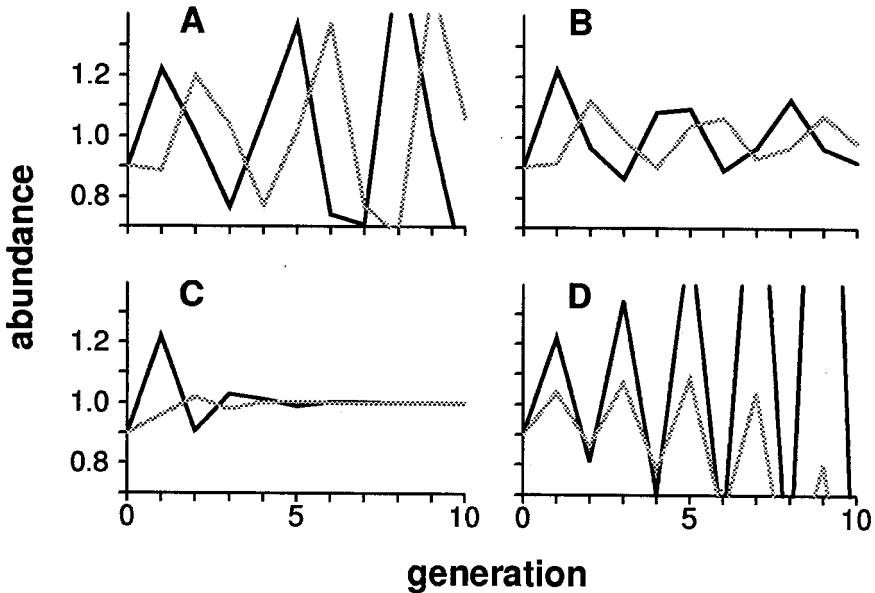


FIG. 4.—Example trajectories for host-density-dependent parasitoid yield (eqq. [1] and [3]), showing the effects of differing degrees of host-density dependence. In all cases,  $r = 4$ ,  $q = 0.4$ , and  $k = 2$ . Host trajectories are shown by solid black lines, parasitoids by gray lines; abundances are shown as proportions of equilibrium values. Initial abundances were  $0.9 \times$  equilibria. A,  $c_1 = 0$  (no host-density dependence of parasitoid yield); B,  $c_1 = 0.2$  (very weak dependence); C,  $c_1 = 0.5$  (moderate dependence); and D,  $c_1 = 1$  (strong dependence).

The effects of host-density dependence of parasitoid recruitment, for systems with the host equilibrium well below carrying capacity (i.e., small  $q$ ), are shown by the trajectories in figure 4. When parasitoid recruitment does not vary with host density (fig. 4A), dynamics are similar to those with weak dependence of recruitment on parasitoid density (fig. 2A): responses of parasitoid abundance to changes in host abundance are substantially delayed and thus overshoot, producing diverging oscillations. Dependence of parasitoid recruitment on host density reduces the lag: parasitoid abundance increases more rapidly when host abundance is low (but increasing) and decreases more rapidly when host abundance is high (but decreasing). When mild (e.g., fig. 4B, C), this produces damped oscillations, much as with scramble within-host parasitoid competition (e.g., fig. 2B). Stronger host-density dependence of parasitoid recruitment entirely eliminates the lag between host and parasitoid fluctuations but results in excessive overcompensation and diverging (in-phase) oscillations (fig. 4D).

Qualitatively similar effects to those described earlier are found also in models with overcompensating parasitoid competition. Specifically, models based on equation (2), but with either  $c$  or  $y$  dependent on host density (as  $c$  is in eq. [3]), produce stability boundaries similar to those in figure 3. Stronger dependence of parasitoid per-host recruitment on host density again enhances stability at low  $q$

but (when intense) eliminates stability at high  $q$  and moderate  $r$ . The principal difference from the results shown in figure 3 is that since scramble parasitoid competition allows stability at very low  $q$  (and  $k > 1$ ) even without dependence of parasitoid per-host recruitment on host density (as in fig. 1B–D), this also occurs when parasitoid recruitment does depend on host density. The low- $q$  enhancement of stability by dependence of parasitoid recruitment on host density thus is reflected in an expansion of the stable region at moderately low  $q$  (e.g., 0.1–0.3) rather than very low  $q$ .

#### DISCUSSION

The dynamic effects of density-dependent variation in parasitoid “yield” (recruitment per parasitized host) clearly can be substantial, as shown, for instance, in the striking differences in stability regions between figure 4A (with density-independent recruitment) and figures 2D and 4D (with strongly density-dependent recruitment). These effects also are complex. Under many circumstances (most notably, strong suppression of host abundance but only modest aggregation of parasitism), such variation is stabilizing. Under other circumstances, however, stronger density dependence in parasitoid recruitment can be destabilizing. This occurs primarily at moderate levels of host suppression and moderate to high host reproductive rates when the recruitment variation depends on parasitoid density, while with host-density-dependent recruitment, it affects systems with slight host suppression and moderate host reproductive rates.

These results constitute clear exceptions to the general conclusion, obtained from models with constant parasitoid yield (Beddington et al. 1975, 1976, 1978; May et al. 1981; Bernstein 1986; Hochberg and Lawton 1990; Ives 1992), that strongly aggregated parasitism (e.g.,  $k < 1$ ) is necessary and sufficient for stabilization of parasitoid-host systems with hosts suppressed substantially below their carrying capacity. Seen in the context of previous studies of density-dependent variation in recruitment, however, the present results are not so exceptional. It has been shown previously that dependence of parasitoid recruitment on parasitoid density usually is stabilizing but can be destabilizing if too strong and that it accentuates the effect of aggregation of parasitism (Hassell et al. 1983; Taylor 1988*b*). It has separately been shown that dependence of parasitoid recruitment on either parasitoid or host density can stabilize systems with very low host abundances but also that stability may be lost in systems with higher host abundances (Comins and Wellings 1985). The main results of the present article essentially are a combination of these previous findings, in a more comprehensive model framework addressing all three factors (density-dependent recruitment, aggregation of risk, and host suppression) at once. Because of this consistency with previous results and results for variants of the current models (as noted in Results), the results reported here seem likely to be fairly robust, despite having been obtained using models almost entirely lacking specific empirical justification.

In all these models of density-dependent per-host recruitment, the underlying mechanism is stronger regulation of parasitoid abundance. That is, the growth of

the parasitoid population when hosts are abundant but declining (or about to decline) because of intense parasitism is slowed, while the decline in parasitoid abundance when hosts are scarce but increasing (or about to increase) because of low levels of parasitism, is also lessened. Because of the nearly synchronous dynamics of hosts and parasitoids in these models, these effects of parasitoid "regulation" (broadly defined) occur whether the changes in parasitoid recruitment respond to host density, to the slightly later peaks and troughs in parasitoid density, or even to the yet later ups and downs in the ratio of parasitoids to hosts (Hassell et al. 1983; Comins and Wellings 1985). The typical result of this damping of the parasitoid response to host fluctuations is that the parasitoids do not overshoot the oscillations in host abundance and the fluctuations die out: the system is stabilized. The destabilization that sometimes occurs results from an exaggeration of the same process: just as in single-population models, strongly overcompensating competition can cause excessive declines from population peaks and excessive increases from lows, leading to diverging two-generation cycles, with hosts and parasitoid oscillating in phase (e.g., fig. 4D). This can happen without direct host density dependence but only under extreme conditions (Taylor 1988b); addition of scramble host competition produces it over a much wider range of parameter values.

These theoretical results suggest several potentially fruitful lines of empirical study. Apart from the reasonably large body of literature relating to variation in parasitoid clutch sizes and sex ratios, there is a striking scarcity of quantitative data on parasitoid recruitment per parasitized host in relation to population densities, levels of superparasitism, and so forth. Such data obviously often will be difficult to obtain under natural conditions, but even laboratory studies would be valuable as a starting point for assessing the reasonableness of the models used in this article, and thus the importance of their results, and possibly for suggesting ways to improve them.

In addition to investigating the assumptions of the models, it obviously would be valuable to test their conclusions. Although doing so experimentally (e.g., by manipulating the form of recruitment density dependence) does not seem possible, a comparative approach could be adopted. For instance, the most significant prediction from these models is that among systems in which the parasitoid suppresses the host population substantially below its carrying capacity, those in which there is fairly strong overcompensating dependence of parasitoid yield on parasitoid and/or host densities are more likely to be stable (e.g., constant or resilient) than are systems without this source of regulation. Description of both the per-host dynamics of parasitism and the overall temporal dynamics of the populations in a large number of real systems could permit this prediction to be tested. Alternatively, generalizations may eventually be possible concerning when certain forms of per-host recruitment patterns might be expected, for instance, in relation to taxonomic or life-history groupings of parasitoids. If so, such categorizations might be substituted for direct knowledge of recruitment dynamics to provide more (though less direct) data to test the predictions obtained from these models.

More generally, the fundamental message of this study, for future empirical

and theoretical work alike, is that attention must be paid to the dynamics of the parasitoid population. The major effects shown in this article suggest that the density dependence (or lack thereof) of parasitoid per-host recruitment is worth examining in future empirical attempts to understand the dynamics of real parasitoid-host interactions and also in theoretical explorations of the effects of other factors. In empirical studies, if per-host recruitment cannot be directly studied, the dynamics of parasitoid abundance, rather than simply parasitism, should at least be determined. At the very least, the results reported here indicate that theoretical conclusions based on an assumption that parasitoid yield does not vary with densities should be applied to real systems with considerable caution unless there is evidence to support this assumption.

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