

HOST-FEEDING AND OVIPOSITION BY PARASITOIDS IN RELATION TO HOST STAGE: CONSEQUENCES FOR PARASITOID-HOST POPULATION DYNAMICS

N. A. C. KIDD and M. A. JERVIS

School of Pure & Applied Biology, University of Wales College of Cardiff, P.O. Box 915,
Cardiff CF1 3TL, Wales, U.K.

SUMMARY

Among parasitoids which host-feed destructively, there is a tendency for females to partition their feeding and oviposition behaviour in relation to different host stages, feeding preferentially or exclusively on earlier host stages and ovipositing preferentially or exclusively in (or on) later ones. We explored the dynamic implications of this behaviour for parasitoid-host population dynamics, using modifications of the age-structured simulation models of Kidd and Jervis (1989, 1991).

Using the new versions of the models, we compared the situation where parasitoids practice host stage discrimination with respect to feeding and oviposition, with the situation where they do not. Additionally, we examined the effects of host stage discrimination on populations by (a) having generations either discrete or overlapping, (b) varying initial age structure, (c) having varying degrees of density dependence acting on host adult mortality, and (d) varying parasitoid development times in relation to the length of host development.

With either discrete or overlapping generations of the host population, a reduction in the parasitoid development time had a destabilizing influence on the parasitoid-host population interaction. With discrete generations stage discrimination had no effect on the risk of extinction, irrespective of either the degree of density dependence acting on the host population, or the initial age structure of the host population. When parasitoid search was uncoupled from the insect's adult energy requirements, the interaction was always unstable. With continuous generations, stage discrimination affected stability at certain parasitoid development times, but not at others. The relative lengths of parasitoid and host development times also influenced the tendency of the host population to show discrete or overlapping generations.

KEY WORDS: parasitoids, host-feeding, oviposition, population dynamics, modelling

INTRODUCTION

Host-feeding—the consumption of host materials by adult female parasitoids—is an apparently widespread habit amongst insect parasitoids, having been recorded in several families of Hymenoptera (Jervis and Kidd, 1986) and in the Dipteran family Tachinidae (Nettles, 1987). Among those parasitoids which feed destructively upon hosts there is a tendency for females to partition their feeding and oviposition behaviour in relation to different host stages. This divergence in host stage utilization often takes the form of feeding preferentially or exclusively on earlier host stages and of ovipositing preferentially or exclusively in (or on) later ones (Kidd and Jervis, 1991).

In a recent paper (Kidd and Jervis, 1991) we explored, using computer simulation models, the relative advantages to host-feeding parasitoids of a number of possible host stage selection strategies. We concluded from these models that the advantage to be gained from feeding on earlier host stages and ovipositing in later ones is likely to be associated with: 1) reduced handling times of feeding on early stage hosts; 2) reduced wastage of progeny from factors other than host-feeding by the parent parasitoid, by confining oviposition to late host stages; and 3) reduced probability of progeny mortality resulting from the parent's host-feeding activities.

The partitioning of feeding and oviposition in relation to host stage also has potentially important practical and theoretical implications for parasitoid-host population dynamics. For example, biological control workers already recognize that some parasitoid introductions may fail unless a suitable age structure is present in the host population. Hussey (1985) noted that where *Encarsia formosa* Gahan attacks a whitefly population with a preponderance of young stages, the mortality from host-feeding may prevent the whitefly population from increasing, so preventing the establishment of the parasitoid. Equally likely, the lack of older host stages for oviposition can contribute to parasitoid failure.

One important theoretical implication of partitioning behaviour arises from recent work showing that in host populations with overlapping generations an age class invulnerable to parasitism can act as a stabilizing mechanism, but at the same time raising the host equilibrium (thereby interfering with pest suppression) (Murdoch, 1989; Murdoch et al., 1987). It therefore seems likely that in the case of host-feeding parasitoids, invulnerability of some stages to parasitism and others to feeding could have equally interesting dynamic consequences.

In this paper we therefore explore the dynamic implications of stage discrimination for parasitoid feeding and oviposition, using modifications of our earlier age-structured simulation models for host-feeding parasitoids (Kidd and Jervis, 1989, 1991).

THE SIMULATION MODELS

The modelling approach we have adopted is described in detail in an earlier paper (Kidd and Jervis, 1989), so we present only a summarized version here. The models simulate the dynamic interaction between an all-female population of parasitoids and a host population, the individuals of which they may use for either feeding or oviposition. A time-step of one day was used with the host population (N) consisting of a set number of 1-day age groups (eggs, larvae and reproducing adults) with a reproductive rate of R eggs/adult/day. All adult hosts were assumed to be female and to reproduce at the same rate irrespective of age. A density-dependent mortality factor acted on each adult age group prior to reproduction, taking the form:

$$S_i = 1 - b(\log X_i + 1)$$

where X was the density of adults in the i -th age group, and b , the coefficient of density-dependence, took values between 0.1 and 0.25 in the simulations, the higher the value the greater the density-dependent mortality.

The parasitoids also comprised a number of 1-day age groups of developing larvae and a population of adults (P) whose longevity was dependent on available energy reserves. Each parasitoid was made to search at random for hosts distributed at random amongst a previously defined number (LOC) of host locations (0 or 1 host individual per location). The probability of encounter between an adult parasitoid and a suitable host (larva) of particular age (I) was thus given by $N(I)/LOC$, and the outcome of search determined by a random number generator. Each location searched involved the expenditure of a number of units of energy for search and maintenance, but energy stocks could be replenished by host-feeding instead of oviposition. A constant amount of energy (HE) was gained from feeding on each host. The decision whether to oviposit or feed on an encountered host was determined partly by available energy reserves (T) and partly on the probability of encounter (P_e), with oviposition occurring above a certain threshold value of ' T ' and feeding below it. The type of host-feeding exhibited by the parasitoids was thus "non-concurrent destructive", according to the terminology proposed by Jervis and Kidd (1986). Death of an adult parasitoid occurred when its energy reserves fell below the level required to sustain maintenance and search.

In the most advanced versions of our earlier models, critical shortage of energy resources could be circumvented at least temporarily by resorption of mature eggs, an adaptation which has been widely observed in synovigenic parasitoids (Jervis and Kidd, 1986). We were able to show, however, that this trait, together with egg limitation, has an important destabilizing influence on the parasitoid-host interaction (Kidd and Jervis, 1989). Thus to avoid the complicating effects of these factors obscuring answers to the questions of current interest, our present models assume an unlimited egg supply and no egg resorption.

The parasitoids searched sequentially by a queuing system, the process being repeated continuously until all the parasitoids had used up their total time allocation for the day. Each parasitoid was allowed 10 hours of searching time each day, "efficiency of search" also being constrained by handling times (assumed constant) for feeding and oviposition.

In our previous models (Kidd and Jervis, 1989) the parasitoids simply treated all of the host larval age groups as a homogeneous resource, feeding and ovipositing indiscriminately in each. Here, we are interested in comparing this situation with that in which parasitoids discriminate between early and later larval stages, feeding exclusively in the former and ovipositing exclusively in the latter. In each simulation, we therefore presented four 1-day larval age groups to the parasitoid. In the stage discrimination treatments, host-feeding was confined to larval stages 1 and 2, and oviposition to stages 3 and 4, except in one important respect. If encounters with age groups 3 and 4 coincided with energy reserves falling below the threshold (T), then the parasitoids were forced to feed instead of oviposit. In one series of simulations, however, we removed this exception to examine the case of complete discrimination irrespective of energy levels.

Complete discrimination between stages, as we have portrayed it in our models may, however, be rare in nature. Our survey of the literature in Kidd and Jervis (1991) suggests that among host-feeding parasitoids there is a tendency for females to prefer feeding on early stage hosts and ovipositing on later stage ones, but there may be considerable overlap. Our models deliberately exaggerate this tendency into complete discrimination in order to highlight any interesting dynamic consequences.

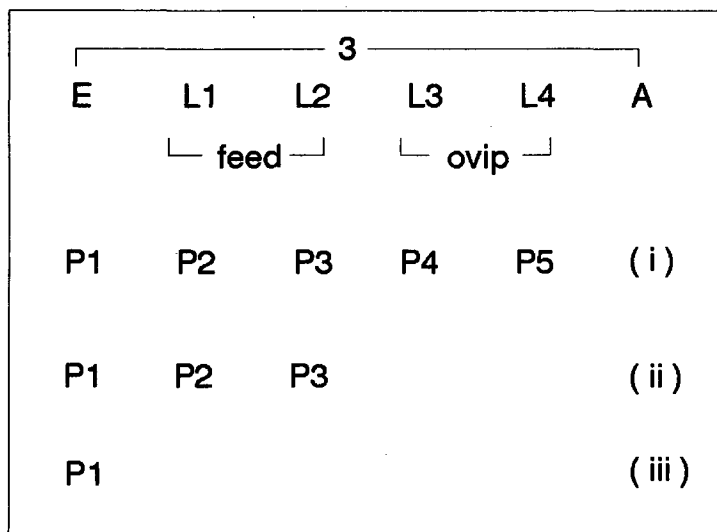
To achieve a comprehensive analysis we also examined the effects of stage discrimination on populations by (a) having generations either discrete or overlapping, (b) varying initial host age structure, (c) having varying degrees of density dependence acting on host adult mortality, and (d) varying parasitoid development times in relation to the length of host development.

RESULTS

Discrete Generations

To produce a host population with discrete generations egg development was set to 1 day, larval development to 4 days and adult lifespan to 1 day, with 3 eggs produced per day (Fig. 1a). This gave a total development time of 5 days and a lifespan of 6 days. Initially, parasitoid development was also set at 5 days, but we later tested the effects of changing this to 3 days and 1 day respectively (see Fig. 1a). Fifteen simulations were run over 100 days for each treatment and the proportion of interactions which resulted in the "extinction" of parasitoid or host was calculated. Extinction, in the present context, meant the elimination of either population, or alternatively, a density of >200 parasitoids (overexploitation).

a.



b.

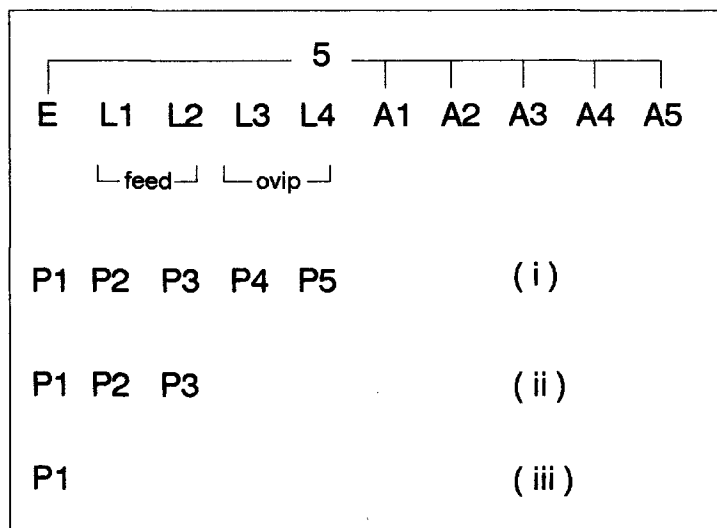


Fig. 1. The life history characteristics of the host used to generate (a) discrete host generations, (b) continuous host generations. E=host eggs; L1-L4=host larval age groups; A=host adult age groups. i-iii=the variations in parasitoid development time (P1-P5) examined.

Whether the parasitoids discriminated or not between host age groups for feeding and oviposition was found to have no significant effect on the proportion of populations which became extinct. This was so irrespective of the degree of density dependence acting on the interaction (Fig. 2; $P > 0.05$ for all χ^2 and Fisher exact tests), and of the

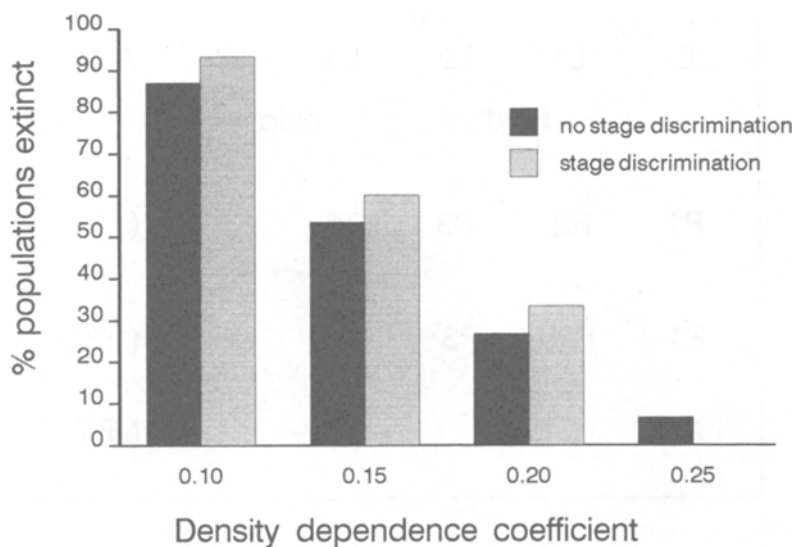


Fig. 2. The effect of stage discrimination on the proportion of population interactions ($n=15$) becoming extinct during 100 days at different levels of density dependent mortality acting on the host.

initial age structure of the population (Fig. 3; $P>0.05$ for all χ^2 and Fisher exact tests). The population interactions typically showed numerical fluctuations on 2 scales—primary fluctuations corresponding to generation turnover and secondary fluctuations induced by the parasitoid (Fig. 4). These secondary fluctuations either increased or decreased in amplitude depending on the degree of density-dependence, while the ratio of parasitoid/host numbers always remained low, a characteristic of host-feeding parasitoids (Kidd and Jervis, 1989).

In these simulations a density-dependence coefficient of 0.15 resulted in extinction in approximately 50% of interactions. To examine the effects of further modifications to the discrete host generation model, we used the simple expedient of holding the coefficient at 0.15 and again noting the proportion of interactions becoming extinct. Increases in the proportion of extinctions indicated a reduction (and decreases an improvement) in the stability or persistence of the interactions.

Energy-independent age group discrimination. When parasitoids fed only on larval age groups 1 and 2, and oviposited only in age groups 3 and 4 (i.e. complete discrimination irrespective of energy levels) the interactions invariably resulted in the extinction of the parasitoid population, usually within 20 days. This significant decrease in the stability and persistence of the interaction was a consequence of uncoupling the decision whether to feed or oviposit from the parasitoid's immediate energetic needs whilst searching. It is clearly in the parasitoid's interests to retain some degree of flexibility over which age groups it feeds on, in order to avoid premature death and a consequent reduction in fitness. This flexibility in feeding behaviour of the parasitoid

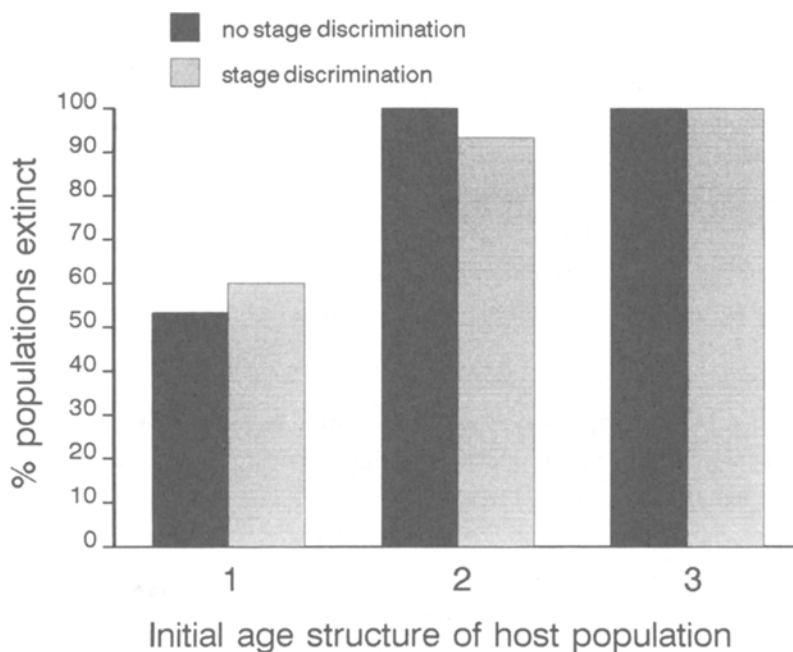


Fig. 3. The effect of stage discrimination on the proportion of population interactions ($n=15$) becoming extinct during 100 days with an initial host age structure of (1) 0, 200, 0, 0, 0, 0; (2) 100, 50, 20, 10, 5, 2; (3) 30, 30, 30, 30, 30, 30 in each age group respectively.

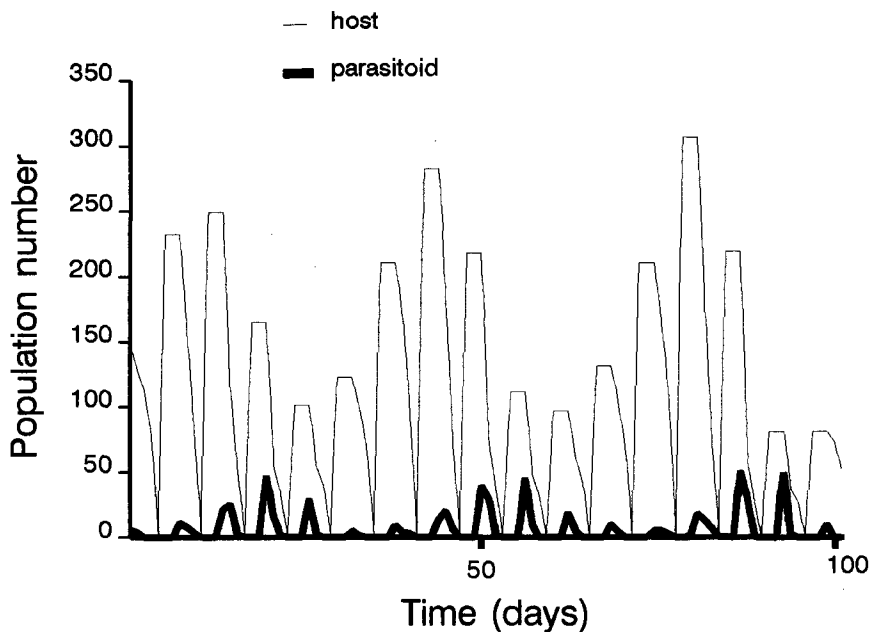


Fig. 4. A typical population interaction between the parasitoid and host, the latter with the discrete generation life history characteristics shown in Fig. 1a (i) and the following initial conditions: Age structure = 0, 200, 0, 0, 0, 0; $P=12$; density dependence coefficient = 0.15.

would also appear to be an important stabilizing influence on the population interaction with its host.

The effect of parasitoid development time. To test how varying the parasitoid's development time might influence the interactions, we ran one series of simulations with a parasitoid development time of 3 days and another with a development time of 1 day (see Fig. 1a). In all cases, irrespective of whether the parasitoids discriminated between age groups or not, the interactions resulted in extinction. Also, varying the initial age structure of the host population (following Fig. 3), made no difference. The interactions again invariably resulted in extinction.

Overlapping Generations

To produce a host population with overlapping generations we expanded the number of host age groups to 10, whilst retaining a development time of 5 days. The five host adult age groups reproduced at a rate of 1 egg/adult/day (Fig. 1b). In these simulations the density-dependent coefficient used to stabilize the interactions was 0.25. In the absence of parasitism, host population growth conformed to an approximately logistic model, initial minor irregularities caused by different numbers

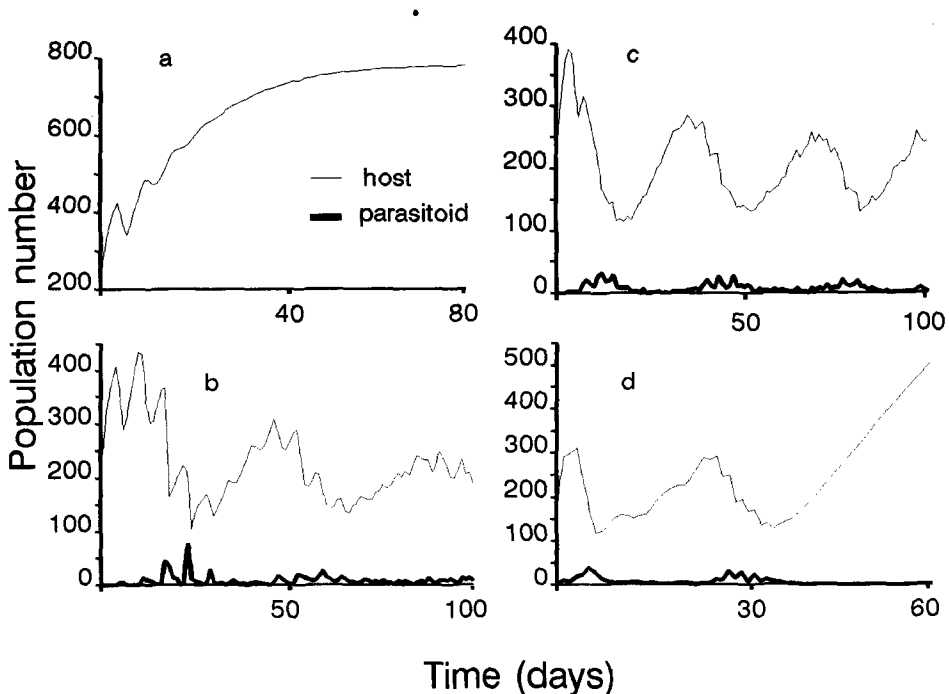


Fig. 5. Population interactions between parasitoid and host, the latter with the continuous generation life history characteristics shown in Fig. 1b and a density-dependent mortality coefficient of 0.25. Host dynamics (a) in the absence of the parasitoid, and (b–d) in the presence of the parasitoid, with different parasitoid development times: (b) 5 days, (c) 3 days, and (d) 1 day. (same initial conditions throughout).

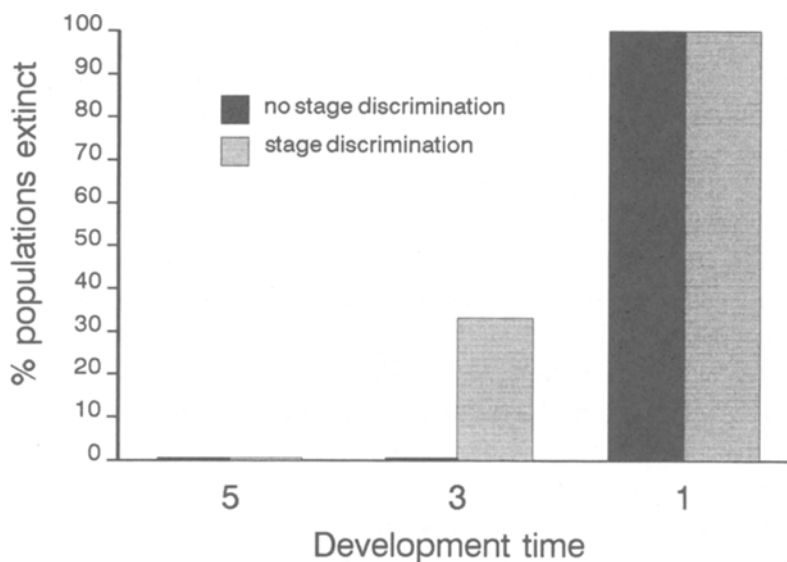


Fig. 6. The effect of stage discrimination on the proportion of population interactions ($n=12$) becoming extinct during 100 days, where parasitoid development time varied between 1 and 5 days.

in each are group damping out as the population achieved a stable age distribution (Fig. 5a).

The presence of the parasitoid, however, induced complex fluctuations in the numbers of both populations—a) primary fluctuations of approximately 30 time units periodicity, damping with time, and b) secondary fluctuations corresponding initially to the generation time of the host and parasitoid (5 time units), but becoming more erratic as time progressed (Fig. 5b).

The effect of parasitoid development time. Reducing the development time of the parasitoid relative to that of the host had two effects—a) a progressive destabilization of the interaction (Figs. 5c, d) and b) a reduction in the secondary generation time fluctuations (compare Figs. 5b, c, d).

Parasitoid development time also affected the stability of the interaction through stage discrimination, but only at certain restricted values. For example, stage discrimination with respect to feeding and oviposition had no effect on the proportion of extinctions at parasitoid development times of 5 and 1 time units, whereas it did when the parasitoid larval development time was 3 time units (Fig. 6; Fisher exact test $P=0.046$).

DISCUSSION

It needs to be emphasized at this point that our models are somewhat oversimplified, in that synovigeny (including egg resorption and egg limitation) are

omitted. These components have, as we have previously shown (Kidd and Jervis, 1989), important destabilizing influences. Therefore, their effects needed to be excluded in the present analysis to prevent them from obscuring the possible effects of stage discrimination. In the absence of synovigeny, the following major effects become apparent.

Firstly, with either discrete or overlapping generations of the host population, a reduction in the parasitoid development time had a destabilizing influence on the interaction. Secondly, there is the potential of host stage discrimination to influence dynamics. With discrete generations stage discrimination had no effect on the risk of extinction, irrespective of either the degree of density dependence acting on the host population, or the initial age structure of the host population. When parasitoid search was uncoupled from the insect's adult energy requirements, however, the interaction was always unstable.

With continuous generations, stage discrimination affected stability at certain parasitoid development times, but not at others. The relative lengths of parasitoid and host development times were also found to influence the tendency of the host population to show discrete or overlapping generations. Whilst this result was qualitatively similar to those of Godfray and Hassell (1989), our findings nevertheless differed in detail. This is perhaps not too surprising in that our model was constructed differently and incorporated different assumptions, in particular, that adult lifespan is open-ended rather than fixed (see below).

Data obtained for the dryinid wasp *Dicondylus indianus* Olmi (Sahragard et al., 1991) and the chalcid *Aphelinus asychis* Walker (Mackauer, 1982) suggest a lengthening of adult reproductive lifespan when hosts are relatively scarce (but not rare). Also, in both of these host-feeding species (and, interestingly, in the non-host-feeding dryinid *Aphelopus atratus* (Dalman) (L. Munroe, unpublished data)) the period of intensive egg-laying tends to be shorter at relatively high host densities than at low ones, i.e. there is a shift in the fecundity schedule of the parasitoid towards an earlier age. Lengthening of reproductive lifespan was shown by the models of Godfray and Hassell (1989) to promote continuous generations in a host population, while short reproductive lifespans promote discrete generations. Therefore, in the above-mentioned parasitoid species, it is possible that adult lifespan may be reciprocally decreased at high host densities, thus promoting discrete generations. In our models we take account of this tendency, in as much as adult parasitoid lifespan can be prolonged at low host densities by an increase in host-feeding activity at the expense of oviposition. There is indeed some evidence from the population cycles shown in Fig. 5 to suggest that the discretization of generations is promoted at higher host densities, and suppressed at low host densities.

As mentioned in our introduction, the presence in a continuous-generation host population of an age class invulnerable to parasitism will promote stability, according to models developed by Murdoch et al. (1987). We can also demonstrate this in our

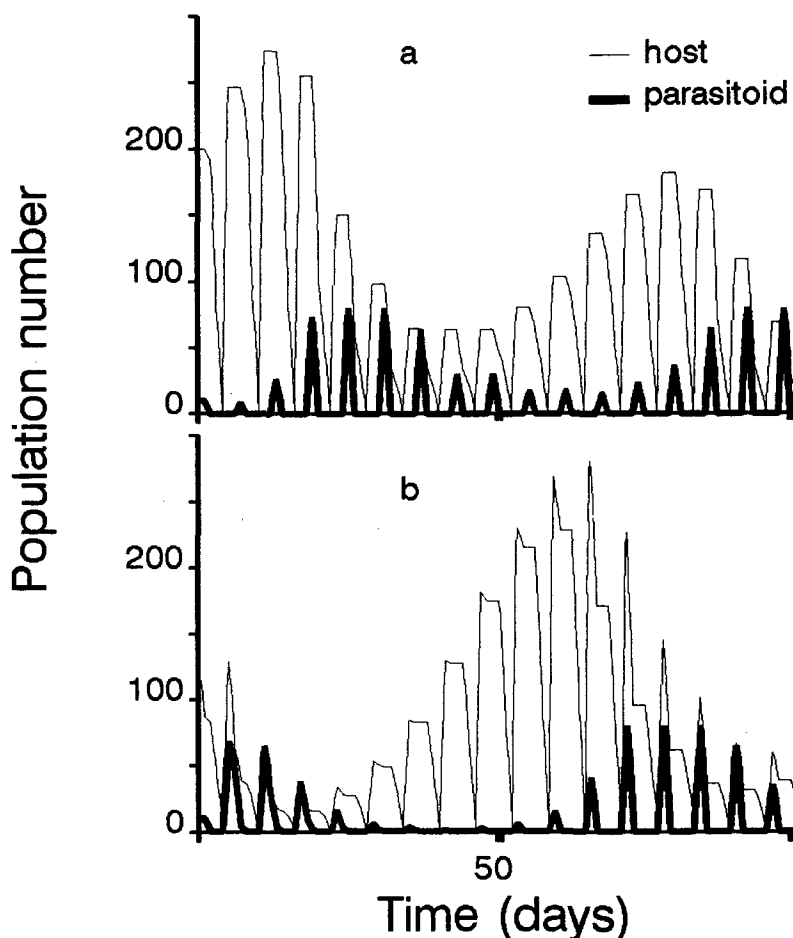


Fig. 7. Typical interactions between the parasitoid and a continuous generation host population with (a) age groups 1, 2 and 3 invulnerable to parasitism, and (b) all age groups vulnerable to parasitism. (No host-feeding)

present models. Stability occurs where parasitoids oviposit only in late stages (Fig. 7a), while the interaction is unstable in the case where all larval stages are attacked (Fig. 7b). The invulnerable age class theory would thus appear to provide some potential insights into the stabilizing effects of host-feeding through stage discrimination. In effect, by feeding on age classes unused for oviposition, which is the tendency amongst destructive host-feeders (Kidd and Jervis, 1991) the parasitoid increases the vulnerability of the host to mortality, thus decreasing stability. However, there are dangers inherent in drawing such parallels with Murdoch et al.'s (1987) studies. One of the major reasons why destructive feeders prefer to oviposit in late stage hosts is to avoid destructively feeding on their own progeny. Non-host feeding parasitoids, on the other hand, may oviposit specifically in any one or a number of host stages, as even a cursory examination of the literature can demonstrate

(Clausen, 1940; Askew, 1971). It is therefore unrealistic to compare a stage discriminating host-feeding parasitoid with a non-host-feeder. It is only strictly appropriate to compare a stage discriminating host-feeder with one that does not practice discrimination. The implications of this comparison for stability have already been fully explored.

In conclusion, we hope to have shown that the tendency for destructively host-feeding parasitoids to partition their feeding and oviposition behaviour to different host stages has potentially important consequences for parasitoid-host population dynamics. Parasitoids that display such behaviour include some important biological control agents e.g. *Epidinocarsis lopezi* (De Santis), a parasitoid of the cassava mealybug, *Phaenococcus manihoti* Matile-Ferrero (Neuenschwander and Madojemu, 1986). The tendency for host-feeding parasitoids to stage-discriminate may ultimately prove to be an important criterion, at least under certain restricted circumstances (see above), in the selection of biological control agents.

REFERENCES

- Askew, R. R. (1971) *Parasitic Insects*. Heinemann, London.
- Clausen, C. P. (1940) *Entomophagous Insects*. McGraw-Hill, New York.
- Godfray, C. J. and M. P. Hassell (1989) Discrete and continuous insect populations in tropical environments. *J. Anim. Ecol.* **58**: 153–174.
- Hussey, N. W. (1985) Whitefly control by parasites. 104–115. In N. W. Hussey and N. Scopes (eds). *Biological Control: the Glasshouse Experience*. Blandford Press, Poole.
- Jervis, M. A. and N. A. C. Kidd (1986) Host-feeding strategies in hymenopteran parasitoids. *Biol. Rev.* **61**: 395–434.
- Kidd, N. A. C. and M. A. Jervis (1989) The effects of host-feeding behaviour on the dynamics of parasitoid-host interactions, and the implications for biological control. *Res. Popul. Ecol.* **31**: 235–274.
- Kidd, N. A. C. and M. A. Jervis (1991) Host-feeding and oviposition strategies of parasitoids in relation to host stage. *Res. Popul. Ecol.* **33**: (in press).
- Mackauer, M. (1982) Fecundity and host utilization of the aphid parasite *Aphelinus semiflavus* (Hymenoptera: Aphelinidae) at two host densities. *Can. Ent.* **114**: 721–726.
- Murdoch, W. W. (1989) The relevance of pest-enemy models to biological control. 1–24. In M. Mackauer, L. E. Ehler and J. Roland (eds) *Critical Issues in Biological Control*, Intercept, Andover.
- Murdoch, W. W., R. M. Nisbet, S. P. Blythe, W. S. C. Gurney and J. D. Reeve (1987) An invulnerable age class and stability in delay-differential parasitoid-host models. *Am. Nat.* **129**: 263–282.
- Nettles, W. C. (1987) *Eucelatoria bryani* (Diptera: Tachinidae): Effect on fecundity of feeding on hosts. *Environ. Entomol.* **16**: 437–440.
- Neuenschwander, P. and E. Madojemu (1986) Mortality of the cassava mealybug, *Phaenococcus manihoti* Mat.-Ferr. (Hom., Pseudococcidae), associated with an attack by *Epidinocarsis lopezi* (Hym., Encyrtidae). *Mitt. Schweiz. Ent. Gesell.* **59**: 57–62.
- Sahragard, A., M. A. Jervis and N. A. C. Kidd (1991) Influence of host availability on rates of oviposition and host-feeding, and on longevity in *Dicondylus indianus* Olmi (Hym; Dryinidae), a

parasitoid of the Rice Brown Planthopper, *Nilaparvata lugens* Stål (Hem; Delphacidae). *J. app. Ent.* (in press).

寄主の発育段階に依存する捕食寄生者の寄主摂食および産卵行動：
寄生者-寄主の個体群動態への影響

N. A. C. KIDD · M. A. JERVIS

破壊的に寄主摂食をする捕食寄生者は、その摂食と産卵行動を寄主の発育段階に応じて振分ける傾向がある。つまり、前の段階を好んで(あるいは専門的に)食い、後の段階に好んで(あるいは専門的に)産卵する。我々は、Kidd and Jervis (1989, 1991) の令構成シミュレーションモデルを修正して、この行動が寄生者-寄主の個体群動態にどう影響するかを調べた。

修正モデルを使って、寄生者が寄主の発育段階を区別して摂食と産卵を振分ける場合とそうでない場合を比較した。さらに、(a) 離散世代と重複世代、(b) 初期令構成、(c) 寄主の成体死亡率の密度依存性の程度、(d) 寄主の発育段階によって生じる寄生者の発育期間、を変えて寄主の発育段階を区別することが個体群動態にどう影響するかを調べた。

寄主個体群が離散世代であるか重複世代かにかかわらず、寄生者の発育期間の短縮は、寄生者-寄主の個体群相互作用を不安定化する効果があった。離散世代のときは、寄主個体群の密度依存性の程度や初期令構成がどうであろうと、発育段階を区別することは捕食寄生者の絶滅確立に全く影響しなかった。寄生者の探索行動がエネルギー要求と無関係だとすると、相互作用は常に不安定となった。連続世代のときは、寄生者がある範囲の発育期間をとるときに、発育段階の区別が個体群の安定性に影響したが、別の発育期間ではそうならなかった。また、寄生者と寄主の発育期間の相対的な違いは、寄生個体群が離散世代か連続世代のどちらになりやすいかに影響した。