Individual behaviour and population dynamics: lessons from aphid parasitoids

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Abstract

An increasing number of researchers are studying behaviour in the hopes of understanding population dynamics or improving biological control efforts of insect pests by natural enemies. However, it is unclear exactly how behavioural studies will improve our understanding of these population level processes. In this paper we argue that in order to understand population level processes, the problem must be approached from a population biology perspective. A comprehensive understanding of certain behaviours will provide little towards our understanding of host-natural enemy interactions. For example, using an aphid-parasitoid model, we examined the effect that a commonly studied behaviour, variance in host selection by aphid parasitoids, has on aphid-parasitoid population dynamics. Differential host selection does not qualitatively alter classic Nicholson-Bailey dynamics, but only results in quantitative differences in aphid-parasitoid population sizes. Irrespective of the degree of aphid instar preference, a large increase in the number of aphids is followed by a large increase in the number of parasitoids, decimating the aphid population. Thus, studying some behaviours, such as variance in host selection, will not contribute substantially to an understanding of aphid-parasitoid population dynamics.

Introduction

Aphid population dynamics have long been of interest to scientists and crop producers alike, because of the destruction aphids cause in agricultural crops. Not only do aphids remove phloem from the plants, but they are also capable of transmitting plant viruses (Taylor, 1986). Natural enemies such as predators, parasitoids, and hyperparasitoids can also be found in the agro-ecosystem, resulting in complex host and natural enemy population dynamics (Horn, 1989). Thus, if our goal is to better understand these population level processes, either from a strictly ecological standpoint or as a means of improving biological control efforts, how do we go about elucidating these complex population processes?

One approach, which we could term ‘bottom-up’, focuses on host and/or natural enemy behaviours in an effort to understand population dynamics. Three key events have occurred in the past 40 years that have directed our attention towards the importance of behavioural processes in population processes. First, C.S. Holling introduced the notion of the functional response (Holling, 1966). He showed that a few easily observed behavioural components could be used to determine predation rates. Secondly, Hassell and associates reevaluated Nicholson-Bailey models and demonstrated how various behavioural components could stabilize host-parasitoid interactions (Hassell, 1971). Finally, the introduction of behavioural ecology showed that natural enemy behaviour could be deduced by functional analyses, i.e., from an evolutionary perspective (Krebs & Davies, 1978). For example, optimal foraging theory, a sub-field of behavioural ecology, has been instrumental in deriving host acceptance theory for a broad range of predators and parasitoids.

These three events, among others, have caused us to consider behaviour more seriously than we might have otherwise. For example, there have been liter-
ally thousands of behavioural studies (e.g., functional response studies) conducted under the guise of better understanding population dynamics or improving biological control, but in many cases it is unclear exactly how these studies achieve this goal. In fact, we believe that in some instances population dynamicists and biological control practitioners have focused so strongly on behaviour, that they may have ‘missed the forest while focusing on the trees’.

In this paper, we argue that in order to understand host-natural enemy population level processes, it is essential to start with a ‘top-down’ perspective. The problem must initially be approached from a population biology perspective, by building general models of parasite-host interactions that incorporate descriptors of behaviour that facilitate these interactions. This is followed by numerical analysis, and if a particular behaviour is identified as a key component, only then should a detailed analysis be initiated. For in some instances, even detailed knowledge of certain behaviours will not provide us with any additional understanding of population level processes. Further, it is not prudent to assume that simply by studying different behaviours and assembling them into a cohesive unit that one can achieve a comprehensive understanding of population or community level processes.

Materials and methods

Part 1: The standard model

We constructed a simulation model based roughly on the Acyrthosiphon pisum–Aphidius smithi system, although we are not claiming exact duplication. Our intent in constructing this model was not to duplicate nature, but rather, to use the model as a tool to determine how knowledge of a particular behaviour affects our understanding of population level processes. Using this model, we manipulated only one behavioural component of host exploitation, variance in host selection. We then evaluated how this behaviour altered aphid-parasitoid population dynamics within a single season. This is a valid objective, since many aphid parasitoids are highly discriminating amongst instars (Mackauer & Völkl, 1993). Behavioural ecology also tells us that discrimination should vary under different circumstances (Mangel & Clark, 1988; van Alphen & Visser, 1990). Furthermore, aphid populations are age structured and any discrimination might effectively create stage or age specific refugia (Murdoch et al., 1987; Mangel & Roitberg, 1992), with the effect of small changes in behaviour culminating in large-scale changes in population dynamics.

To obtain moderate resolution, we broke our time scale into quarter-instar periods or quips (Frazer & Gilbert, 1976), which roughly translate into 12-h periods. We chose to run our model for a finite time of 500 quips, which is approximately 250 days. We ran the model for less than one year, to examine the population dynamics that would occur within a single growing season. Substantially different dynamics might be obtained if the model was set to run over many years. We chose to address single season dynamics, as this time frame is of key interest to producers and biological control practitioners.

Constants were employed for several model parameters (Table 1). Our next objective was to construct age structured models of an aphid and its parasitoid. To do this we constructed Lewis-Leslie matrices (Begon & Mortimer, 1986; Caswell, 1989) for both aphids and parasitoids. The aphid transition matrix and age distribution vector comprised 70 quips. Since aphid instars are 4 quips each, quips 1–16 characterized instars 1–4, quips 17–21 characterized pre-reproductive adults, and quips 22–70 characterized reproductive adults (Campbell, 1974). Age specific fecundity values for mature aphids were drawn from a fecundity schedule taken from lab studies by Mondor & Roitberg (unpubl.). Age specific survivorship was determined by the product of two processes: (i) constant age-specific survivorship ($\mu_b$) from background predation:

$$\mu_i = \mu_b - \bar{\psi}\phi,$$

where $\mu_b$ = background survivorship, $i$ = instar and $\phi$ = a constant, and (ii) age and circumstance dependent attacks by parasitoids as described below.

Three transition matrices were used to evaluate parasitoid dynamics, one for each parasitoid as a function of initial host instar, i.e., 2nd, 3rd or 4th instar. Each of those hosts produces parasitoids with different age-specific survivorship (Sequeira, 1991), hence a separate transition matrix and age distribution vector was developed for each parasitoid class. All parasitoid age distribution vectors consisted of 16 quips.

We assumed no parasitoid age specific fecundity in our model, that parasitoids were not egg limited (Mackauer & Völkl, 1993), and that parasitoids forage for 6 hours each day. Before each quip, parasitoids adjust their host selection preference to account for new host availability. The potential types of hosts
Table 1. A list of model parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
<th>References for parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival of adult aphids from predation per quip</td>
<td>$\mu_b$</td>
<td>0.95</td>
<td>Assumption</td>
</tr>
<tr>
<td>Holling’s search rate parameter</td>
<td>$\alpha$</td>
<td>0.0006</td>
<td>Mackauer, 1983</td>
</tr>
<tr>
<td>Mummy survival per quip</td>
<td>$\mu_m$</td>
<td>0.98</td>
<td>Assumption</td>
</tr>
<tr>
<td>Per quip survival of parasite adult reared from small host</td>
<td>$\mu_{sp}$</td>
<td>0.950</td>
<td>Sequeira, 1991</td>
</tr>
<tr>
<td></td>
<td></td>
<td>*0.898</td>
<td></td>
</tr>
<tr>
<td>Per quip survival of parasite adult reared from medium host</td>
<td>$\mu_{mp}$</td>
<td>0.895</td>
<td>Sequeira, 1991</td>
</tr>
<tr>
<td></td>
<td></td>
<td>*0.798</td>
<td></td>
</tr>
<tr>
<td>Per quip survival of parasite adult reared from large host</td>
<td>$\mu_{lp}$</td>
<td>0.954</td>
<td>Sequeira, 1991</td>
</tr>
<tr>
<td></td>
<td></td>
<td>*0.905</td>
<td></td>
</tr>
<tr>
<td>Reduces aphid fecundity as population grows in size</td>
<td>$\theta$</td>
<td>0.038</td>
<td>Assumption</td>
</tr>
<tr>
<td>Time required to parasitize a host</td>
<td>$t_o$</td>
<td>0.0013</td>
<td>Assumption</td>
</tr>
<tr>
<td>Time required to assess then reject a host</td>
<td>$t_r$</td>
<td>0.0005</td>
<td>Assumption</td>
</tr>
</tbody>
</table>

*Lab data were halved in the second run of the model to more accurately indicate parasitoid survivorship under field conditions.

Available to the parasitoids for oviposition, in order of acceptance as a function of host quality, are as follows: healthy (i.e., unparasitized) second instar, healthy fourth instar, healthy third instar, parasitized second instar, parasitized fourth instar, and parasitized third instar (Sequeira, 1991). A 70% drop in host value occurs between non-parasitized vs. parasitized same instar aphids (McBrien, 1991). In our model we assumed that first instar aphids would be inspected but rejected, and that adult aphids would be rejected at a distance and never inspected, although we realize that different authors report different instar preferences for parasitoids (Mackauer & Chow, 1986).

Aphid and parasitoid populations were then connected by employing a version of Holling’s Disc Equation, i.e., the functional response (Holling, 1966). Holling’s original version of the equation for one time unit is:

$$N_a = aN/(1 + aNt_h),$$

where $a$ = area of discovery, $t_h$ = handling time, and $N$ = number of hosts available.

In our system we have several host stages and varying levels of host discrimination, thus for any given stage, the functional response is:

$$NA_Q = \frac{aN_Q}{1 + a\sum_{Q=5}^{16} p_Qt_o + a\sum_{Q=5}^{16} (1 - p_Q)t_r},$$

where $a$ = search rate, $p$ = probability to parasitize, $t_o$ = time to parasitize, $t_r$ = time to reject.

For each quip we update the aphid and the parasitoid matrices, before beginning the next quip.

The model was run with fixed thresholds of acceptance (e.g., 2nd instars only, 2nds and 4ths, etc.). Under full acceptance, parasitoids oviposit in 2nd, 3rd, and 4th instar aphids, both unparasitized and parasitized. For each run of the model we computed the total number of aphids and parasitoids in each quip and we also calculated ‘cumulative damage’ estimates, which were roughly the number of aphid days of feeding on a crop. We use cumulative damage estimates as another indicator of the size of aphid populations in a single growing season. This information may be the most useful to growers as it provides an indicator of the level of crop damage that could be anticipated under the different aphid-parasitoid scenarios.

Note that we assume no explicit spatial structure to the environment aside from a uniform distribution of aphids across 100 plants. Under real field conditions, spatial structure may result in very different dynamics than we see in our simulation. However, our intention was to consider the dynamics arising directly from different levels of parasitoid discrimination. Thus, we chose to remove other ecological parameters and focus exclusively on population dynamics that result from changes in parasitoid exploitation behaviour.

Part 2: Reducing aphid fecundity and parasitoid survivorship

In a second run of the model, we analyzed the aphid-parasitoid population dynamics that result when halv-
Figure 1. Population dynamics of aphids and parasitoids under different levels of host acceptance: (a) 2nd instars, (b) 2nd and 4th instars, and (c) 2nd, 4th and 3rd instars, respectively.

Results

Part 1: The standard model

Variance in host selection by parasitoids did not qualitatively alter aphid or parasitoid population dynamics (Figure 1). However, both peak aphid numbers and peak parasitoid numbers declined as parasitoids became less choosy. Aphid populations also declined earlier in the season as parasitoids accepted more host instars in which to oviposit. Cumulative damage estimates also declined as parasitoids attacked more host instars (Table 2). Superparasitism had little effect on either qualitative or quantitative aphid-parasitoid dynamics. The numbers of aphids and parasitoids, and cumulative damage estimates, did not change substantially as parasitoids became less choosy, when all healthy instars were also selected. Given the relatively low oviposition and rejection times (28 and 11 s, respectively) and the very high eggloads (effectively unlimited in these simulations) a large population of parasitized aphids increases over time regardless of degree of discrimination. Upon emergence, the parasitoids eventually decimate the aphid population. Superparasitism does not appreciably change the overall dynamics because aphids are killed regardless of whether parasitized or superparasitized. Meanwhile only one parasitoid emerges from a host regardless of the number of parasitoid eggs placed in an aphid.

Part 2: Reducing aphid fecundity and parasitoid survivorship

Aphid and parasitoid dynamics were different from the original run of the model in one main way (Figure 2), aphid numbers increased more gradually and took longer to decline as opposed to our original model. This gradual increase and decrease in aphid numbers resulted in larger aphid cumulative damage estimates for all thresholds tested (Table 2). But, like the original runs, there was qualitatively no difference in the aphid-parasitoid dynamics under different fixed host selection thresholds. Once again, superparasitism had little effect on either qualitative or quantitative aphid-parasitoid dynamics.

Discussion

Irrespective of the values that we use for aphid fecundity or parasitoid longevity in our pea aphid-Aphidius model, what we generate is classic predator-prey population dynamics (Hassell, 1978). The aphid population grows rapidly, the parasitoid population lags behind but eventually begins to grow and it reduces the aphid population to near zero, at which point the parasitoids also decline in number because there are so few hosts left to parasitize. Variation in host
Figure 2. Population dynamics of aphids and parasitoids under different levels of host acceptance: (a) 2nd instars, (b) 2nd and 4th instars, and (c) 2nd, 4th and 3rd instars, respectively, when aphid fecundity and parasitoid survivorship were halved.

Selection by parasitoids has relatively minor effects on within-season aphid-parasitoid population dynamics, although it may be important with respect to the amount of crop damage done by aphids. As parasitoids become more choosy, crop damage (as measured in the cumulative number of days of aphid feeding) increases dramatically.

It was surprising that degree of host acceptance had so little impact on aphid-parasitoid population dynamics. We originally believed that invulnerable aphid instars would have a larger effect on aphid-parasitoid dynamics, for as previously mentioned, other studies have shown that the presence of invulnerable classes of individuals can lead to large changes in population level processes. For example, while examining the long term stability of predator-prey interactions, both Murdock et al. (1987) and Mangel & Roitberg (1992) found that invulnerable age classes could have dramatic effects on Nicholson–Bailey dynamics, ranging from stable cycles to chaotic numerical change.

While we were focusing more specifically on short term mean host and parasitoid densities, we believe that our aphid-parasitoid system also has fundamental differences from these previous studies, resulting in much different aphid-parasitoid dynamics. In our model, it takes 8 days (16 quips) to go from a parasitoid egg to an adult, and during that time, more and more aphids are being produced that serve as hosts for parasitoids. The parasitoid population builds up until eventually they reach such high numbers that they decimate the entire aphid population. The large number of parasitoids far outweighs any effects that behaviour (i.e., discrimination), might place on the system. Furthermore, unlike the aforementioned studies, the vulnerable age class comes in the middle of the host’s life cycle. Aphids that are invulnerable when young, must still proceed into the vulnerable age classes. Fewer and fewer adult aphids make it through the vulnerable stages without being parasitized, as the number of parasitoids increases. And indeed, it is just these types of dynamics that have been seen in field studies of aphid populations (e.g., Gilbert & Hughes, 1971).

It is important to clarify that some behaviours may be very important for aphid-parasitoid population dynamics. For example, immigration/emigration may function in an analogous manner to a spatial refuge, which may allow populations of aphids to persist, when others aphid populations have been decimated (Weisser et al., 1997). Thus, our model may be questioned on the grounds that it was so simplistic as to not represent what is really happening under field conditions. What happens if we put in more realistic descriptors from nature (e.g., physical structure to the field)? That is exactly the point: amalgamating behaviours may not give appropriate population dynamics without some means of scaling up from individuals to the population level.

As we mentioned at the outset, our contention is that it is important to study population level processes from a population biology perspective, and if a behaviour turns out to be important, then detailed studies of that particular behaviour are warranted. Behaviour can be very important to population level processes and understanding the efficacy of biological control agents, but before researchers study everything about a natural enemy they should first think about the context within which their study is initiated.
Table 2. Cumulative damage estimates for altered parasitoid host selection behaviour

<table>
<thead>
<tr>
<th>Variance in host selection behaviour</th>
<th>Cumulative damage (aphid days)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Part 1: The standard model</strong></td>
<td></td>
</tr>
<tr>
<td>Unparasitized instar 2 accepted</td>
<td>550,000</td>
</tr>
<tr>
<td>Unparasitized instar 2, 4 accepted</td>
<td>355,000</td>
</tr>
<tr>
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<tr>
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<tr>
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<tr>
<td>Unparasitized instar 2, 4, 3 accepted, Parasitized 2, 4, 3 accepted</td>
<td>195,000</td>
</tr>
<tr>
<td><strong>Part 2: Reducing aphid fecundity and parasitoid survivorship</strong></td>
<td></td>
</tr>
<tr>
<td>Unparasitized instar 2 accepted</td>
<td>1,350,000</td>
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<tr>
<td>Unparasitized instar 2, 4 accepted</td>
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</tr>
<tr>
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References


