Generation Time Ratios—Determinants of Prey Abundance in Insect Predator–Prey Interactions

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The potential fitness of an adult insect predator depends mainly on the future trends in resource availability throughout the period of development of its larvae, because they, unlike the adult, are confined to a patch. Thus, adult oviposition strategy is likely to be determined by the bottlenecks in resources that occur during the period of its offsprings' development. Therefore, the longer the developmental time of a predator, the smaller the degree of depletion of the patch by that predator species. As a consequence, the relative "efficiency" of predators as biological control agents is negatively correlated with their generation time relative to that of their prey. © 1999 Academic Press

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INTRODUCTION

There is an increasing awareness of the importance of individual behavior in population dynamics (Luck, 1990). If the predictions of optimal foraging theory are incorporated into classical predator–prey models, certain phenomena accounted for by these models are explained and therefore the models become much more realistic (Kacelnik *et al.,* 1992). In optimal foraging theory, the predator revenue per unit time is maximized based on the present quality of the patch (Stephens and Krebs, 1986). This neglects an important fact: predators breed in the patches and the optimum foraging strategy may therefore depend not only on the present state of a patch of prey but also, and maybe more importantly, on the quality of the patch in the future. This is especially relevant when considering arthropod predators, including the polyphagous, whose larvae are confined to a patch for the duration of their development. The fitness of the larvae depends on the future patch quality. Here we discuss the consequences of the future trends in the patch quality for the optimal foraging strategy of a predator and subsequently for predator–prey population dynamics.

CONSEQUENCES OF PATCH QUALITY PROJECTION FOR PREDATOR–PREY POPULATION DYNAMICS

The oviposition strategy of arthropod predators, and their evolutionarily stable number of eggs laid per patch, depends on the larval competition curve, defined as larval survival multiplied by their adult fecundity if they are females or by mating success if they are males (Ives, 1989). The larval competition curve, however, depends primarily on bottlenecks in prey abundance during larval development, particularly the periods when the expected prey abundance is lowest (Dixon and Kindlmann, 1995; Hemptinne *et al.,* 1993). The optimum oviposition strategy is therefore determined mainly by expectations of future bottlenecks in prey abundance. The strategy of a predator with a long larval developmental time will depend on a longer projection of the future prey abundance in the patch and will therefore include more bottlenecks or higher probability of a bottleneck than a predator with a short developmental time (Fig. 1). Thus, assuming that everything else is the same, including the degree of prey depletion during the bottlenecks, a predator with a short developmental time can deplete the prey more than a species with a relatively long developmental time. In general, changes in numbers of individuals tend to be large if generation time of the species is short and vice versa, because short-living species are able to complete more generations per unit time than long-living species. Therefore, the longer the developmental time of a predator relative to that of its prey, the less finely it can follow the prey density and therefore the smaller the degree to which it can deplete a patch. Interestingly, Godfray and Hassell (1987) also stressed, in a different context, that the generation times of prey and predator have potentially important implications for biological control. Their simulations indicate a slight increase in pest equilibrium population density
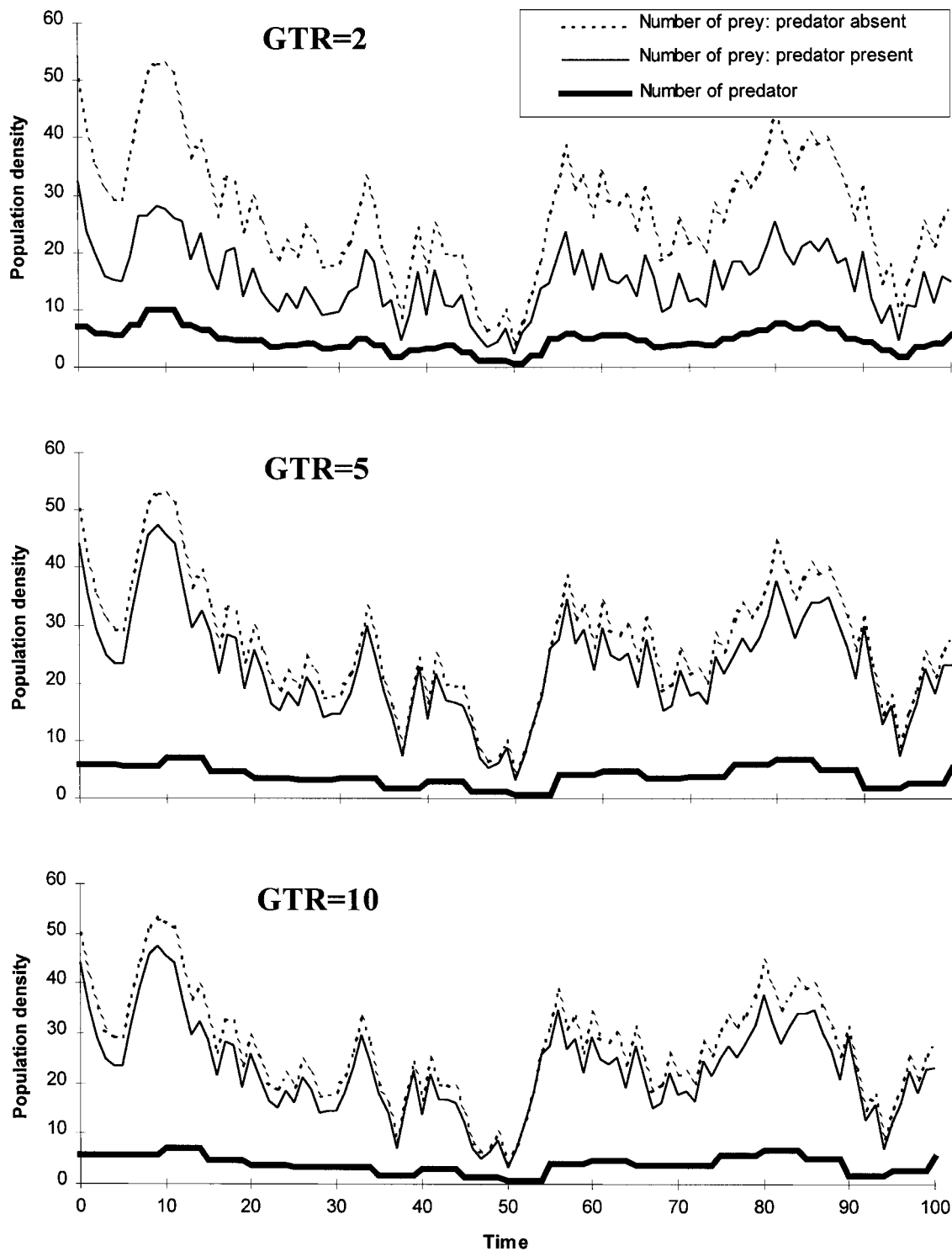
FIG. 1. Population trends in the abundance of prey with and without predators, with three different generation time ratios (GTR), and in the abundance of the predator in time. Parameters: $K = 10$, $v = 5$; for $t \bmod D = 0$: $F_t = y_{t-1}$; for D = GTR—see insets.

when the generation time ratio (GTR) is larger than one. Because they were considering the effects of parasitoids rather than predators, they did not use GTR values larger than 1.2.

This is visually illustrated by a simplistic discrete-

time modification of Ives' (1989) model (Fig. 1). To avoid any specific assumptions, the predator-free prey density at time t, x_t, was assumed to be a random walk, $x_{t+1} = x_t + \epsilon$, where ϵ is a random number between $-K$ and K. This includes both the intrinsic dynamics of prey

and the influence of environmental conditions, other species, etc. The prey generation time is therefore 1 time unit. The generation time of the predator is D time units, and it needs ν prey items for successful completion of its larval development. Assuming discrete predator generations, the predator numbers change only when $t = 0$, D, 2D, 3D, . . . when the larvae become adult and leave the patch and different F females arrive to lay their eggs. Following Ives (1989), the larval competition curve was assumed to be of the form $s(y) = \mu(1 - \alpha y)$ for $y < 1/\alpha$ and $s(y) = 0$ for $y \geq 1/\alpha$, where y is the number of eggs laid by all the females in the patch, s is the probability of survival to adults of larvae born from these eggs multiplied by their adult fecundity, and μ and α are parameters. According to Ives (1989), the evolutionarily stable number of eggs laid per patch is then equal to $y_t = 1/\alpha(F + 1)$. To account for the prey trajectory projection, $\alpha = \nu/\min_{\tau \in (t, t+D)} x_\tau$, a consequence of which is that the fitness of the larvae is positively correlated with the minimum expected number of prey in the absence of predators, relative to their voracity.

The simulations for different ratios of generation times of the predator and its prey (GTR = D/1 here) in Fig. 1 clearly illustrate that the effect on the prey population density is inversely related to the developmental time of the predator. This results from the differences in the speeds of the predator and prey dynamics.

In biological terms, this theory predicts that, given a prey species and two predators differing only in developmental times, the predator with the longer developmental time will have less effect on prey abundance. Or, given a predator species and two prey species, the predator whose trajectory shows less violent oscillations from the predator's point of view is more effective in reducing the abundance of the prey.

Three questions need to be addressed before this theory can gain general acceptance: (1) Are there empirical data to support the above predictions? (2) If such data exist, how are predators able to accommodate to bottlenecks in the long-term projections of prey trajectories? (3) Can the predator's strategy be explained in terms of maximizing fitness at the individual level? These questions are addressed in the following sections.

OPTIMAL FORAGING STRATEGY OF A LONG-LIVED PREDATOR EATING A SHORT-LIVED PREY

Predators are generally considered to be less effective in suppressing herbivore abundance than are parasites (Beddington *et al.,* 1976; DeBach, 1964; van den Bosch and Messenger, 1973). For example, in the field, the reduction of aphid density below the parasitoid-free value (the q values) by parasitoids can be in the range of 0.01 (Beddington *et al.,* 1978), whereas the reductions due to predators are usually less by approximately one order of magnitude (Table 1). This is also

TABLE 1

Estimated q Values for Predators

q Value	Predator	Prey	Source
0.02–0.33	Complex of species	*Aphis fabae*	Frazer and Gilbert, 1976
~0.1–0.2	*Coccinella trifasciata*	*Acyrthosiphon pisum*	Milne, 1988
>0.25	Complex of species	*Therioaphis trifolii*	Nawrocka, 1988
0.2–0.4	Syrphids	*Brevicoryne brassicae*	Kauffman and Schwalbe, 1991
~0.05–0.2	*C. septempunctata*	*Aphis fabae*	Campbell and Cone, 1994
~0.01–0.05	Complex of species	*Phorodon humuli*	Tenhumberg and Poehling, 1995
0.5	Syrphids	*Metopolophium dirhodum*	Putman, 1955

true for other predator–prey and parasite–host systems (e.g., Murdoch, 1994). Why are predators much less effective than parasites in reducing the abundance of herbivores?

The developmental time of aphidophagous predators like coccinellids often spans several aphid generations (Hemptinne *et al.,* 1993); so their GTR is large. The existence of an aphid colony is time limited and often similar in duration to the developmental time of ladybird larvae, which, unlike the adults, are confined to a colony. Oviposition characteristically occurs over a short period, the "egg window," early in the development of each patch (Hemptinne *et al.,* 1992, 1993; Kindlmann and Dixon, 1993). There appear to be two reasons for this, both based on the expectation of the future trends in patch quality. The first is that it ensures sufficient time for ladybird larvae to complete their development.

The second reason is that cannibalism is common in ladybirds (Agarwala and Dixon, 1993; Fox, 1975; Hodek, 1973). Cannibalism is adaptive in their case (Osawa, 1991), as eating conspecific competitors will increase the fitness of a ladybird larva that, due to the prey trajectory projection, may be short of food toward the end of its development, when the aphid colony that it is attacking declines in abundance. This situation differs significantly from that of parasites in which, by ovipositing in young aphids, parasites can ensure that there is sufficient food for the development of their offspring. Therefore, eggs laid by ladybirds late in the existence of an aphid colony are at a further disadvantage, as they are highly likely to be eaten by conspecific larvae that hatched from the first eggs to be laid. Indeed, the egg number reduction due to cannibalism in the field steeply increases at high coccinellid densities (Mills, 1982). Even if late-laid eggs complete their development, the resultant adults are likely to be small because of competition for resources with older conspe-

cifics. Small adults have a low fitness (Dixon and Guo, 1993). Thus, by not laying eggs in patches that are already exploited by larvae, ladybirds increase their fitness by reducing the risks of cannibalism and of competition with older conspecifics. Recent empirical data on ladybirds and other long-lived insect predators have confirmed that the presence of conspecific larvae acts as an oviposition inhibitor and causes adults to leave the patch (Hemptinne *et al.,* 1992, 1993; Růžička, 1994). The existence of the egg window is also indirectly supported by the inverse density-dependent response to aphid abundance that is shown by these predators, which has commonly been recorded in the field (Pschorn-Walcher and Zwölfer, 1956; Hafez, 1961; Hughes, 1963; Kuchlein, 1966; Coderre, 1988; Chambers, 1991; Ofuya, 1991).

The short egg window also reduces the number of eggs laid per patch. The relatively low number of ladybird larvae, which is also not added to later in the existence of the aphid colony, is not able to substantially reduce the rapidly increasing number of aphids. This is a consequence of the large GTR. Egg windows, inverse numerical responses, and large q values are characteristic of ladybird–aphid systems (Pschorn-Walcher and Zwölfer, 1956; Hafez, 1961; Hughes, 1963; Kuchlein, 1966; Coderre, 1988; Chambers, 1991; Ofuya, 1991) but occur also in other systems in which the generation time of the natural enemy spans several prey generations (e.g., Blaustein, 1992). In parasite–host and acarine predator–prey systems, the generation times of the natural enemy and prey are comparable and the q values are small (Beddington *et al.,* 1978). In *Aphytis*–coccid systems, in which the natural enemy can complete several generations per host generation, the q value is less than 0.01 (Murdoch, 1994).

LONG-LIVED PREDATOR EATING A LONG-LIVED PREY

In the field, long-lived predators like ladybirds or syrphids in general are successful in controlling coccids (DeBach, 1964) but not aphids (Bombosch and Tokmagoklu, 1966; Frazer and Gilbert, 1976; Milne, 1988; Nawrocka, 1988; Kaufmann and Schwalbe, 1991; Campbell and Cone, 1994; Tenhumberg and Poehling, 1995) nor mites (Putman, 1955). In the *Rodolia cardinalis* (Mulsant)–cottony cushion scale system (DeBach, 1964), the ladybird lays an egg under an adult female coccid or its egg mass, and the larva can complete its development by consuming this coccid and its eggs (Clausen, 1940). That is, the generation times of the predator and prey in this system are comparable—the GTR is small. As the food availability is ensured, coccid-feeding ladybirds follow the trajectory of their prey more closely than aphid-feeding ladybirds.

THE EVOLUTIONARILY STABLE NUMBER OF EGGS LAID PER PATCH: SIMULTANEOUS VS SEQUENTIAL PREDATOR ARRIVAL

Unlike adults, immature predators are usually unable to move between patches. In predator–prey systems in which the GTR is large, several prey generations elapse before the predator matures. During this time, the abundance of prey within a patch may change dramatically and prey is likely to become scarce. This may be a deterministic event, either patch depletion or prey emigration, or a consequence of variation in the long-term prey population dynamics or both. Hence, it is not unreasonable to assume that a predator's fitness will decline with an increase in the number of predator eggs that are already present in a patch at the instant of its birth. Although the exact reasons for this decline in fitness might differ for different groups of predators (cannibalism, etc.), nevertheless the presence of other conspecifics increases competition for prey and the younger and weaker individuals are at greater risk. At any instant, ovipositing predators should weigh the profit from reproduction in a patch that is being exploited against the prospects of finding a more suitable patch; their evolutionarily stable strategy is likely to be based on the prey trajectory projection. The egg window of aphidophagous ladybirds is a measurable result of this decision.

It is predicted that when offspring fitness declines with increase in the number of eggs laid in a patch, the evolutionarily stable number of eggs laid per adult female in a patch will depend on the larval competion function (Ives, 1989). This prediction is based on the assumption that predators arrive in a patch simultaneously, which is very unlikely. When the predators arrive in a patch sequentially, as is assumed in the theory presented here, the predators should cease laying eggs when threat from cannibalism makes it more profitable to look for another patch; the egg window is closed.

The reluctance of predators to reproduce where predators are already present and the resultant inverse density dependence results in these predators being poor biocontrol agents. Thus, the important feature of a potential biocontrol agent is its generation time relative to that of its prey. Herbivore–plant systems are very similar in that the plants can be overexploited. In these systems there is also evidence (Thiery and Gabel, 1993) that herbivores avoid laying eggs on plants that are already colonized by conspecifics.

THE QUESTION OF PRUDENCE

Although seductive, it would be rash to conclude from the above that long-lived predators behave prudently and harvest prey populations in an optimal way. In systems in which predators show an inverse density-

dependent response to increase in prey abundance, the survival of immature predators is safeguarded when the prey population decreases. This is not achieved, however, via group selection but by responding to cues which maximize each individual's fitness.

Both the empirical data and the theory indicate that differences between the generation times of the natural enemies and their prey result in a range of GTRs and q values. A natural enemy that lays additional eggs above the "optimal" number has a greatly reduced fitness. This is because of the sequential arrival and reproduction by predators in a patch.

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