

When and why top-down regulation fails in arthropod predator-prey systems

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Received May 1, 2001 · Accepted July 25, 2001

Abstract

The existence of top-down regulation in predator-prey models is a result of the functional and numerical responses included in the model. Examples are given of arthropod predator-prey systems where functional and numerical responses may be irrelevant for the system dynamics, or relevant for only a part of the population. It is argued that there are advantages in using a patch dynamics approach, when describing the feeding and oviposition behaviour of adult predators.

This leads to predictions that in arthropod predator-prey systems, in which the predator has a long generation time relative to that of its prey, predator reproduction should be correlated with the age of a prey patch rather than the number of prey present, and top-down regulation does not occur. The predictions are tested against data for various species of aphids, coccids, mites, mosquitoes and their predators and the effectiveness of different species in biological control.

In Räuber-Beute-Modellen ist das Vorhandensein einer „top-down“-Regulation das Ergebnis der funktionellen und numerischen Reaktionen, die in dem Modell enthalten sind. Es werden Beispiele von Räuber-Beute-Systemen angeführt, in denen die funktionellen und numerischen Antworten für die Dynamik der Systeme unbedeutend sein können, oder nur für einen Teil der Population von Bedeutung sind. Es wird erörtert, dass bei der Beschreibung des Fraß- und Eiablageverhaltens adulter Prädatoren die Anwendung eines „patch“-Dynamik Ansatzes vorteilhaft ist. Dies führt zu den Vorhersagen, dass in Räuber-Beute-Systemen bei Arthropoden, in denen der Räuber im Verhältnis zur Beute eine lange Generationszeit aufweist, die Reproduktion des Räubers mit dem Alter des Beute-„patch“ und nicht mit der Anzahl der vorhandenen Beute korreliert und so „top-down“-Regulation nicht stattfindet. Die Vorhersagen werden mit Daten von verschiedenen Arten von Blattläusen, Schildläusen, Milben, Mücken und ihren Feinden getestet, sowie die Effektivität der biologischen Kontrolle verschiedener Arten betrachtet.

Key words: Predator-prey models – patch models – life histories – aphids – ladybirds – aphidophagous predators – population regulation

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Top-down regulation and negative feedbacks

Top-down regulation is a characteristic feature of most predator-prey models. This is because predator fecundity is a function of the amount of food consumed (numerical response – Hassell & Varley 1969, May 1976), and the amount of prey eaten per unit time by one predator is dependent mainly on prey density (Holling 1959a, b, May 1976, Hassell 1978, – prey dependent functional response) and sometimes also on the density of the predator (Thompson 1939, Beddington 1975, DeAngelis et al. 1975, Frazer & Gilbert 1976, Arditi & Ginzburg 1989, Ruxton et al. 1992, Cosner et al. 1999). If these assumptions are valid then when prey is scarce, theory predicts that predators reproduce less and decline in numbers, which allows the prey to increase. As far as we are aware, the existence of top-down regulation in any model is always a result of some form of functional and/or numerical response.

Problems with functional and numerical responses

In many natural situations, functional and numerical responses may not shape the dynamics of the system, or are relevant for only a part of the population. Insect predator-prey systems are a typical example: juvenile and adult insects differ in that the latter can fly while the former cannot. Thus it is important to incorporate this fact into models of insect population dynamics: juveniles (larvae) stay within one patch of prey, while adults may not, and therefore juveniles and adults have to be considered as two different entities. Patch in this sense means the space that the larva of a predator can reach by walking, usually one or only a few adjacent plants, or even only a part of an individual plant as in trees.

Thus the functional response of a larva is determined by the situation it finds in the patch of prey it occupies, while the functional response of an adult is determined by the prey availability in the overall population. Adults can easily fly from one patch to another, and are very effective at finding prey patches. Therefore, food availability seems to be much less limiting for adults than for juveniles, which are confined to one patch. Thus although adult insect predators show a functional response to food availability, in most natural situations they are likely to find enough prey for satiation and therefore food availability is unlikely to be the main limiting factor for adults. In other words, their perception of prey density is that it is in the region where the functional response levels off.

An even larger difference between juveniles and adults exists in their numerical responses, as juveniles do not reproduce, while adults do. Moreover, adult fecundity is a function of the amount of prey eaten, but their potential fitness is determined by the number of offspring that *survive to adulthood*. Therefore, in situations where juvenile mortality is large, the adult oviposition strategy becomes very important. This strategy is likely to have been shaped by bottlenecks in the availability of resources that occur during the period of development of the larvae, because they, unlike the adult, are confined to a patch. That is, the numerical response of an adult, in theory at least, should 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 (Kindlmann & Dixon 1999a, b).

In the simplest and most widely used models (e.g., Holling 1959a, b, Hassell & Varley, 1969, Beddington 1975, DeAngelis et al. 1975, May 1976, Hassell 1978), a stable age distribution is assumed, which allows one to ignore the individual life stages. Similarly, all predators and prey are assumed to interact with each other, thus other patches with the same species, and migration between patches, are ignored in the hope that the population dynamics will be similar everywhere. These assumptions may be satisfied in confined and limited spaces (e.g., a greenhouse), aquatic predator-prey systems (Major 1978, Partridge et al. 1983, Arditi et al. 1991, Arditi & Saiah 1992, Diehl et al. 1993, Blaine & DeAngelis 1997), in insect host-parasitoid systems (Holling 1959a, b, Hassell & Varley 1969, Hassell 1978) and maybe in some vertebrate predator-prey systems (Rubenstein 1978, Packer & Ruttan 1988), for which these models were originally developed. In these systems, the predators may – in theory – complete their development within one patch of prey, reproduce there and coexist with the prey for several generations. This may result in an asymptotic approach to a stable age distribution and no migration. When space is unlimited, and arthropod predator-prey systems are considered, in which the prey rapidly changes in numbers, the picture is completely different.

Foraging theory and egg windows

In arthropod predator-prey systems, a predator patch dynamics approach best describes the feeding and oviposition behaviour of adult predators. The patch model in optimal foraging theory, which also does not distinguish between juveniles and adults, predicts that an individual should stay in a patch, until it depletes it to a level when it becomes advantageous to travel to

another patch (Stephens & Krebs 1986). If a patch of prey is perceived by a juvenile predator as a set of prey colonies of different densities, then optimal foraging theory might be applicable to the foraging behaviour of juveniles.

However, it is doubtful, whether such an approach is useful for studying the foraging behaviour of adults. They can move freely not only between prey colonies, but also between prey patches in our sense, which makes it easier for them to find enough prey for satiation. Therefore, food availability is unlikely to be the main limiting factor for adults. Most arthropod predators are highly fecund and potentially capable of producing hundreds, or even thousands of eggs during their adult life. As their populations are not steadily increasing, therefore – by definition – on average only one offspring per adult (two offspring per one mother, assuming a 1:1 sex ratio) survives and reproduces. This means that offspring survival is likely to be very low in insect predators – about 1% or less. Thus there should be a strong selection pressure on adults to optimise the distribution of their eggs: any oviposition strategy that even slightly increases offspring survival results in a big increase in fitness (Kindlmann & Dixon 1993). For example, when larval survival is 1%, then a strategy that increases survival by only 1% doubles larval survival! Thus foraging theory, which deals with maximising of food intake and not the optimal distribution of offspring, is not relevant to the searching behaviour of adult insect predators, where potential fitness seems to be mainly determined by their oviposition strategy.

If the patches of prey are ephemeral and highly variable in quality (number of prey present), and the generation time ratio (GTR, defined as the ratio of generation time of the predator to that of its prey – Kindlmann & Dixon 1999b) is large, then it is advantageous for predators to lay only few eggs per prey patch (Kindlmann & Dixon 1999b). This is because of the bottlenecks in resource availability that occur during the development of the larvae, rather than the state of the patch of prey at the instant of oviposition. That is, the long-term future of a patch of prey becomes important for an ovipositing predator in large-GTR systems (Kindlmann & Dixon 1999a, b). The oviposition strategy should also maximise the probability that the patch will exist at least for the period of development of the offspring. If patches of prey are ephemeral, then oviposition should occur only during a short “egg window”, early in the existence of each patch of prey (Hemptinne et al. 1992). An interesting corollary follows from the above: the predator should have a low impact on the prey species, that is, the strength of top-down regulation should be low (Kindlmann & Dixon 1999b).

Another important factor determining the oviposition strategy is likely to be cannibalism, which is advantageous and likely to have been selected for in systems that during development experience bottlenecks in prey availability. Eating conspecifics is likely to increase the chance of survival of the cannibal, but also reduces competition for a limited resource.

Predictions

The above results can be summarised in the following predictions for arthropod predator-prey systems:

1. Predators should reproduce only in prey patches that are likely to survive long enough to sustain the development of their offspring – this usually means that predators should oviposit early in the development of a prey patch. Thus – contrary to the usual assumptions – predator reproduction should be correlated with the age of the prey patch, rather than the number of prey present.
 - 1.1. Corollary: If patches of prey are ephemeral and their dynamics typically described by a curve with only one peak, then – contrary to the predictions of optimal foraging theory and of models including functional and numerical responses – eggs of predators should be found in young patches of prey, where the prey is less numerous and not in older patches, where prey is likely to be more abundant.
2. The larger the GTR, the weaker is top-down regulation. That is, in systems with a large GTR, prey is not regulated by predation, but by auto-regulation or bottom-up processes.
 - 2.2. Corollary: Arthropod predators should have a relatively low impact on prey dynamics in large GTR systems.
3. Cannibalism should be common in arthropod predator-prey systems, especially those that experience bottlenecks in prey abundance, that is, in systems with a large GTR. In addition, it is the most vulnerable stages of the predator, such as eggs, which are likely to be eaten.

Empirical evidence

Numerical responses

Inverse numerical responses (prediction 1 and corollary 1.1) are characteristic of ladybird-aphid systems (Pschorn-Walcher & Zwölfer 1956, Hafez 1961, Hughes 1963, Kuchlein 1966, Coderre 1988, Chambers 1991, Ofuya 1991), but also occur in other systems, where the generation time of the natural enemy spans several prey generations (e.g., Blaustein 1992).

Ladybirds, chrysopids and hoverflies avoid ovipositing where larvae of their own species are already present (Hemptinne et al. 1993, Ruzicka 1994). That is, they reproduce only in patches of prey, which have only existed for a short period and therefore insufficient time has elapsed for conspecific larvae to develop. This conforms with prediction 1 and corollary 1.1 that they should only oviposit early in the development of a patch of prey and that oviposition is correlated with the age of a patch rather than on the number of prey present.

By moving between patches of prey adults optimise the distribution of their eggs (numerical response), rather than optimise foraging in the terms of maximising food consumption per unit time (functional response). The numerical response, however, reflects the ages of the patches of prey, rather than the amount of food they contain. It is surprising that this was completely ignored in the models of predator-prey population dynamics.

Tree-dwelling aphids

Tree-dwelling aphids are suitable model groups for studying the above. Their population dynamics have been studied over long periods of time and in considerable detail (Dixon 1963, 1966, 1969, 1970, 1971, 1975, Taylor 1977, Dixon 1979, Dixon & Barlow 1979, Barlow & Dixon 1980, Dixon & Mercer 1983, Chambers et al. 1985, Wellings et al. 1985, Dixon 1990, Turchin 1990, Turchin & Taylor 1992, Dixon et al. 1993, Kindlmann & Dixon 1996, Dixon et al. 1996). During spring and summer all the generations are parthenogenetic and short lived (2–4 weeks). In autumn, sexuals are also produced, which mate and give rise to the overwintering eggs that hatch the following spring and give rise to fundatrices, the first parthenogenetic generation. In the case of the Turkey-oak aphid, for example, there is an initial dramatic in-

crease in population size in spring followed by a steep decline in abundance during summer, when they become so scarce that they are not able to support the survival of immature predators. Sometimes there is a further increase in autumn (Fig. 1). Thus the period when they are suitable for the development of predators is typically described by a curve with only one peak. In other species, such as the sycamore aphid, there are usually two such periods during one season.

In contrast to most other groups, empirical data do not lend support to a marked effect of natural enemies (top-down regulation) on these aphids (Kindlmann & Dixon 1999a,b, Dixon et al. 1995, 1997). Predators tend to lay their eggs when these aphid populations are increasing in abundance (Fig. 1, Hemptinne et al. 1992), which conforms with prediction 1.1.

Although the parasitoids of aphids have a GTR close to 1, they are regulated by their hyperparasitoids (Mackauer & Völkl 1993), and therefore unable to respond to an increase in aphid abundance.

Food quality determines the rate of development and size of an individual aphid more than intraspecific competition. Food quality follows a seasonal pattern and is not affected by aphid numbers substantially, which means that aphid numbers are not regulated by bottom-up processes (Dixon et al. 1995, 1997). Analysis of the empirical data has revealed the regulatory mechanism that is responsible for the summer decline in numbers: migration. This increases linearly with density and declines with improving food quality (Kindlmann & Dixon 1996). Therefore the dynamics of several species of tree-dwelling aphids is self-regulated. That is, natural enemies do not play a substantial role in regulating the abundance of these aphids, which accords with corollary 2.1.

Ladybirds and their prey

In the field, predators like ladybirds and syrphids, which have a long developmental time, are successful in controlling the abundance of coccids, which take a similar period of time to develop, but not aphids, which develop in a much shorter period of time (De-Bach 1964, Bombosch & Tokmakoglu 1966, Frazer & Gilbert 1976, Milne 1988, Nawrocka 1988, Kaufmann & Schwalbe 1991, Campbell & Cone 1994, Tenhumberg & Poehling 1995, Dixon et al. 1997, Dixon 2000). This accords with prediction 2 – ladybirds successfully control their prey when the GTR is small but not when it is large (Fig. 2.).

Cannibalism is common in aphidophagous ladybirds (Hodek 1973, Fox 1975, Mills 1982, Agarwala & Dixon 1993, Dixon 2000). A high probability of egg cannibalism (Mills 1982) makes it advantageous for ladybirds to avoid oviposition in patches of prey

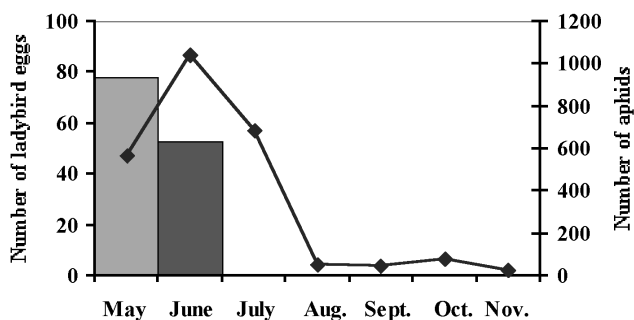


Fig. 1. Average yearly profile of the Turkey-oak aphid dynamics in Norwich (UK)-line, and number of coccinellid eggs laid in the aphid colonies-columns.

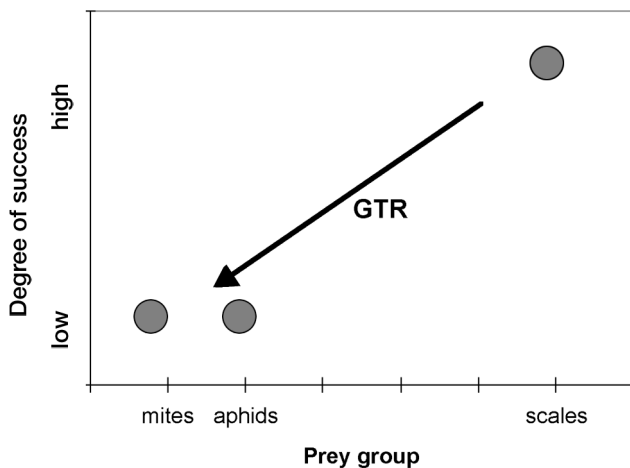


Fig. 2. Degree of success of ladybirds in depressing the abundance of mites, aphids and scale insects. The arrow indicates increasing GTR.

already occupied by conspecific larvae. In addition, empirical field data indicate that cannibalism also serves subsequently to regulate the numbers of ladybird larvae within a patch (Mills 1982, Osawa 1989, 1991, 1992, Hironori & Katsuhiko 1997, Kindlmann et al. 2000, Yasuda et al. submitted), which conforms with the prediction 3.

General results on insect predator-prey systems

Predators are generally considered to be less effective in suppressing herbivore abundance than are parasitoids (DeBach 1964, Beddington et al. 1976, Van den Bosch & Messenger 1973, Waage & Mills 1992, Dixon 2000). For example, out of 93 cases of "substantial" or "complete" biological control reported by Van den Bosch & Messenger (1973), only 10 cases of "substantial" and 2 of "complete" control involved only predators. Of the 419 species of predatory Coleoptera used in biological control only 14 species were successful, whereas of the 1317 species of parasitic Hymenoptera 97 species were successful (Greathead & Greathead 1992).

Parasitoids can reduce herbivore density to about 1% (Beddington et al. 1978), whereas predators are usually approximately one order of magnitude less effective (Kindlmann & Dixon 1999a). This is also true for other predator-prey and parasite-host systems (e.g., Murdoch 1994).

The famous exception is the control of the cottony-cushion scale, *Icerya purchasi*, by the ladybird beetle, *Rodolia cardinalis*, in California (DeBach 1964). The duration of development of the larvae of *Rodolia* is, however, considerably shorter than that of their prey (Dixon et al. 1997).

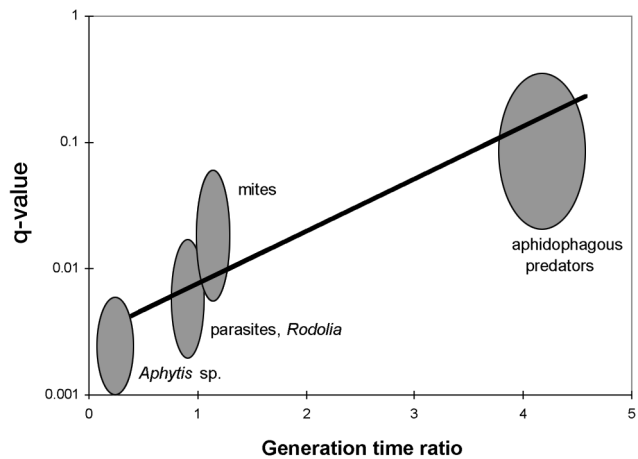


Fig. 3. The trend in q-values relative to the generation time ratio for various arthropod predator-prey systems.

Predatory mites are also frequently recorded as good to excellent at keeping populations of herbivorous mites below economic thresholds (Croft & MacRae 1992). As in the *Rodolia*-coccid system, the generation time ratio in the predatory mite – herbivorous mite systems is much lower than that in aphidophagous ladybird – aphid systems. In *Aphytis*-scale systems, where the natural enemy can complete several generations per one host generation, the parasite often overexploits its host resulting in local extinction (Murdoch 1994).

Thus, in accord with prediction 2, there is a continuum of ratios of the generation times of the natural enemies to those of their prey (GTR), which is correlated with the q-values, where q-value is defined as the degree, to which a predator can reduce prey density below the parasitoid-free value (Beddington et al. 1978) – see Figure 3. In natural enemy – prey systems where the GTR is much larger than one, the corresponding q-values are large. In parasites, predatory mites and *Rodolia cardinalis*, the GTR is close to 1 and the corresponding q-values are likely to be small. In *Aphytis*-scale systems the GTR is much smaller than one, and the q-values are close to zero.

Successful control in large GTR systems

Larvivorous fish, like *Gambusia*, are a highly successful in controlling mosquitoes and the GTR in this system is much larger than one (Murdoch et al. 1985). However, mosquitoes are not an important component of *Gambusia*'s diet and its population dynamics are largely independent of those of the mosquito. Many of the environments where this occurs are temporary, and the fish have to be restocked each season

(Murdoch et al. 1985). Thus, this cannot be seen as a natural form of control.

Water ecosystems, however, are much more suitable for using large-GTR predators for controlling herbivore abundance. Unlike in terrestrial systems, the predators (e.g., fish) cannot leave the ponds and therefore may be quite effective, especially if their numbers are maintained artificially. In this respect such systems resemble glasshouses, where large-GTR predators are frequently used to control the abundance of pests. In natural conditions, however, large-GTR predators, even in water ecosystems, are unlikely to be effective in regulating prey abundance. This is supported by three recent (1991–1995) attempts to control mosquitoes using *Gambusia*, all of which failed (Todd & Giglioli 1983, Blaustein 1992, Lardeux 1992). Similarly *Notonecta*, another predator of mosquitoes, which is a successful biocontrol agent in semi-natural conditions, is not effective in natural conditions (Murdoch et al. 1985).

Conclusions

In arthropod predator-prey systems, adult predators are able to move between patches of prey, while juveniles cannot. Predators are highly fecund, and especially in systems where GTR is large juveniles experience bottlenecks in prey availability. This results in cannibalism in juveniles and their high mortality. Therefore, there is a strong selection pressure on adults to optimise the distribution of their eggs in a way that maximises the likelihood of survival of their offspring. The optimum oviposition strategy is to lay eggs only early in the existence of the patch of prey; the “egg window”. The mechanism that enables many species of insect predators to achieve this is to avoid laying eggs in patches of prey that contain conspecific larvae. As well as enabling them to avoid laying eggs in “old patches” the mechanism also greatly reduces the number of eggs that are likely to be laid in a patch. As a consequence of this and cannibalism, top-down regulation fails.

The challenges for the future are to determine how the theory of classical predator-prey systems can be adapted for arthropod predator-prey systems and to document fully the mechanisms that enable insect predators to forage and oviposit in ways that often come close to optimum.

References

- Agarwala BK, Dixon AFG (1993) Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* 90: 45–50.
- Arditi R, Ginzburg LR (1989) Coupling in predator-prey dynamics: Ratio dependence. *Journal of Theoretical Biology* 139: 311–326.
- Arditi R, Perrin N, Saiah H (1991) Functional responses and heterogeneities. An experimental test with cladocerans. *Oikos* 60: 69–75.
- Arditi R, Saiah H (1992) Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* 73: 1544–1551.
- Barlow ND, Dixon AFG (1980) Simulation of lime aphid population dynamics. Pudoc, Wageningen.
- Beddington JR (1975) Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology* 44: 331–340.
- Beddington JR, Free CA, Lawton JH (1976) Concepts of stability and resilience in predator-prey models. *Journal of Animal Ecology* 45: 791–816.
- Beddington JR, Free CA, Lawton JH (1978) Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273: 513–519.
- Blaine TW, DeAngelis DL (1997) The interaction of spatial scale and predator-prey functional response. *Ecological Modelling* 95: 3 19–328.
- Blaustein L (1992) Larvivorous fishes fail to control mosquitos in experimental rice plots. *Hydrobiologia* 232: 219–232.
- Bombosch S, Tokmakoglu O (1966) The efficiency of aphidophagous insects in control of *Aphis fabae* Scop. In: Hodek I (ed) *Ecology of Aphidophagous Insects*. Academia, Prague, pp 271–273.
- Campbell CAM, Cone WW (1994) Influence of predators on population development of *Phorodon humuli* (Homoptera, Aphididae) on hops. *Environmental Entomology* 23: 1391–1396.
- Chambers RJ (1991) Oviposition by aphidophagous hoverflies (Diptera: Syrphidae) in relation to aphid density and distribution in winter wheat. In: Polgar L, Chambers RJ, Dixon AFG, Hodek I (eds) *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague, pp 115–121.
- Chambers RJ, Wellings PW, Dixon AFG (1985) Sycamore aphid numbers and population density 11. Some processes. *Journal of Animal Ecology* 54: 425–442.
- Coderre D (1988) The numerical response of predators to aphid availability in maize: why coccinellids fail? In: Niemczyk E, Dixon AFG (eds) *Ecology and Effectiveness of Aphidophaga*. SPB Academic Publishing, The Hague, pp 219–223.
- Cosner C, DeAngelis DL, Ault JS, Olson DB (1999) Effects of spatial grouping on the functional response of predators. *Theoretical Population Biology* 56: 65–75.
- Croft BA, MacRae IV (1992) Biological control of apple mites by mixed populations of *Metaseiulus occidentalis* (Nesbitt) and *Typhlodromus pyri* Scheuten (Acari, Phytoseiidae). *Environmental Entomology* 21: 202–209.
- DeAngelis DL, Goldstein RA, O'Neill RV (1975) A model for trophic interaction. *Ecology* 56: 881–892.
- DeBach P (1964) *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London.
- Diehl SP, Lundberg PA, Gardfjell H, Oksanen L, Persson L (1993) Daphnia-phytoplankton interactions in lakes: Is there

- a need for ratio-dependent consumer-resource models? *American Naturalist* 142: 1052–1061.
- Dixon AFG (1963) Reproductive activity of the sycamore aphid, *Drepanosiphum platanoides* (Schr.) (Hemiptera: Aphididae). *Journal of Animal Ecology* 32: 33–48.
- Dixon AFG (1966) The effect of population density and nutritive status of the host on the summer reproductive activity of the sycamore aphid, *Drepanosiphum platanoides* (Schr.). *Journal of Animal Ecology* 35: 105–112.
- Dixon AFG (1969) Population dynamics of the sycamore aphid *Drepanosiphum platanoides* (Schr.) (Hemiptera: Aphididae): Migratory and trivial flight activity. *Journal of Animal Ecology* 38: 585–606.
- Dixon AFG (1970) Stabilisation of aphid populations by an aphid induced plant factor. *Nature* 227: 1368–1369.
- Dixon AFG (1971) The role of intra-specific mechanisms and predation in regulating the numbers of the lime aphid, *Eucallipterus tiliae* L. *Oecologia* 8: 179–193.
- Dixon AFG (1975) Effect of population density and food quality on autumnal reproductive activity in the sycamore aphid, *Drepanosiphum platanoides* (Schr.). *Journal of Animal Ecology* 44: 297–304
- Dixon AFG (1979) Sycamore aphid numbers: The role of weather, host and aphid. In: Anderson RM, Turner BD, Taylor LR (eds) *Population Dynamics*, Blackwell Scientific Publications, Oxford, pp 105–121.
- Dixon AFG (1990) Population dynamics and abundance of deciduous tree-dwelling aphids. In: Hunter M, Kidd N, Leather SR, Watt AD (eds) *Population Dynamics of Forest Insects*. Intercept Ltd., Andover, pp 11–23.
- Dixon AFG (2000) *Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control*. Cambridge University Press, Cambridge.
- Dixon AFG, Barlow ND (1979) Population regulation in the lime aphid. *Zoological Journal of the Linnean Society* 67: 225–237.
- Dixon AFG, Hemptinne JL, Kindlmann P (1995) The ladybird fantasy – prospects and limits to their use in the bio-control of aphids. *Züchtungsforschung* 1: 395–397.
- Dixon AFG, Hemptinne JL, Kindlmann P (1997) Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga* 42: 71–83.
- Dixon AFG, Kindlmann P, Sequeira R (1996) Population regulation in aphids. In: Floyd RB, Sheppard AW, De Barro PJ (eds) *Frontiers of Population Ecology*. CSIRO Publishing, Melbourne, pp 103–14.
- Dixon AFG, Mercer DR (1983) Flight behaviour in the sycamore aphid: factors affecting take-off. *Entomologia Experimentalis et Applicata* 33: 43–49.
- Dixon AFG, Wellings PW, Carter C, Nichols JFA (1993) The role of food quality and competition in shaping the seasonal cycle in the reproductive activity of the sycamore aphid. *Oecologia* (Berlin) 95: 89–92.
- Fox LR (1975) Cannibalism in natural populations. *Annual Review of Ecology and Systematics* 6: 87–106.
- Frazer BD, Gilbert N (1976) Coccinellids and aphids: A quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *Journal of the Entomological Society of British Columbia* 73: 33–59.
- Greathead DJ, Greathead AH (1992) Biological control of insect pests by insect parasitoids and predators: the BIO-CAT database. *Biocontrol News and Information* 13: 61N–68N.
- Hafez M (1961) Seasonal fluctuation of population density of the cabbage aphid, *Brevicoryne brassicae* (L.), in the Netherlands and the role of parasite, *Aphidius* (Diaeretiella) rapae (Curtis). *Tijdschrift Plantziekten* 67: 445–548.
- Hassell MP (1978) *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, New Jersey.
- Hassell MP, Varley GC (1969) New inductive population model for insect parasites and its bearing on biological control. *Nature* 223: 1133–1137.
- Hemptinne JL, Dixon AFG, Coffin J (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238–245.
- Hemptinne JL, Dixon AFG, Doucet JL, Petersen JE (1993) Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms. *European Journal of Entomology* 90: 451–455.
- Hironori Y, Katsuhiko S (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 153–163.
- Hodek I (1973) *Biology of Coccinellidae*. Academia, Prague and Jungk, The Hague.
- Holling CS (1959a) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 293–320.
- Holling CS (1959b) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385–398.
- Hughes RD (1963) Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). *Journal of Animal Ecology* 32: 393–424.
- Kauffman WC, Schwalbe CP (1991) Plant growth responses to *Aphis fabae* injury: importance of predation by *Coccinella septempunctata* (Coleoptera: Coccinellidae). In: Polgar L, Chambers RJ, Dixon AFG, Hodek I (eds) *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague, pp 167–175.
- Kindlmann P, Dixon AFG (1993) Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* 90: 443–450.
- Kindlmann P, Dixon AFG (1996) Population dynamics of tree-dwelling aphids: from individuals to populations. *Ecological Modelling* 89: 23–30.
- Kindlmann P, Dixon AFG (1999a) Generation time ratios – determinants of prey abundance in insect predator – prey interactions. *Biological Control* 16: 133–138.
- Kindlmann P, Dixon AFG (1999b) Strategies of aphidophagous predators: lessons for modelling insect predator-prey dynamics. *Journal of Applied Entomology* 123: 397–399.
- Kindlmann P, Yasuda H, Sato S, Shinya K (2000) Key life stages of two predatory ladybird species. *European Journal of Entomology* 97: 495–499.
- Kuchlein JH (1966) Some aspects of the predator-prey relation. In: Hodek I (ed) *Ecology of Aphidophagous Insects*. Academia, Prague, pp 237–242.

- Lardeux F (1992) Biological-control of Culicidae with the Copepod *Mesocyclops aspericornis* and larvivorous fish (Poeciliidae) in a village of French-Polynesia. *Medical and Veterinary Entomology* 6: 9–15.
- Mackauer M, Völkl W (1993) Regulation of aphid population by aphidiid wasps: does parasitoid foraging behaviour or hyperparasitism limit impact? *Oecologia* 94: 339–350.
- Major PE (1978) Predator-prey interactions in two schooling fishes, *Carnax ignobilis* and *Stolephorus purpureus*. *Animal Behaviour* 26: 760–777.
- May RM (1976) *Theoretical Ecology*. Blackwell Scientific Publications, Oxford.
- Mills NJ (1982) Voracity, cannibalism and coccinellid predation. *Annals of Applied Biology* 101: 144–148.
- Milne WM (1988) Effectiveness of aphidophagous insects in lucerne. In: Niemczyk E, Dixon AFG (eds) *Ecology and Effectiveness of Aphidophaga* SPB Academic Publishing, The Hague, pp 203–210.
- Murdoch WW (1994) Population regulation in theory and practice. *Ecology* 75: 271–287.
- Murdoch WW, Chesson J, Chesson PL (1985) Biological control in theory and practice *American Naturalist* 125: 344–366.
- Nawrocka B (1988) Effectiveness of the aphidophagous syrphids in controlling the cabbage aphid *Brevicoryne brassicae* L. In: Niemczyk E, Dixon AFG (eds) *Ecology and Effectiveness of Aphidophaga*. SPB Academic Publishing, The Hague, pp 289–294.
- Ofuya TI (1991) Aspects of the ecology of predation in two coccinellid species on the cowpea aphid in Nigeria. In: Polgar L, Chambers RJ, Dixon AFG, Hodek I (eds) *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague, pp 213–220.
- Osawa N (1989) Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. *Researches on Population Ecology* 31: 153–160.
- Osawa N (1991) Consequences of sibling cannibalism for the fitness of mother and offspring of the ladybirds beetle *Harmonia axyridis*. In: Polgar L, Chambers RJ, Dixon AFG, Hodek I (eds) *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague, pp 221–225.
- Osawa N (1992) Sibling cannibalism in the ladybird beetle *Harmonia axyridis*: fitness consequences for mother and offspring. *Researches on Population Ecology* 34: 45–55.
- Packer C, Ruttan L (1988) The evolution of cooperative hunting. *American Naturalist* 132: 159–198.
- Partridge BL, Johannson J, Kalish J (1983) The structure of schools of giant bluefin tuna in Cape Cod Bay. *Environmental Biology of Fishes* 9: 253–262.
- Pschorn-Walcher H, Zwölfer H (1956) The predator complex of the white-fir woolly aphids (Genus *Dreyfusia*, Adelgidae). *Journal of Applied Entomology* 39: 63–75.
- Rubenstein DI (1978) On predation, competition, and the advantages of group living. *Perspectives in Ethology* 3: 205–231.
- Ruxton G, Gurney WSC, DeRoos A (1992) Interference and generation cycles. *Theoretical Population Biology* 42: 235–253.
- Ruzicka Z (1994) Oviposition – deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *European Journal of Entomology* 91: 361–370.
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- Taylor LR (1977) Migration and the spatial dynamics of an aphid, *Myzus persicae*. *Journal of Animal Ecology* 46: 411–423.
- Tenhumberg B, Poehling HM (1995) Syrphids as natural enemies of cereal aphids in Germany – aspects of their biology and efficacy in different years and regions. *Agriculture, Ecosystems and Environment* 52: 39–43.
- Thompson WR (1939) Biological control and the theories of the interaction of populations. *Parasitology* 31: 299–388.
- Todd RG, Giglioli MEC (1983) The failure of *Gambusia puncticulata* and other minnows to control *Aedes taeniorhynchus* in a mangrove swamp on Grand-Cayman, WI. *Mosquito News* 43: 419–425.
- Turchin P (1990) Rarity of density dependence or population regulation with lags? *Nature* 344: 660–663.
- Turchin P, Taylor AD (1992) Complex dynamics in ecological time series. *Ecology* 73: 289–305.
- Van den Bosch R, Messenger PS (1973) *Biological Control*. Intext, New York.
- Waage JK, Mills NJ (1992) Biological control. In: Crawley MJ (ed) *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*. Blackwell Scientific Publications, Oxford, pp 412–430.
- Wellings PW, Chambers RJ, Dixon AFG, Aikman DP (1985) Sycamore aphid numbers and population density 1. Some patterns. *Journal of Animal Ecology* 54: 411–424.
- Yasuda H, Kindlmann P, Shinya K, Sato S (submitted) Intra and interspecific interactions on survival of two predatory ladybirds in relation to prey abundance: competition or predation. *Biological Control*.