

University of South Bohemia
Faculty of Science



Modelling the population dynamics
and prey-predator interactions
in an aphid-ladybird system

Kateřina Kintrová

Ph.D. Thesis

Supervisor: **Prof. RNDr. Pavel Kindlmann, DrSc.**

Faculty of Science, University of South Bohemia, České Budějovice
&
Institute of Systems Biology and Ecology, Czech Academy of Sciences,
České Budějovice

České Budějovice/Brno

2009

Declaration – Prohlášení

I hereby declare that I worked out this Ph.D. thesis on my own, or in collaboration with the co-author of the presented papers and manuscript, and only using the cited literature.

I declare that in accordance with the Czech legal code § 47b law No. 111/1998 in its valid version, I consent to the publication of my Ph.D. thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně nebo ve spolupráci se spoluautorem přiložených prací, pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce (v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou) elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách.

Brno, 28th September, 2009

Kateřina Kintrová

Author contribution statement

Kateřina Kintrová, born Houdková, author of this Ph.D. thesis, is the first author of one paper, one manuscript and the preliminary results and wrote the substantial part of them. She created the source code of the model and performed all the simulations and analyses. She managed an extended observational field experiment on aphids and their predators which became a background to the other published model (Paper II). There, Pavel Kindlmann is the author of the model of intraguild predation and the first author of the paper. As a supervisor, he helped with the text of paper I and guided ideas of paper III (manuscript).

The co-author hereby consents to the publication of the papers in the Ph.D. thesis of Kateřina Kintrová and supports it by his signature:

Pavel Kindlmann

Kintrová, K., 2009. *Modelling the population dynamics and prey-predator interactions in an aphid-ladybird system.* Ph.D. Thesis, in English, 94 p. Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic.

Annotation:

Population dynamics of a prey-predator system was studied on an aphid-ladybird model using mechanistic and analytic approaches of modelling. Simulations of the population dynamics were scaled up to a metapopulation level and extended to a long-term model. The effect of a specific oviposition strategy of predatory females on the aphid population was investigated and the efficiency of predators as biological control agents was considered.

Key-words:

Population dynamics, modelling, metapopulations, predator-prey interactions, oviposition strategy, intraguild predation, biological control.

Financial support:

Work on the thesis was supported by FRVŠ grant project 3258/2005, the grant LC06073 of the Czech Ministry of Education and the long-term research programme MSM 0021622416 (Masaryk University, Brno).

Poděkování – Acknowledgements

Během let mého doktorského studování na univerzitě v Českých Budějovicích se staly události pro můj život bezvýznamné i zcela zásadní. Rozhodně je na co vzpomínat i za co děkovat. Nejspíše je tedy toto poděkování záznam mé paměti, abych na to hned tak nezapomněla.

Mé díky a vzpomínky patří jistě Tonymu a June Dixonovým, báječným Angličanům, kteří mi otevřeli dveře k vědeckému nadšení, svému jazyku i svým srdcím. Nepotkala bych ovšem Tonyho bez mého školitele, Pavla Kindlmanna, který mě neváhal vypravit do Anglie a povláčel mě po různých koutech světa. Děkuji mu hlavně za cennou životní lekci, které se mi dostalo. Z lidí a lidiček, které jsem potkala v budějovickém pupku světa, s vděčností vzpomínám především na kolegynky Adrianu, Ivku a Janu, Lauru, kamarády z Větrné, a také na Petra, bez kterého by bylo všechno jinak. Zvláštní dík patří Davidovi, jehož životní cesta se překvapivě promítla i do mého osudu. K moravskému dílu mého studování neodmyslitelně patří Majka i další kolegové z Řečkovic, jimž velmi vděčím za stálý přísun optimismu a odhodlání.

Moje poděkování rodičům, Brašnovi a manželovi není žádnou formalitou, ale upřímnou oslavou našeho umění být spolu a mít se rádi. Tuto práci bych ráda věnovala mámě a tátovi.

I am grateful to Pavel Kindlmann, Tony Dixon and friends from České Budějovice and Brno. A special thanks to my husband, brother and parents to whom I would like to dedicate this thesis.

Table of Contents

General introduction	7
Modelling the population dynamics	13
References	17
Paper I Scaling up population dynamics processes in a ladybird-aphid system	23
Houdková, K. & Kindlmann, P. 2006. <i>Population Ecology</i> 48: 323–332.	
Shrnutí	
Paper II Intraguild predation: fiction or reality?	25
Kindlmann, P. & Houdková, K. 2006. <i>Population Ecology</i> 48: 317–322.	
Shrnutí	
Paper III Modelling of metapopulation dynamics in an aphid-coccinellid system on a long-term scale	27
Kintrová, K. & Kindlmann, P. (submitted).	
Shrnutí	
Preliminary results: Effect of increasing temperature on the dynamics of an aphid-ladybird system.	59
Summary of results	67
Shrnutí práce	71

General Introduction

Aphids have fascinated biologists for over 250 years, whether by the prodigious rate of increase, peculiar siphunculi or sense of host alternation (Dixon 2004). Up today, there have been about 4700 described species of the largest aphid family Aphididae (Hemiptera: Aphidoidea) in the world (Remaudière and Remaudière 1997). Scientists have uncovered the secret of aphid reproduction and various yearly cycles in alternating different morphs and hosts, but many questions are still to be answered and new have been asked. However, most of the research in the last 50 years has been stimulated by a pest status of aphids (Dixon 2004). About 450 species have been recorded from crop plants, nevertheless only about 100 have successfully exploited the agricultural environment to the extent that they are of a significant economic importance (Blackman and Eastop 2000). Feeding on the phloem of crop plants, aphids cause yield decreases, sometimes of considerable proportions (Irwin et al. 2007). In addition, aphids transmit plant-debilitating viruses that can, in turn, wreak havoc on a crop and its potential harvest (Irwin et al. 2007).

To protect their crops, humans have utilized various pesticides and repellent effects of some plants since ancient times. The use of modern synthetic pesticides began in the 1940s, after an insecticide potential of DDT was discovered. Twenty years later, the negative consequences of widespread use of DDT on bird populations were uncovered (e.g., Carson 1962). Tracing DDT over several trophic levels up to a top predator – human – has astounded and cautioned people against injudicious interventions in complex natural systems. More attention was focused on research of relations among the trophic levels above as well as below pest species and an alternative, natural way of controlling pests was expected to be found. The interest of entomologists in biology of aphids and their natural enemies has been since then much more granted. A promising case of successful control of the cottony cushion scale (*Icerya purchasi*) by the vedalia ladybird (*Rodolia cardinalis*) on Californian citrus orchards in 1888 – 1889 has encouraged ‘aphidologists’ to experiment with releasing a large amount of predatory and parasitic species to crop fields and introducing alien species with features appropriate to the successful control (e.g., Obrycki and Kring 1998). One of these species is *Harmonia axyridis*, a voracious ladybird that originated from Southeast Asia, which recently attracted attention also in the Czech Republic (Brown et al. 2008, Nedvěd 2008). It has been released extensively for classical biological control in North America since 1916 (Koch 2003), but a standalone established population was not documented until 1988. After the first detection, *H. axyridis* spread rapidly across North America (Koch 2003). An initial enthusiasm over the

effective biocontrol agent was soon dampened by reports on decreasing abundances of native ladybird species (Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002). Moreover, *H. axyridis* has established in Germany in 1999 and spreads itself rapidly to surrounding states. Today, twenty years after the American seeming success, *H. axyridis* has become a human nuisance, a grape and wine pest and a threat to native biodiversity (Kenis et al. 2008).

The above examples of unexpected consequences of human interventions to natural processes are just two of many. They point out the necessity of understanding the complex relations among species within the studied ecosystem, processes operating at different trophic levels as well as abiotic factors influencing the dynamics in the system.

FEATURES OF APHID BIONOMY

Aphids (Aphididae) are plant-sucking insects, which occur throughout the world. The greatest number of species is to be found in the temperate regions, where only few higher plants are free from aphids (Dixon 1977). Although the best-known pest aphid species are polyphagous, most aphids are relatively host specific (Blackman and Eastop 2007). A significant feature of life cycles of many aphid species is a host alternation (heteroecy). This, together with alternating sexual and asexual reproduction and formation of several different morphs makes the aphid biology very complex.

A typical life cycle of a host-alternating aphid in the temperate zone is holocyclic, i.e., with at least one sexual generation in a year cycle, starting with an egg overwintering on a primary host plant, usually in a bark of some woody species. In spring, as temperature rises, a female nymph hatches from the egg. The timing of hatching is well synchronized with the host plant phenology so the small nymphs feed on nutritionally rich germinating buds. The aphid moults through four larval instars to the imago (incomplete metamorphosis). The mature female, called fundatrix, is parthenogenetic and viviparous. One or few generations of wingless females (fundatrigeniae) reproduce parthenogenetically on the primary host plant. Then winged morphs (alatae) are produced to migrate to secondary host plants.

The secondary host plant is often of a different family than the primary host. Here, aphids continue to reproduce parthenogenetically and can become very abundant. It is this phase of the life cycle that usually causes damage to crops. Aphids' prodigious rate of increase is enabled by an evolutionary invention of 'telescoping generations' (Dixon 1987, Kindlmann and Dixon 1989). During their larval development, aphids invest in both somatic and gonadal growth. This results

in the development of gonads that contain embryos, many of which are ready to be born when an aphid matures (Dixon 1987). Thus, the development of an aphid from birth to maturity takes approximately one week, whereas other similar sized insects need about three weeks (Dixon 2005). Aphids can achieve high densities in a short time, especially under favourable conditions. When overcrowded, aphids produce more winged individuals (alatae), which migrate to other host plants and settle new colonies (McVean et al. 1999, Müller et al. 2001). A similar switch in production of alate morphs is induced by deteriorating nutritional quality of the host plant in mid-summer (e.g., Ba-Angood and Stewart 1980, Howard and Dixon 1992, McVean et al. 1999, Karley et al. 2003) when a collapse of aphid populations usually occurs. Alate aphids are less fecund than the apterae because they invest the energy to the flying apparatus and lipoidal reserves (Wratten 1977, Dixon and Kindlmann 1999). In addition, alatae do not reproduce in the maternal colony, which heavily affects the population growth on summer hosts. Enhanced emigration, reduced birth rate and elevated mortality caused by natural enemies are considered as the key population processes underlying the mid-summer crash in aphid populations (Karley et al. 2004).

The alatae migrate from the summer host plants back to the primary host where the sexual reproduction takes place. Here, winged gynoparae give birth to sexual females (oviparae), which then mate with winged males and produce the overwintering eggs. The mortality during autumn migrations is high. Aphids are drifted by air masses more or less passively and influence only the landing part of the drift (Pettersson et al. 2007). It has been estimated that only 0.2 – 1 % of the migrants succeed in locating the host (Taylor 1977, Ward et al. 1998).

NATURAL ENEMIES OF APHIDS

Natural enemies of aphids have been studied especially with respect to their potential to control aphid populations in the agricultural crops. Ladybirds are well known and popular all around the world. In the context of biological control in greenhouses, the parasitic wasps have got in gardeners' awareness. However, the range of aphid enemies is much wider. Beside ladybirds (Coleoptera: Coccinellidae), also hoverflies (Diptera: Syrphidae) and lacewings (Neuroptera: Chrysopidae) belong to often-studied families. In open fields, the potential of ground predators (e.g., Coleoptera: Carabidae), predatory bugs (e.g., Heteroptera: Anthracoridae, Nabidae) and spiders have been investigated (e.g., Sunderland et al. 1986, Denoth et al. 2002, Vichitbandha and Wise 2002, Östman et al. 2003). In greenhouses, especially the aphid midge, *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) and hymenopterous parasitoids belonging to the Aphidiinae

(Hymenoptera: Braconidae) and Aphelinidae (Hymenoptera) are used for biological control of aphids. Fungal pathogens are a further group of interest. All these are often collectively termed Aphidophaga.

The greatest potential for suppressing aphid populations is to be expected from species, that are specialized predators of aphids or their offspring feeds predominantly on aphids. Aphids are very abundant and ubiquitous prey but their predators (mainly ladybirds and larvae of hoverflies and lacewings) have to adapt to the ephemeral and extremely fast dynamics within aphid colonies. Adult predators can move easily among the colonies and so are able to find the patchily distributed prey. However, the juveniles develop predominantly within the colony they were born in and are confronted with the bottleneck in prey resources that occurs during the massive emigration of aphids back to the primary host. Hence, cannibalism on eggs or smaller larvae may occur, as it may supply a source of food and remove potential competitors (Hemptinne and Dixon 2000). Consequently, there should be a strong selection pressure in aphidophagous females to lay eggs only in young aphid colonies, which are not yet occupied by other predators (Hemptinne et al. 1992, 1993, Hemptinne & Dixon 2000). Such colonies do not contain other predatory larvae threatening the currently laid eggs or the youngest larvae hatched later, and are likely to be rich in aphids during the whole larval development. Ladybirds and lacewings have developed an efficient strategy to deal with this situation: olfactory tracks of predatory larvae in the colony act as a signal for the predatory females to cease oviposition and leave the colony (Hemptinne et al. 1992, 1993; Růžička 1998, 2001). Similarly, hoverflies are known to inspect aphid colonies visually and avoid colonies with alate aphids indicating onset of emigration (Kan and Sasakawa 1986, Kan 1988).

The lifetime fecundity of aphidophagous ladybirds varies greatly among species from slightly more than 100 to more than 1500 eggs per female (e.g., Omkar and Srivastava 2003, Omkar and James 2004). Eggs are usually laid in clusters (on average 11 – 30 eggs, depending on the species). Developmental time is species specific and is influenced by temperature, the amount of food consumed, and prey species (e.g., Hukusima and Kamei 1970, Omkar and Srivastava 2003, Omkar and James 2004). In *Coccinella septempunctata* (7-spot ladybird), the egg to adult development of individual fed on *Myzus persicae* took approximately from 70.4 to 10.4 days under constant temperature of 14°C and 32°C, respectively (Obrycki and Tauber 1981, Katsarou et al. 2005). The development of ladybirds can prolong even twice when fed on different aphid diet (Omkar and Srivastava 2003). Similarly, the fecundity of *C. septempunctata* differs significantly under various diets, e.g., 1764 eggs on the mustard aphid *Lipaphis erysimi*, 1060 on the pea aphid, *Aphis craccivora*, but only 203 on the toxic oleander aphid, *Aphis nerii*

(Omkar and Srivastava 2003). Digestibility and toxicity of aphids depends also on the toxicity of their host plants.

Most ladybird species in temperate regions hibernate as adults. They aggregate on selected elevated sites (hibernaculum), where can be found in large numbers. South-oriented and aerated sites are preferred, probably as a prevention of spread of pathogens during winter (Honěk 1989). Big, strong-flying ladybirds invade hibernacula in higher altitudes (up to about 4000 meters a. s. l.), whereas small and less mobile individuals seek hibernacula at the edges of the breeding sites (Honěk 1989). However, ladybirds gather up from large area every autumn and spread again next spring, so losses in one 'microregion' may be supplemented again in the next season.

Aphid parasitoids deposit their eggs separately to the aphid host. The infested aphid is usually killed in few days; the parasitoid larva devours the soft portions of the aphid's body, with only the cuticle remaining. The cuticle of the aphid (the 'mummy') serves as a shelter, within or under which the parasitoid pupates. Aphid parasitoids are often attacked by hyperparasitoids and various predators. Therefore, parasitoid females avoid ovipositing in the colonies with higher rate of parasitism because of the higher risk of hyperparasitism (Mackauer and Völkl 1993).

It is obvious that the trophic interactions within an aphid community are dense and complex. Many studies on aphids deal with the intraguild predation (IGP), i.e., predatory interactions between protagonists that occupy the same trophic level and thus compete for similar prey/hosts (e.g., Brodeur and Rosenheim 2000, Colfer and Rosenheim 2001, Hindayana et al. 2001, Denoth et al. 2002, Sato and Dixon 2004, Straub et al. 2008). However, due to the complexity of interactions, most of these studies have focused only on one taxonomic group of Aphidophaga, ignoring the others. There occur also interactions mutualistic with aphids, e.g., ants attending aphid colonies. Ants feed on honeydew of aphids and often protect the aphid colonies from attacks of predators and parasitoids (reviewed by Stadler and Dixon 2005).

STUDYING THE POPULATION DYNAMICS OF APHIDS

Over the last fifty years an intensive research on aphids has been carried out. Dozens of laboratory and fields experiments were conducted to describe effects of various factors on aphids and their enemies. In the laboratory and some small-scale field experiments, we can study the insect biology at an individual level and interactions of two or more species under simplified conditions. These experiments

are often short-term and the measured parameters are described with considerable preciseness. Extensive field experiments deal with the dynamics on a wider scale and the results are often just approximate. Especially when the system is opened (i.e., experimental colonies are not caged) many factors have to be taken into account. This type of studies should be, by my opinion, accompanied by detailed and frequent inspections of the studied environment in order to record important changes and impulses to aphid colonies. A correct interpretation of results is still a challenge in the aphid research.

Modelling the population dynamics of aphids and their enemies represents another way to understanding the complexity of the system. Contemporary models usually involve only seasonal dynamics and are very simplified in terms of the level of trophic interactions and the biotic and abiotic factors involved. This may be of a great advantage: a well made model can reveal a nub and consequences of interactions, because not obscured by natural noise. When modelling, we are looking for some patterns rather than testing a hypothesis. The resulting concepts should be then verified in natural systems.

The validation probably remains to be the most serious problem of the modelling approach. As the insect migrate between hosts or prey, it is almost impossible to get census data on period longer than few weeks. Furthermore, the populations of aphids and their enemies affect each other and the interactions work from the individual- to metapopulation-scale not only in space, but also in time. Today, rough estimates of aphid abundances all around the year are available (e.g., Sequeira and Dixon 1997, Thacker et al. 1997, Alyokhin et al. 2005, Dixon 2000, Bommarco et al. 2007, data from suction traps). However, there is an acute shortage of long-term data on aphid enemies, preferably accompanying the aphid data in the same region so that the mutual interactions could be studied. Moreover, some phases of the aphids' life cycle are poorly known, e.g., the autumn migration, success in a primary host finding and mating, and winter survival.

In spite of all these difficulties, I believe that modelling is a reasonable and valuable way, how to study aphidophagous communities.

Modelling the aphid–ladybird population dynamics

The thesis extends the previously published model of aphid population dynamics (Kindlmann 1985, Kindlmann and Okrouhlá 1986, Kindlmann and Dixon 1996, Kindlmann and Dixon 2003, Kindlmann et al. 2004), which is based on the mechanism of the negative response of the intrinsic aphid dynamics to the cumulative density within the colony. I aimed to scale up the model from a single prey colony to a metapopulation level, simulate the oviposition strategy of predatory females and study effects of selected parameters on overall dynamics of the system. The originally one-season model was extended to simulate the aphid–ladybird population dynamics for many years.

The model was built on the following assumptions:

a. The aphid species conforms to the host-alternating life cycle with one sexual generation in autumn and overwintering eggs.

Host-alternating aphid species migrate twice a year. Thus, the aphid abundance on a particular patch of summer host in any season is not directly linked either with that in the previous or the subsequent season ('season' means the dynamics between the spring and autumn migrations in the model). The migration brings an important consequence to the modelling of long-term dynamics: the winged aphids emigrating from the summer host plants must be counted because they establish the population in the next season. This assumption differentiates the model from the model of Kindlmann and Dixon (2003), where a tree-dwelling aphid species was considered. Mortalities during autumn migration and winter survival are supposed to be high (Taylor 1977, Ward et al. 1998).

b. The main driving factor of aphid population dynamics is the cumulative density within the colony.

The steep increase in numbers of aphids in spring is often derived from the exponential growth (Mack and Smilowitz 1982, Kindlmann et al. 2004). The summer collapse of populations has been then modelled as a deterministic process driven either by the nutritional stage of the host plant or by interactions with predators and/or parasitoids (e.g., Bommarco 2001, Ma and Bechinski 2008). It has been observed (Dixon 2005) that the summer decline in aphid abundances occurs even if predators are absent and it is characteristic to the aphid population dynamics. Kindlmann and Okrouhlá (1986) suggested a simple model, in which the cumulative density within an aphid colony is the driving process of the decline. This model fits well to empirical data and explains the switch to alatae production by a natural intrinsic mechanism of aphid dynamics (Kindlmann et al. 2004).

c. The aphidophagous predator is univoltine and reproduces only in aphid colonies. Its larvae are cannibalistic. Females follow the oviposition strategy to minimize a risk of death of their offspring.

Ladybirds in central Europe are known to have mostly one generation per year (Hagen 1962, Honěk 1989). The assumptions of exclusive feeding on the aphid prey are applied mainly to keep the model simple. Cannibalism is frequent in aphidophagous predators. Newly hatched larvae feed on sibling eggs thus increase their own probability of survival (e.g., Gagné et al. 2002). Larvae of older instars may be intraguild predators (e.g., *Harmonia axyridis*) or cannibalise on conspecific larvae when prey is scarce (Osawa 2002, Sato et al. 2003). In the model, a non-preferential variant of foraging behaviour of larvae is implemented, i.e., the larva devours whatever it encounters, be it aphid or a conspecific larva ('meet & eat' hypothesis, Kindlmann and Dixon 2003). The selection pressure leads predators to the preference of young aphid colonies without conspecific predators. This period in a life of prey colony has been described as an 'egg window' (Hemptinne et al. 1992, 1993). There are also empirical data supporting this hypothesis (Hironori and Katsuhiko 1997, Kindlmann et al. 2000).

d. Predators migrate to hibernacula in autumn.

The autumnal migration to characteristic sites is known in ladybirds (e.g., Hagen 1962, Hodek 1973, Honěk 1989). This process is important in the model, as it enables to redistribute all predators among patches every season similarly as aphids are redistributed.

In the model, both mechanistic and analytic approaches are combined and also some degree of stochasticity is included. The mechanistic approach with a stochastic element is used after the spring migration (the settling phase) where a destiny of each individual contributes significantly into the overall dynamics later in the season. On the contrary, the dynamics of an already settled colony is modelled analytically by a set of differential equations because the interactions between predators and prey are simpler and an individual does not play such an important role. The model consists of three phases:

- 1. Egg-window dynamics** – at the beginning of this phase the prey immigrates to the virtual landscape from the winter host and starts to reproduce. Predatory females enter the system during the first few days, fly randomly from patch to patch, feed on the prey and lay their eggs in suitable patches according to the optimization rules mentioned above. The random distribution of aphids among patches, as well as the random foraging and oviposition of the females introduce some stochasticity into the model.

- 2. Within-season dynamics** – in this phase we use the prey and predator numbers in each patch, as they were set in the egg-window phase, and simulate the intrinsic dynamics of each patch separately until a new generation of young predators emerges from their pupae. During this period, further immigration of either the prey or predator is neglected assuming it to be small compared to the intrinsic system dynamics.
- 3. Between-season dynamics** – this phase imitates the winter survival, when prey faces unfavourable conditions as eggs, and predators hibernate as adults. The outgoing numbers of overwintering insects are used as initial abundances in the first phase of the next season.

In the latest extension (**Paper III**), the model is governed by a set of parameters, some of them are based on published data on aphids and ladybirds (e.g., rate of increase under various temperatures, number of eggs per batch in ladybirds, duration of larval development), others are set artificially since the real measured values are not yet available. Duration of the egg window, larval voracity, and temperature were studied. The model in more details is described in Houdková and Kindlmann (2006) (**Paper I**) and Kintrová and Kindlmann (**Paper III**).

The model of Kindlmann and Dixon (1996, 2003) was intended for the dynamics of tree-dwelling aphid species (the sycamore aphid, *Drepanosiphum platanoides*, and the Turkey-oak aphid, *Myzocallis boernerii*). It revealed that migration is the regulatory mechanism responsible for the summer decline in aphid numbers. In the model, the tendency to migrate was determined by changes in food quality of host plants in a rather complicated way (Kindlmann and Dixon 1996). The modelling of predator's effect on an aphid population was outlined in Kindlmann and Dixon (2003). It was based on the assumption that the optimum oviposition strategy of predatory females is more important than the functional response to prey. This is substantial especially in the case of the aphid–ladybird system where the development of a ladybird larva lasts approximately as long as the existence of an aphid colony (Hemptinne et al. 1992). Resulting trends in numbers of aphids and ladybirds during a summer season predicted by the model (e.g., Fig. 1 in Houdková and Kindlmann 2006) support the hypothesis of 'generation time ratio', GTR (Kindlmann and Dixon 1999). This hypothesis derives the efficiency of a predator from the ratio of predator's developmental time to that of its prey. It is supposed that the larger is the ratio of the developmental times (great GTR), the less finely the predator can follow the prey density and therefore the smaller is the degree, to which it can deplete a patch. As a consequence, the relative effectiveness of predators as biological control agents is negatively correlated with their generation time relative to that of their prey (Dixon et al. 1995, 1997, Kindlmann and Dixon 1999a, 1999b).

QUESTIONS OF INTEREST

Concerning the model presented here, further questions were asked:

If the simulation extends from a single colony to the metapopulation level, how will the dynamics of the system change? Predators were found to be inefficient in the single prey colony model (Kindlmann and Dixon 2003). Will they have an effect on the metapopulation level? And if yes, then what phase of the year-round dynamics will it occur in? **(Paper I)**

On a long-term scale, cyclical oscillations in aphid abundance have been described in several aphid species (e.g., Sequeira and Dixon 1997, Thacker et al. 1997, Alyokhin et al. 2005, Dixon 2005, Bommarco et al. 2007, Lankin-Vega et al. 2008). Random as well as density-dependent processes were studied but the underlying mechanisms are still unknown (Thacker et al. 1997; Alyokhin et al. 2005; Bommarco et al. 2007). The introduced simulation model produces a range of oscillations in abundances of both prey and predator characterized by a median abundance, amplitude and length of the cycles. A question arises, whether these oscillations are comparable with those described in literature and which mechanism is responsible for oscillations under simplified model conditions. **(Paper III)**

Climate change has attracted attention of many scientists in the last decade. The effect of increasing temperature on population dynamics of insects, especially the pest species and pathogen vectors, seems to be of a great importance. Existing studies suggest that direct effects of temperature on insect herbivores are likely to be larger and more important than any other factor (Bale et al. 2002). Two important parameters in the model are directly influenced by a 'system' temperature: the growth rate of aphids and the developmental time of ladybirds. How will the increasing temperature influence the predator-prey interactions? **(Preliminary results)**

In biological control, intraguild predation has become a major research topic. Theoretical treatments have suggested that intraguild predation has a uniformly negative effect on the ability of predatory biological control agents to suppress populations of herbivores in agroecosystems (Rosenheim and Harmon 2006). There is strong evidence that intraguild interactions are widespread in aphid-parasitoid or aphid-parasitoid-predator systems and mostly detrimental to aphid parasitoids (Brodeur and Rosenheim 2000, Colfer and Rosenheim 2001). But how often do intraguild interactions really occur among aphid predators in a field? **(Paper II)**

References

- Alyokhin, A., Drummond, F.A. & Sewell, G. (2005) Density-dependent regulation in populations of potato-colonizing aphids. *Population Ecology* **47**: 257–266.
- Ba-Angood, S.A. & Stewart, R.K. (1980) Occurrence, development, and distribution of cereal aphids on early and late cultivars of wheat, barley, and oats in southwestern Quebec. *Canadian Entomologist* **112**(6): 615–620.
- Bale, J.S. *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**: 1–16.
- Blackman, R.L. & Eastop, V.F. (2000) *Aphids on the World's Crops*. John Wiley & Sons, Ltd., Chichester.
- Blackman, R.L. & Eastop, V.F. (2007) *Aphids on the World's Herbaceous Plants and Shrubs*. John Wiley & Sons, Ltd., Chichester.
- Bommarco, R. (2001) Using matrix models to explore the influence of temperature on population growth of arthropod pests. *Agricultural and Forest Entomology* **3**: 275–283.
- Bommarco, R., Wetterlind, S. & Sigvald, R. (2007) Cereal aphid populations in non-crop habitats show strong density dependence. *Journal of Applied Ecology* **44**: 1013–1022.
- Brodeur, J. & Rosenheim, J.A. (2000) Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* **97**: 93–108.
- Brown, M.W. & Miller, S.S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News* **109**(2): 143–151.
- Brown, P.M.J. *et al.* (2008) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *BioControl* **53**: 5–21.
- Carson, R.L. (1962) *Silent Spring*. Houghton-Mifflin, Boston.
- Colfer, R.G. & Rosenheim, J.A. (2001) Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* **126**: 292–304.
- Colunga-Garcia, M. & Gage, S.H. (1998) Arrival, Establishment, and Habitat Use of the Multicolored Asian Lady Beetle (Coleoptera: Coccinellidae) in a Michigan Landscape. *Environmental Entomology* **27**(6): 1574–1580.
- Denoth, M., Frid, L. & Myers, J.H. (2002) Multiple agents in biological control: improving the odds? *Biological Control* **24**: 20–30.
- Dixon, A.F.G. (1987) Parthenogenetic reproduction and the rate of increase in aphids. In: *Aphids, their biology, natural enemies and control*. Minks, A.K. & Harrewijn, P. (eds.), Elsevier, Amsterdam, pp. 269–287.
- Dixon, A.F.G. (2000) *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge University Press, Cambridge.
- Dixon, A.F.G. (2004) Past and future of aphid biology. In: *Aphids in a new millennium*. Simon, J.C., Dedryver, C.A., Rispe, C. & Hullé, M. (eds.), INRA, Paris, pp. 17–25.
- Dixon, A.F.G. (2005) *Insect herbivore-host dynamics: Tree-dwelling aphids*. Cambridge University Press, Cambridge.
- Dixon, A.F.G. & Kindlmann, P. (1999) Cost of flight apparatus and optimum body size of aphid migrants. *Ecology* **80**(5): 1678–1690.

References

- Dixon, A.F.G., Hemptinne, J.-L. & Kindlmann, P. (1995) The ladybird fantasy - prospects and limits to their use in the biocontrol of aphids. *Züchtungsforschung* **1**: 395–397.
- Dixon, A.F.G., Hemptinne, J.-L. & Kindlmann, P. (1997) Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga* **42**: 71–83.
- Gagné, I., Coderre, D. & Mauffette, Y. (2002) Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecological Entomology* **27**: 285–291.
- Hagen, K.S. (1962) Biology and Ecology of Predaceous Coccinellidae. *Annual Review of Entomology* **7**: 289–326.
- Hemptinne, J.-L. & Dixon, A.F.G. (2000) Defence, oviposition and sex: semiochemical parsimony in two species of ladybird beetles (Coleoptera, Coccinellidae)? A short review. *European Journal of Entomology* **97**(4): 443–447.
- Hemptinne, J.-L., Dixon, A.F.G. & Goffin, J. (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* **90**: 238–245.
- Hemptinne, J.-L., Dixon, A.F.G., Doucet, J.L. & Petersen, J.E. (1993) Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *European Journal of Entomology* **90**(4): 451–455.
- Hindayana, D., Meyhöfer, R., Scholz, D. & Poehling, H.-M. (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biological Control* **20**: 236–246.
- 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.
- Honěk, A. (1989) Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). *Acta Entomologica Bohemoslovaca* **86**: 179–192.
- Howard, M.T. & Dixon, A.F.G. (1992) The effect of plant phenology on the induction of alatae and the development of populations of *Metopolophium dirhodum* (Walker), the rose-grain aphid, on winter wheat. *Annals of Applied Biology* **120**(2): 203–213.
- Irwin, M.E., Kampmeier, G.E. & Weiser, W.W. (2007) Aphid movement: Process and consequences. In: *Aphids as crop pests*. van Emden, H.F. & Harrington, R. (eds.), CABI, London, pp. 153–186.
- Kan, E. (1988) Assessment of aphid colonies by hoverflies. II pea aphids and 3 syrphid species; *Betasyrphus serarius* (Wiedemann), *Metasyrphus frequens* Matsumura and *Syrphus vitripennis* (Meigen) (Diptera: Syrphidae). *Journal of Ethology* **6**(2): 135–142.
- Kan E. & Sasakawa, M. (1986) Assessment of the maple aphid colony by the hover fly, *Episyrphus balteatus* (de Geer) (Diptera: Syrphidae). *Journal of Ethology* **4**(2): 121–127.
- Karley, A.J., Pitchford, J.W., Douglas, A.E., Parker, W.E. & Howard, J.J. (2003) The causes and processes of the midsummer population crash of potato aphids *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer)

- (Hemiptera: Aphididae). *Bulletin of Entomological Research* **93**(5): 425–437.
- Karley, A.J., Parker, W.E., Pitchford, J.W. & Douglas, A.E. (2004) The mid-season crash in aphid populations: why and how does it occur? *Ecological Entomology* **28**: 383–388.
- Katsarou, I., Margaritopoulos, J.T., Tsitsipis, J.A., Perdakis, D.Ch. & Zarpas, K.D. (2005) Effect of temperature on development, growth and feeding of *Coccinella septempunctata* and *Hippodamia convergens* reared on the tobacco aphid, *Myzus persicae nicotianae*. *BioControl* **50**: 565–588.
- Kenis, M., Roy, H.E., Zindel, R. & Majerus, M.E.N. (2008) Current and potential management strategies against *Harmonia axyridis*. *BioControl* **53**(1), 235–252.
- Kindlmann, P. (1985) A model of aphid population with age structure. In: *Mathematics in Biology and Medicine*. Capasso, V., Grosso, E. & Paveri-Fontana, S.L. (eds.). Series: Lecture Notes in Biomathematics **57** Springer, Berlin, pp. 72–77.
- Kindlmann, P. & Dixon, A.F.G. (1989) Developmental constraints in the evolution of reproductive strategies: Telescoping of generations in parthenogenetic aphids. *Functional Ecology* **3**(5): 531–537.
- Kindlmann, P. & Dixon, A.F.G. (1993) Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* **90**(4): 443–450.
- Kindlmann, P. & Dixon, A.F.G. (1996) Population dynamics of tree-dwelling aphids: from individual to population. *Ecological Modelling* **89**: 23–30.
- Kindlmann, P. & Dixon, A.F.G. (1999a) Generation time ratios – determinants of prey abundance in insect predator-prey interactions. *Biological Control* **16**: 133–138.
- Kindlmann, P. & Dixon, A.F.G. (1999b) Strategies of aphidophagous predators: lessons for modelling insect predator-prey dynamics. *Journal of Applied Entomology* **123**: 397–399.
- Kindlmann, P. & Dixon, A.F.G. (2003) Insect predator-prey dynamics and the biological control of aphids by ladybirds. In: *Proceedings of the 1st International Symposium on Biological Control of Arthropods*. USDA, Forest Service, Honolulu/Morgantown, pp 118–124.
- Kindlmann, P. & Okrouhlá, M. (1986) Simulation of the population dynamics of a laboratory aphid coccinellid system. In: *Ecology of Aphidophaga II*. Hodek, I. (ed.), Academia, Praha, pp. 357–362.
- Kindlmann, P., Yasuda, H., Sato, S. & Shinya, K. (2000) Key life stages of two predatory ladybird species (Coleoptera: Coccinellidae). *European Journal of Entomology* **97**: 495–499.
- Kindlmann, P., Arditi, R. & Dixon, A.F.G. (2004) A simple aphid population model. In: *Aphids in a new millennium*. Simon, J.C., Dedryver, C.A., Rispe, C. & Hullé, M. (eds.), INRA, Paris, pp. 325–330.
- Kindlmann P., Jarošík V. & Dixon A.F.G. (2006) Population dynamics. In: *Aphids as crop pests*. van Emden, H.F. & Harrington, R. (eds.), CABI, London, pp. 311–329.
- Koch, R.L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science* **3**: 32, 16pp. Available online: insectscience.org/3.32

- Lankin-Vega, G., Worner, S.P. & Teulon, D.A.J. (2008) An ensemble model for predicting *Rhopalosiphum padi* abundance. *Entomologia Experimentalis et Applicata* **129**: 308–315.
- Ma, Z. & Bechinski, E.J. (2008) A survival-analysis-based simulation model for Russian wheat aphid population dynamics. *Ecological Modelling* **216**: 323–332.
- Mack, T.P. & Smilowitz, Z. (1982) CMACSIM, a temperature-dependent predator-prey model simulating the impact of *Coleomegilla maculata* (DeGeer) on green peach aphids on potato plants. *Environmental Entomology* **11**: 1193–1201.
- Mackauer, M. & Völkl, W. (1993) Regulation of aphid populations by aphidiid wasps: does parasitoid foraging behaviour or hyperparasitism limit impact? *Oecologia* **94**: 339–350.
- McVean, R.I.K., Dixon, A.F.G. & Harrington, R. (1999) Causes of regional and yearly variation in pea aphid numbers in eastern England. *Journal of Applied Entomology* **123**(8): 495–502.
- Michaud, J.P. (2002) Invasion of the Florida Citrus Ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and Asymmetric Competition with a Native Species, *Cycloneda sanguinea*. *Environmental Entomology* **31**(5): 827–835.
- Müller, C.B., Williams, I.S. & Hardie, J. (2001) The role of nutrition, crowding and interspecific interactions in the development of winged aphids. *Ecological Entomology* **26**: 330–340.
- Nedvěd, O. (2008) Invazní slunéčko *Harmonia axyridis*.
<http://zoo.bf.jcu.cz/kz/harmonia.htm>
- Obrycki, J.J. & Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology* **43**: 295–321.
- Obrycki, J.J. & Tauber, M.J. (1981) Phenology of three coccinellid species: Thermal requirements for development. *Annals of Entomological Society of America* **74**: 31–36.
- Omkar & James, B.E. (2004) Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae). *Journal of Applied Entomology* **128**(2): 150–157.
- Omkar & Srivastava, S. (2003) Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. *BioControl* **48**(4): 379–393.
- Osawa, N. (2002) Sex dependent effects of sibling cannibalism on life history traits of the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Journal of the Linnean Society* **76**: 349–360.
- Östman, Ö., Ekblom, B. & Bengtsson, J. (2003) Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics* **45**: 149–158.
- Pettersson, J., Tjallingii, W.F. & Hardie, J. (2007) Host-plant selection and feeding. In: *Aphids as crop pests*. van Emden, H.F. & Harrington, R. (eds.), CABI, London, pp. 87–113.
- Plantegenest, M., Pierre, J.S., Dedryver, C.A. & Kindlmann, P. (2001) Assessment of the relative impact of different natural enemies on population dynamics of the grain aphid *Sitobion avenae* in the field. *Ecological Entomology* **26**: 404–410.

- Remaudière, G. & Remaudière, M. (1997) Catalogue of the World's Aphididae (Homoptera, Aphidoidea). INRA, Versailles, France.
- Rosenheim, J.A. & Harmon, J.P. (2006) The influence of intraguild predation on the suppression of a shared prey population: an empirical reassessment. In: *Trophic and Guild Interactions in Biological Control*. Brodeur, J. & Boivin, G. (eds.), Springer, Dordrecht, pp. 1–20.
- Růžička, Z. (1998) Further evidence of oviposition-detering allomone in chrysopids (Neuroptera: Chrysopidae). *European Journal of Entomology* **95**(1): 35–39.
- Růžička, Z. (2001) Oviposition responses of aphidophagous coccinellids to tracks of ladybird (Coleoptera: Coccinellidae) and lacewings (Neuroptera: Chrysopidae) larvae. *European Journal of Entomology* **98**(2): 183–188.
- Sato, S. & Dixon, A.F.G. (2004) Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology* **6**: 21–24.
- Sato, S., Dixon, A.F.G. & Yasuda, H. (2003) Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecological Entomology* **28**: 628–633.
- Sequeira, R. & Dixon, A.F.G. (1997) Population dynamics of tree-dwelling aphids: the importance of seasonality and time scale. *Ecology* **78**: 2603–2610.
- Stadler, B. & Dixon, A.F.G. (2005) Ecology and evolution of aphid-ant interactions. *Annual Review of Ecology, Evolution, and Systematics* **36**: 345–372.
- Straub, C.S., Finke, D.L. & Snyder, W.E. (2008) Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control* **45**: 225–237.
- Sunderland, K.D., Fraser, A.M. & Dixon, A.F.G. (1986) Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. *Journal of Applied Ecology* **23**(2): 433–447.
- Taylor, L.R. (1977) Migration and the spatial dynamics of an aphid, *Myzus persicae*. *Journal of Animal Ecology* **46**(2): 411–423.
- Thacker, J.I., Thieme, T. & Dixon, A.F.G. (1997) Forecasting of periodic fluctuations in annual abundance of the bean aphid: the role of density dependence and weather. *Journal of Applied Entomology* **121**: 137–145.
- Vichitbandha, P. & Wise, D.H. (2002) A field experiment on the effectiveness of spiders and carabid beetles as biocontrol agents in soybean. *Agricultural and Forest Entomology* **4**: 31–38.
- Ward, S.A., Leather, S.R., Pickup, J. & Harrington, R. (1998) Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *Journal of Animal Ecology* **67**: 763–773.
- Wratten, S.D. (1977) Reproductive strategy of winged and wingless morphs of the aphids *Sitobion avenae* and *Metopolophium dirhodum*. *Annals of Applied Biology* **85**(1): 319–331.



Paper I

SCALING UP POPULATION DYNAMIC PROCESSES IN A LADYBIRD–APHID SYSTEM

Kateřina Houdková & Pavel Kindlmann

Population Ecology 48: 323–332, 2006

Abstract

Here, we study how scaling up to the metapopulation level affects predictions of a population dynamics model motivated by an aphidophagous predator–aphid system. The model incorporates optimization of egg distribution in predatory females, cannibalism among their offspring, and self-regulation of the prey population. These factors determine the within-year dynamics of the system and translate the numbers of prey and predator individuals at the beginning of the season into their numbers at the end of the season at the level of one patch – one suitable host plant or a group of these. At the end of each season, all populations of prey and all populations of predators are mixed (this simulates aphid host-alternation and ladybird migration to hibernation sites), and then redistributed at the beginning of the next season. Prey individuals are distributed at random among the patches as a “prey rain”, while adult predators that survived from the previous season optimize the distribution of their offspring, in that they prefer patches with sufficient amount of prey and absence of other predators. This redistribution followed by within–season dynamics is then iterated over many seasons. We look at whether small–scale trends in population dynamics predicted by this model are consistent with large-scale outcomes. Specifically, we show that even on the metapopulation scale, the impact of predators on prey metapopulation is relatively low. We further show how the dates of predator arrival to and departure from the system affect the qualitative behaviour of the model predictions.

Práce I

PROCESY V POPULAČNÍ DYNAMICE SYSTÉMU SLUNĚČKO–MŠICE NA ŠIRŠÍ ŠKÁLE

Kateřina Houdková & Pavel Kindlmann

Population Ecology 48: 323–332, 2006

Shrnutí

V této práci se zabýváme tím, jak rozšíření měřítka na úroveň metapopulace ovlivní předpověď modelu populační dynamiky aplikovaného na systém predátor–mšice. Model zahrnuje optimalizaci rozmístění vajíček samičkami predátorů mezi kolonie kořisti, kanibalismus mezi jejich potomstvem a samoregulaci populace kořisti. Tyto faktory určují dynamiku systému v rámci vegetační sezóny a přenos počtů jedinců kořisti a predátorů ze začátku sezóny do podzimních početností v jednotlivých populacích (koloniích na jedné hostitelské rostlině či jejich skupině). Na konci každé sezóny jsou vzájemně promíchány všechny populace kořisti a populace predátorů (což simuluje střídání hostitele u mšic a migraci na zimoviště u sluněček) a následně znovu rozmístěny na začátku příští sezóny. Jedinci kořisti se rozmisťují náhodně mezi hostitelské rostliny jakožto „déšť kořisti“, zatímco dospělí predátoři, kteří přežili z předešlé sezóny, optimalizují rozmístění svého potomstva. Vybírají si stanoviště s dostatečným množstvím potravy a současně neobsazené jiným predátorem. Přerozdělení jedinců (kořisti i predátorů) a simulace dynamiky v průběhu vegetační sezóny je opakováno v každé následující sezóně. Zaměřujeme se na to, zda trendy v populační dynamice předpovězené tímto modelem na úzké škále odpovídají výsledkům na širší, metapopulační škále. Konkrétně ukazujeme, že také na úrovni metapopulace je dopad predátorů na kořist poměrně slabý. Dále ukazujeme, jak doba příchodu a odchodu predátora ze systému ovlivňuje kvalitu předpovědi modelu.

Autorský podíl K. Houdkové: 60 %.

Paper II

INTRAGUILD PREDATION: FICTION OR REALITY?

Pavel Kindlmann & Kateřina Houdková

Population Ecology 48: 317–322, 2006

Abstract

Intraguild predation has become a major research topic in biological control. Quantification of multipredator interactions and an understanding of the consequences on target prey populations are needed, which only highlights the importance of population dynamics models in this field. However, intraguild predation models are usually based on Lotka–Volterra equations, which have been shown not to be adequate for modeling population dynamics of aphidophagous insects and their prey. Here we use a simple model developed for simulation of population dynamics of aphidophagous insects, which is based on the type of egg distribution made by predatory females, to estimate the real strength of intraguild predation in the aphidophagous insects. The model consists of two components: random egg distribution among aphid colonies, and between-season population dynamics of the predatory species. The model is used to estimate the proportion of predatory individuals that face a conflict with a heterospecific competitor at least once during their life. Based on this, predictions are made on the population dynamics of both predatory species. The predictions are confronted with our data on intraguild predation in ladybirds.

Práce II

PREDACE UVNITŘ SPOLEČENSTVA PREDÁTORŮ: ZDÁNÍ, NEBO SKUTEČNOST?

Pavel Kindlmann & Kateřina Houdková

Population Ecology 48: 317–322, 2006

Shrnutí

Predace uvnitř společenstva predátorů se stala hlavním tématem výzkumu biologické kontroly. Klíčové v této otázce jsou kvantifikace vzájemných interakcí mezi několika predátory a porozumění jejich dopadům na populaci kořisti, což jen podtrhuje důležitost populačně-dynamických modelů v tomto oboru. Bylo však ukázáno, že Lotkovy-Volterrovy rovnice, užívané v těchto modelech, nejsou vhodné pro modelování populační dynamiky mšičožravého hmyzu a jeho kořisti. V této práci používáme jednoduchý model simulující populační dynamiku mšičožravého hmyzu. Podle způsobu rozmístění vajíček samičkami predátorů odhadujeme skutečnou intenzitu predace mezi mšičožravým hmyzem. Model sestává ze dvou složek: náhodné rozmístění vajíček mezi kolonie mšic a meziroční dynamika populací predátorů. Na základě našeho modelu je možné odhadnout podíl dravých jedinců, kteří alespoň jednou za život čelili střetu se soupeřem jiného druhu. Pomocí tohoto modelu jsme určili předpovědi pro populační dynamiku obou soupeřících druhů a porovnali je s našimi experimentálními údaji o interakcích mezi sluněčky.

Autorský podíl K. Houdkové: 40 %.

Paper III

MODELLING OF METAPOPOPULATION DYNAMICS IN AN APHID-COCCINELLID SYSTEM ON A LONG-TERM SCALE

Kateřina Kintrová & Pavel Kindlmann

(submitted)

Abstract

We present here a theoretical simulation model that involves a year-round population dynamics of a host-alternating aphid species and its predator, a coccinellid, particularly a random settling of aphids on a secondary host, oviposition strategy of predatory females, and individually tracked numbers of prey and predators in the colonies. Cumulative density of the prey is the main driving force of the summer population collapse of aphid populations. Winged aphids emigrating from the summer colonies create a basis of abundances in the next year. A simple imitation of autumn migration and overwintering links the individual seasons to a 50-year sequence, enabling to study the dynamics of the aphid-coccinellid system, their interactions and the resulting oscillations in abundance on a long-term scale. The effect of the initial oviposition phase on the overall dynamics is studied. Oscillations with two and three-year cycles occur in abundances of both, prey and predator, when predators linger for long within the prey colonies. However, on a long-term scale, predators maximize their fitness when only 20 % of patches suitable for oviposition are exploited. The meaning and consequences of these results are discussed with empirical data and hypotheses already published.

Práce III

DLOUHODOBÉ MODELOVÁNÍ METAPOPULAČNÍ DYNAMIKY SYSTÉMU MŠICE-SLUNÉČKO

Kateřina Kintrová & Pavel Kindlmann

(nabídnuto k publikaci)

Shrnutí

V této práci představujeme teoretický simulační model, který zahrnuje celoroční populační dynamiku mšice střídající hostitele a jejího predátora, slunéčka, zvláště pak náhodné osidlování letních hostitelů mšicemi, strategii rozmisťování vajíček samičkami predátorů mezi kolonie kořisti a individuálně sledované početnosti predátorů a kořisti v jednotlivých koloniích. Kumulativní hustota mšic je hlavní řídicí silou letního zhroucení jejich populací. Okřídlené mšice, které opouštějí letní kolonie, tvoří základ metapopulace pro příští rok. Jednoduchá simulace podzimní migrace a přezimování propojuje jednotlivé sezóny do 50leté sekvence. To umožňuje studovat dynamiku systému mšice-slunéčko, jejich vztahy a výsledné oscilace v početnosti v dlouhodobém měřítku. Studujeme také vliv počáteční fáze, kdy samičky predátorů umisťují snůšky vajíček do kolonií kořisti, na celkovou dynamiku systému. Zdržují-li se samičky v systému dlouho, objevují se dvou- až tříroční cykly v početnosti mšic i predátorů. Nicméně z dlouhodobého hlediska maximalizují samičky predátorů svou biologickou úspěšnost, pokud využijí pouze 20 % kolonií vhodných pro umístění vajíček. Smysl a širší důsledky těchto výsledků jsou porovnány s empirickými daty a již publikovanými hypotézami.

Autorský podíl K. Kintrové: 80 %.

Modelling of metapopulation dynamics in an aphid-coccinellid system on a long-term scale

Kateřina Kintrová^{1,2} & Pavel Kindlmann^{3,4}

Abstract

We present here a theoretical simulation model that involves a year-round population dynamics of a host-alternating aphid species and its predator, a coccinellid, particularly a random settling of aphids on a secondary host, oviposition strategy of predatory females, and individually tracked numbers of prey and predators in the colonies. Cumulative density of the prey is the main driving force of the summer population collapse of aphid populations. Winged aphids emigrating from the summer colonies create a basis of abundances in the next year. A simple imitation of autumn migration and overwintering links the individual seasons to a 50-year sequence, enabling to study the dynamics of the aphid-coccinellid system, their interactions and the resulting oscillations in abundance on a long-term scale. The effect of the initial oviposition phase on the overall dynamics is studied. Oscillations with two and three-year cycles occur in abundances of both, prey and predator, when predators linger for long within the prey colonies. However, on a long-term scale, predators maximize their fitness when only 20 % of patches suitable for oviposition are exploited. The meaning and consequences of these results are discussed with empirical data and hypotheses already published.

Keywords: metapopulation dynamics, predator-prey interactions, oscillations, oviposition strategy, aphids, ladybirds.

¹Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic.

²Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic.

³Department of Theoretical Ecology, Institute of Systems Biology and Ecology, AS CR, Na Sádkách 7, CZ-370 05 České Budějovice, Czech Republic.

⁴Institute for Environmental Studies, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Prague 2, Czech Republic.

Introduction

As aphids are considered to be serious pests, many attempts were made to build a predictive model of their population dynamics. Much progress has been done in the modelling of intrinsic processes and a great attention has been devoted to the oscillations of aphid abundances during the season, especially to the sudden population crash, which usually occurs in the middle of summer. Karley et al. (2004) summarized a couple of causes most often stated by scientists: deteriorating plant quality and natural enemies. Both of them were used in models with a partial success. Apart from these, a self-regulatory process by a density-induced emigration has been suggested (Dixon 1970; Chambers et al. 1985; Gange 1995; Bommarco et al. 2007) and used to model the mid-summer crash in aphid abundances (Kindlmann & Dixon 1993; McVean et al. 1999; Houdková & Kindlmann 2006; Mashanova et al. 2008). However, what still lacks is a better understanding of the mechanism causing the oscillations in aphid abundances on a long-term scale.

Among the important ecological factors affecting the aphid dynamics during the season, especially the effect of temperature and phenology of host plants on the aphid dynamics were studied (e.g. Siddiqui et al. 1973; Wyatt and Brown 1977; Girma et al. 1990; Zhou and Carter 1992; Davis et al. 2006). Effects of more complex factors, such as atmospheric disturbances, irregularity in landscape use, and specific impact of natural enemies, are usually hard to assess because a single aphid population usually behaves like a metapopulation, i.e., a set of populations scattered over a vast area, which mix during spring and autumn migrations. Then, a change in aphid abundances caused by any factor on a local scale may easily be overridden by the dynamics of the whole metapopulation (Hassell 1987).

The effect of natural enemies on aphid populations has been thoroughly investigated. Many scientists assume that the potential of aphidophagous predators, such as coccinellids or syrphids, in regulation of aphid abundance is significant (e.g., Schmidt et al. 2003; Snyder & Ives 2003; Bommarco et al. 2007; Donaldson et al. 2007; Rhains et al. 2007; Costamagna et al. 2008). However, other studies revealed that the effect of predators is non-significant (Dixon 1970,

2000; Wool 2002; Kindlmann et al. 2005). Theoretical models involving bi- or tri-trophic levels – host plant, aphids, and their natural enemies (Skirvin et al. 1997; Ro & Long 1999; Gosselke et al. 2001; Plantegenest et al. 2001; Houdková & Kindlmann 2006) – indicate that predators can partially, but not substantially, affect the aphid dynamics (Dedryver 1987; Kindlmann & Dixon 1999; 2001). On a long-term and metapopulation scale, only one model of the aphid-coccinellid interaction has been presented until now (Houdková & Kindlmann 2006) but it still awaits empirical verification.

In this study, we further develop our simulation model (Houdková & Kindlmann 2006), which is focused on aphid-coccinellid interactions at the metapopulation level. As an improvement to the previous model, special attention is given to the settling phase of aphid colonies in patches and to the individual dynamics of patches during the season. The long-term dynamics is based on linking individual seasons by a simple imitation of overwintering to a 50-year sequence, thus enabling to study the dynamics of the aphid-coccinellid system, their interactions and the resulting oscillations in abundance on a long-term scale. We focused on the effects two main parameters of the predator activity: the duration of coccinellid oviposition activity and a voracity of coccinellid larvae, which affect the aphid dynamics in the settling phase and the main summer dynamics, respectively. We compare our results with previous studies.

Methods

Biological background

To understand the linking of model parts, let us briefly summarize the context of the aphid-coccinellid interactions. Aphids are characteristic by a parthenogenetic reproduction and vivipary. They usually have only one sexual generation in the autumn, which gives birth to overwintering eggs (Dixon 2005). Some aphid species are obligate tree-dwellers, other (host-alternating) species complete only one or few first spring generations on trees or shrubs (primary hosts) as wingless individuals, and then produce a winged generation migrating to the herbaceous plants – secondary hosts (Blackman & Eastop 1994). Here, a rapid

population increase is often achieved within several generations and an equally steep decline follows together with a production of another winged generation, which migrates back to the primary host (Blackman & Eastop 1994). As migrating, aphids from a 'region-wide' area mix in autumn on the primary host, where the sexual generation mates, and individuals of the new generation spread themselves in spring again. Thus, a regional aphid population is best described as a metapopulation. This approach is used also in the model.

Aphidophagous predators (typically Coccinellidae, Syrphidae and Chrysopidae) feed on temporarily very abundant, but ephemeral prey with an extremely fast dynamics within its colonies. Adult predators move easily among the colonies, but the juveniles develop predominantly within the colony they were born in and are confronted with the bottleneck in prey resources that occurs during the massive emigration of the prey back to the winter host. Concurrently they can forage on eggs or smaller larvae but are faced to cannibalism of older predatory larvae, the pressure of which escalates with disappearance of aphids (Osawa 1993; Hironori & Katsuhiko 1997; Kindlmann et al. 2000). As a direct consequence, there is a high juvenile mortality in aphidophagous predators (up to 95–99 % in Coccinellidae, Osawa 1993; Kindlmann et al. 2000), which has to be compensated by high female fecundity and clever oviposition strategy. There is a strong selection pressure in aphidophagous females to lay eggs only in young aphid colonies, which are not yet occupied by other predators (Kindlmann & Dixon 1993, Hemptinne & Dixon 2000). Such colonies do not contain other predatory larvae threatening the currently laid eggs or the youngest larvae hatched later, and the colony is likely to persist in abundance of aphids during whole larval development. Aphidophagous predators have developed an efficient strategy to deal with this situation: tracks of predatory larvae in the colony act as a signal for the predatory females to cease oviposition and leave the colony. The ability to recognize these oviposition-detering allomones produced by the conspecific larvae has been described in coccinellids and chrysopids (Hemptinne et al. 1992, 1993; Růžička 1998, 2001). Thus predatory females are able to oviposit almost exclusively into aphid colonies, which are in early stage of their development and free of conspecific larvae (Kindlmann and Dixon 1993). The

period, when there are some aphids but no conspecific larvae yet in an aphid colony, is called ‘egg-window’. Such colony is optimal for oviposition. Laboratory studies confirmed that aphidophagous predatory females optimize their oviposition according to these two rules (Dixon 1959; Hemptinne et al. 1992, 1993, Michaud & Jyoti 2007).

Mathematical Model

The model combines both approaches, a mechanistic as well as analytic one, and also includes some stochasticity. The mechanistic approach with the stochastic element is used in the settling phase where, as we believe, a destiny of each individual contributes significantly into the overall dynamics later in the season. On the contrary, the dynamics of a colony already settled is modelled analytically by a set of differential equations because the interactions between predators and prey are simpler and known and the individual does not play such an important role.

The simulation is run in a virtual landscape consisting of p patches suitable for development of aphid colonies. The patch may represent a single shoot, one plant, or a patch of these – depending on the mobility of the animals considered. Any spatial structure of the patches is not incorporated in detail – the distances from patch to patch are all the same, it means that it demands the same energy to fly from a patch to any other patch. Various events in the system are conducted by a set of parameters described later. The model consists of three phases:

1. Egg-window dynamics – at the beginning of this phase the prey immigrates to the system from the winter host and starts to reproduce. Predatory females enter the system during the first few days, fly randomly from patch to patch, feed on prey and lay their eggs in “suitable” patches according to optimization rules mentioned above. The random distribution of aphids among patches, as well as random foraging and oviposition of the females brings some stochasticity into the model.

2. Within-season dynamics – in this phase we use the prey and predator numbers in each patch, as they were set in the egg-window phase, and simulate the intrinsic dynamics of each patch separately until a new generation of young predators emerges from their pupae. During this period, further immigration of either prey or predator is neglected assuming it to be small compared to the intrinsic system dynamics.
3. Between-season dynamics – in this part the winter survival is imitated, when prey faces unfavourable conditions as eggs or hibernating larvae, and predators hibernate as adults. The outgoing numbers of overwintering insects are used as initial abundances in the first phase of the next season.

Egg-Window Dynamics

This phase of the model simulates the basic events in the system early in existence of colonies: the settlement and growth of prey colonies in the virtual landscape and the movement, foraging and oviposition activity of predators (fig. 1). We assume that the individuals of prey immigrate into the patches on the first day of the season, and do not migrate between them. As we suppose the prey to come from the primary host, there is no relationship between the number of prey in one particular patch this year and last year. Prey lands in patches at random and starts to reproduce. The target patch is chosen randomly from a uniform distribution $U(1, p)$. We suppose an exponential reproduction with a constant growth rate, r .

The predator is supposed to be univoltine, so only one egg-window phase in the season is included. We consider only female individuals of the predator. Supposing a 1:1 sex ratio this does not affect the simulation outcome. Females enter the system during the first d days (artificial parameter) of the egg-window phase, the day of arrival is chosen randomly from a uniform distribution $U(1, d)$. “One day” in the simulation corresponds to one day in a development of predatory larva. The activity of predatory females during the egg-window phase is given by a number of flights per day ($freq$, artificial parameter). In every flight, all present females are redistributed among the patches. The target patch is chosen randomly

from the uniform distribution, so it is possible to stay in the same patch or to meet another female. If there is any prey in the target patch, the female feeds on them, but does not eat more than N_{lunch} (estimated parameter) of prey individuals. To control survival and oviposition of females, we introduced an energy budget, E_{mean} (artificial parameter), for each of them (see section Parameter values used). Every prey individual eaten represents one energy unit, which is added to

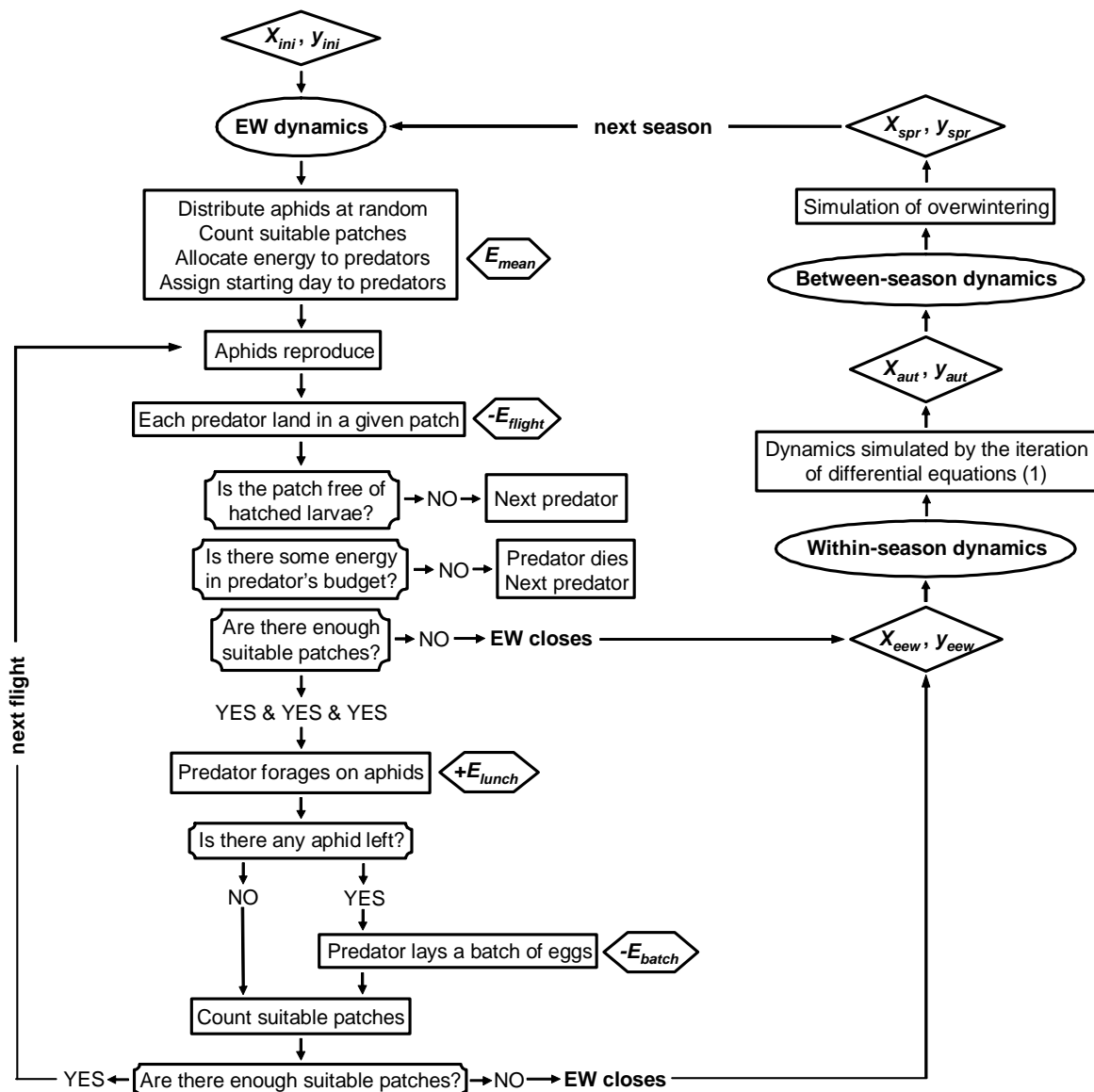


Figure 1. Scheme of the model. The left column describes the mechanistic part of the simulation, the right column outlines the analytic part.

the female's energy budget, and the prey individual is subtracted from the patch. Similarly, a constant cost of every flight (*Eflight*, artificial parameter) is subtracted from the energy amount of each female. If the energy budget of the female is depleted, she dies. Once her energy level reaches a value *Eovi* (artificial parameter), she can lay a *Batch* (estimated parameter) of eggs. The energy needed for oviposition is subtracted from the female's energy budget. According to the optimization rules, females oviposit only in "suitable" patches, which means there is some prey present and no oviposition-detering traces of conspecific larvae met by the female. The traces appear in a patch after larvae emerge from eggs, so it is possible to oviposit in a patch with another batch of yet unhatched eggs. The time of emergence of the first instar larvae is set by parameter *Hatch* (estimated parameter). The patches without prey or with hatched larvae are supposed to be unsuitable for oviposition. Once the proportion of unsuitable patches exceeds a critical value (*unsuit*, studied parameter), the egg-window phase closes and the females leave the system (the smaller *unsuit*, the earlier departure). Nevertheless, the maximum duration of the egg-window phase is set by *EWmax* (artificial parameter). We do not consider the eggs laid later, because most of these larvae would die in a consequence of bottleneck in prey abundance. The final numbers of prey and eggs of predator within every patch are used further in the within-season dynamics modelling.

Within-Season Dynamics

The within-season dynamics is supposed to be driven mainly by cumulative density of prey (Kindlmann 1985; Chambers et al. 1985; Kindlmann & Okrouhlá 1986; McVean et al. 1999; Kindlmann et al. 2004; Rhainds & Messing 2005; Kindlmann et al. 2007; Mashanova et al. 2008) and partially by voracity of predatory larvae. To simulate this phase, we used a modified set of differential equations suggested by Kindlmann and Dixon (2003), who showed that these equations fit well the within-season dynamics in colonies already settled. In contrast to Houdková and Kindlmann (2006), we simulated the dynamics separately for each patch. The system of equations consists of four parts:

(1a) change in cumulative density of wingless prey

$$\frac{dh}{dt} = x, \quad h(0) = 0$$

(1b) change in instant prey density

$$\frac{dx}{dt} = (r - ah)x - \frac{vor \cdot pref \cdot x \cdot y}{b + pref \cdot x + y}, \quad x(0) = x_0$$

(1c) increase in cumulative density of winged prey

$$\frac{dz}{dt} = ahx, \quad z(0) = 0$$

(1d) decrease in predator density due to cannibalism

$$\frac{dy}{dt} = -\frac{vor \cdot y^2}{b + pref \cdot x + y}, \quad y(0) = y_0$$

where $h(t)$ – cumulative density of prey at time t ; $x(t)$ – instant density of prey at time t ; $z(t)$ – cumulative density of winged prey at time t ; a – scaling parameter relating prey cumulative density to its own dynamics; r – maximal potential growth rate of a prey population; $y(t)$ – instant density of predator at time t ; vor – voracity of predatory larvae; b – parameter of the functional response of predator; $pref$ – preference of predatory larvae for prey over conspecific individuals, here set to 1, i.e. no special preference.

We used an iterative approach with a step “one day” to approximate the within-season dynamics. Duration of this phase (i.e. number of steps) is set by time from the end of egg-window phase to emerge of adult predators of the latest-laid eggs (parameter *Temerge*). The following biological assumptions are incorporated in the equations:

- (i) The prey dynamics is derived from the exponential growth (r defines the exponential component of the population growth) but is driven primarily by a negative response of prey to its cumulative density (the term ‘ $- ahx$ ’ in equation 1b), as was described for herbivorous insects e.g. by Kindlmann et al. (2004). The impact of predators is given by voracity and optionally by preference for the prey or conspecific larvae.

Tabulka 1. Parameter values used.

Parameter	Value	Type of parameter, used data
Number of patches	$p = 10,000$	Fixed parameter
Initial number of fundatrices	$x_{ini} = 10,000$	Fixed parameter
Initial number of predators	$y_{ini} = 500$	Fixed parameter
Maximal potential growth rate of prey population	$r = 0.35$	Parameter estimated from data (Siddiqui et al. 1973)
Period of predator arrival	d	Artificial parameter
Number of flights per day	$freq = 8$	Artificial parameter
Average initial energy supply	$E_{mean} = 20$	Artificial parameter of normal distribution
Standard deviation of initial energy supply	$E_{sd} = 2$	Artificial parameter of normal distribution
Cost of one flight	$E_{flight} = 0.5$	Artificial parameter
Minimum energy needed for oviposition	$E_{ovi} = 30$	Artificial parameter
Cost of one batch	$E_{batch} = 10$	Artificial parameter
Food transformation efficiency	$effi = 1$	Changeable parameter
Number of eaten aphids	$N_{lunch} = 5$	Parameter estimated from data and adapted to the energetic balance (Hukusima & Kamei 1970, Michels & Flanders 1992, Omkar & James 2004, Omkar & Srivastava 2003, Soares et al. 2004)
Number of eggs in a batch	$Batch = 20$	Parameter estimated from data (Hukusima & Kamei 1970, Kalushkov & Hodek 2004, Lanzoni et al. 2004, Omkar & James 2004, Omkar & Srivastava 2003, authors' unpublished field data)
Time to hatching of first instar larvae	$Thatch = 5.2$	Parameter estimated from data (Atlihan & Kaydan 2002; Ba M'Hamed & Chemseddine 2001; Hodek 1973; Katsarou et al. 2005; Lanzoni et al. 2004; Miller 1992; Obrycki & Tauber 1981, 1982; Pervez et al. 2005.)
Time to emergence of adults	$Temerge = 31.2$	Parameter estimated from data (Atlihan & Kaydan 2002; Bazzocchi et al. 2004; Bellows et al. 1992; Dixon 2000; El Habi et al. 2000; Hodek 1973; Hukusima & Kamei 1970; Katsarou et al. 2005; Lanzoni et al. 2004; Miller 1992; Miller & Paustian 1992; Mori et al. 2005; Obrycki & Tauber 1981, 1982; Özder & Sağlam 2003; Pervez et al. 2005; Uygun & Atlihan 2000; Yasuda & Dixon 2002)
Proportion of unsuitable patches	$unsuit = 10 - 100 \%$	Studied parameter
Larval voracity	$vor = 0.05 - 0.30$	Studied parameter
Scaling constant of prey dynamics	$a = 0.00005$	Fixed parameter (Kindlmann et al. 2004)
Functional response of predator	$b = 0.01$	Fixed parameter
Probability of winter survival of prey	$survAph = 0.0015$	Fixed parameter
Probability of winter survival of predator	$survLady = 0.8$	Fixed parameter

- (ii) The abundance of prey next season is derived from a number of overwintering eggs. In aphids, this depends on a number of adults mating on the winter host plant, which is given by a number of winged individuals leaving the metapopulations colonies in the summer host plant. In our equations, the amount of emigrating winged prey individuals is described by the term ' ahx ', interpreted this time as a positive contribution to the cumulative number of winged prey (equation 1c).
- (iii) Predators pupating in a patch rarely reproduce within the same patch (Dixon 2000), but adults fly off and reproduce elsewhere. Therefore we assume that the initial density of predators in a patch is defined by the number of eggs laid there by females during the egg-window phase and any changes in the number of larvae within the patch are due to larval cannibalism and not reproduction. Adult predators are not included into the within-season dynamics to simplify calculation.
- (iv) The preference ($pref$) for eating prey or rather conspecific larvae and eggs by predatory larvae is set to 1. It means no special preference for prey, the larvae eat whatever they meet ("meet and eat" hypothesis, Kindlmann & Dixon 2003). The preference does not change with time, only numbers of available prey and larval rivals vary.

Between-Season Dynamics

Cumulative numbers of winged prey over the patches, as well as numbers of mature predators, are summed together. These totals determine the initial abundances of prey and predator next year. Losses during migration between host plants or to hibernation sites and winter survival are imitated by probabilities of prey and predator survival P_x and P_y , respectively (artificial parameters chosen so that the populations in optimal abundances did not go extinct). The resulting counts are used as input data for the egg-window phase next spring.

The simulations were run under the R software (R Development Core Team 2009). The source code is available on request by K.K.

Results of simulations are studied either as changes in abundances within a season and among years, or as changes in 50-year-median of spring abundances with respect to a chosen parameter.

Parameter values used

A detailed list is given in Table 1. The figures x_{ini} and y_{ini} set initial numbers of prey and predators, respectively, for the first year. The activity of predatory females during the egg-window phase is controlled by a set of energy parameters: $E_{mean} \pm E_{sd}$, E_{flight} , E_{ovi} , E_{batch} , and optionally $effi$. These are chosen so that the female survives 4-5 days without nutrition, probably lays one batch of eggs per day, and survives the egg-window phase in an abundance of prey. The model does not suppose that the female necessarily lays all her eggs during the egg-window phase. With food transformation efficiency, $effi$, set to 1, an ingested aphid represents one unit of energy. The initial apportionment of energy along a normal distribution $N(E_{mean}, E_{sd}^2)$ introduces some variability to the model. A mean adult consumption is estimated to 40 aphids eaten daily it means at the most 5 aphids eaten in one patch in the case of 8 flights daily. A consumption of larvae hatched during the egg-window phase is not involved assuming the daily intake of first and second larvae being negligible (Katsarou et al. 2005). The within-season dynamics is specified by parameters a and b which are set in accordance with Kindlmann et al. (2004). The larval voracity (vor) changes in appropriate range to simulate the larval pressure on a prey colony.

Results

Typical trends in numbers in a patch during the within-season dynamics predicted by equations (1) are shown in the figure 2. They correspond very well to the observed ones (Gange 1995; Hironori and Katsuhiko, 1997; Kindlmann *et al.*, 2004; Matis et al. 2008). There is only one peak in the abundance of prey and the individuals respond negatively to their cumulative density resulting in a steep decline in their abundance, which can be interpreted as a bottleneck in prey availability for predators. There is no predator reproduction in the patch;

therefore, their numbers monotonously decline. Because the diet of predatory larvae is defined by mean of the voracity, the decline in predator numbers is more pronounced in scarcity of prey when cannibalism plays its role.

Figure 3 represents relationships between the end of egg-window and autumn abundances of prey and predators as predicted by the equations (1) for various initial numbers of both, prey and predator. The relationship of the autumn abundance of winged prey, i.e. individuals emigrating from a patch, to its end of EW abundance is almost linearly increasing (fig. 3 A). Predatory larvae reduce the expected prey abundance proportionally to their numbers, but their impact on the prey density is feeble (figs. 3 A, B). Predator numbers are strongly affected by prey abundances (fig 3 C). The larvae do best when the prey colony is about 10 individuals at the end of egg-window phase (under a larval voracity = 0.10). In this density, prey is numerous enough to overcome the feeding pressure of larvae, but still sparse, so that there is a fairly long time for the larvae before prey reaches its peak density and becomes rare again. In predator numbers, it generally holds: the more eggs at the beginning, the more adults at the end. However, the initial abundance of the prey influences predator numbers disproportionately (fig. 3 D).

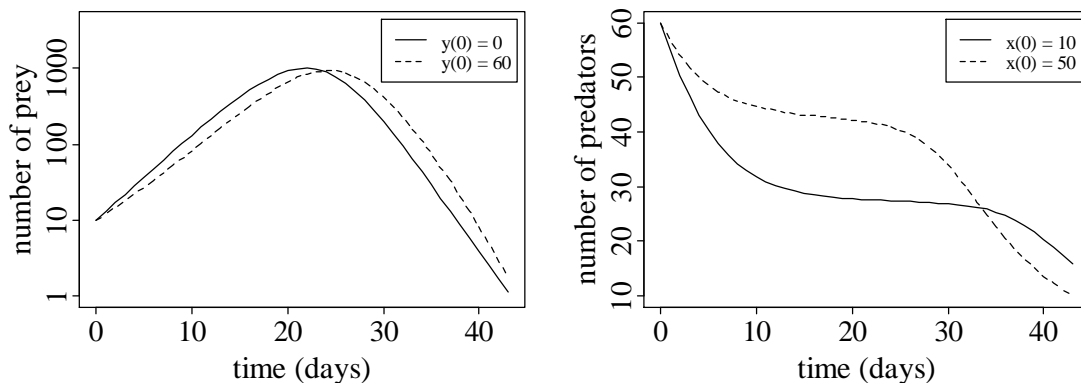


Figure 2. Trends in prey (left) and predator (right) abundances in time predicted by the within-season equations where $a=0.00005$, $r=0.3$, $v=0.1$, $b=0.1$, $e=1$, for $y(0)=0$ and $y(0)=60$ (left) and for $x(0)=10$ and $x(0)=50$ (right) – see insets for line codes.

We studied how larval voracity affects the dynamics of predator within a season. Figure 4 shows the effect of growing voracity on resulting numbers of

mature predators. Not surprisingly, the more voracious larvae, the fewer of them can complete the development to adulthood. When prey is abundant at the end of egg-window phase, the bottleneck in prey availability is more pronounced if voracity is high and the cannibalism of conspecific larvae is more frequent. The impact of larval voracity on the dynamics of prey is negligible. The shape and range of relationship between the autumn abundance of winged prey and numbers of predators (eggs) in the end of EW is almost the same as in figures 3 B and 3 A, respectively. If the larval voracity doubles, the decrease in autumn abundance of winged prey also roughly doubles in respect to the “predator-free” autumn

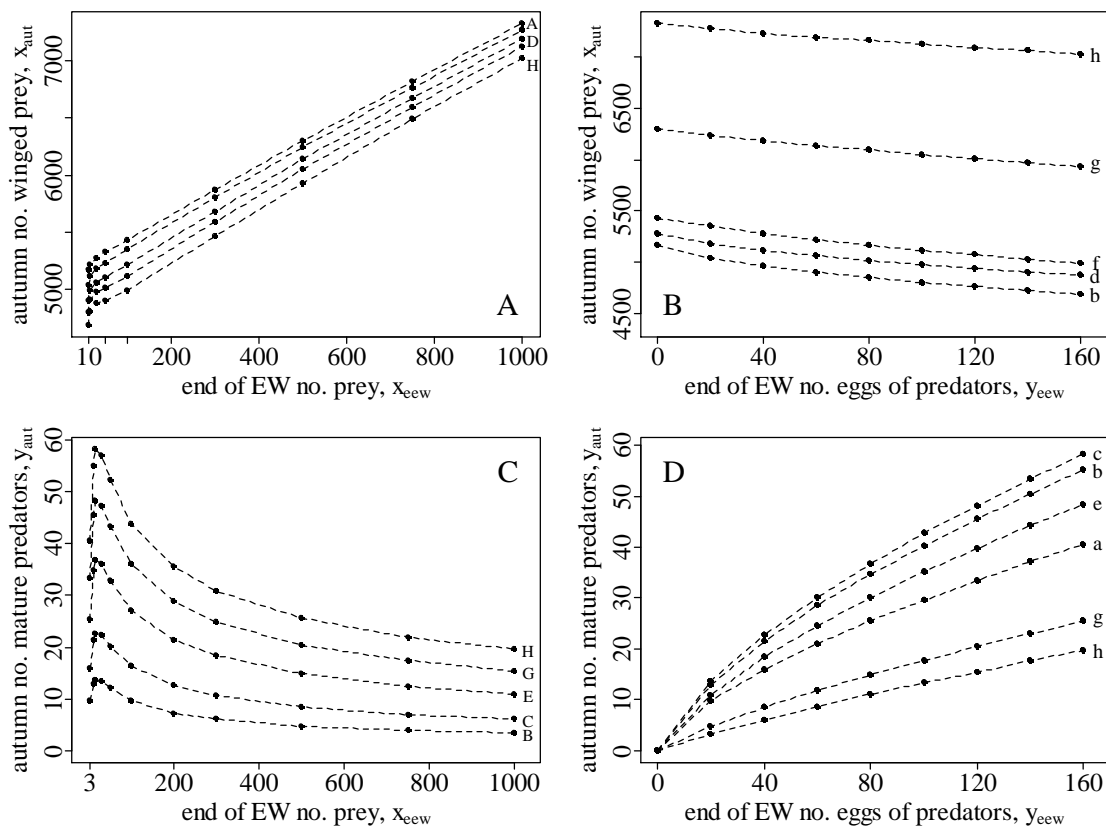


Figure 3. The relationship between the end of egg-window (EW) and autumn abundances of prey and predators as predicted by the equations (1). The larval voracity = 0.10, iteration step = 1 day. A=0, B=20, C=40, D=60, E=80, F=100, G=120, H=160 initial numbers of predator eggs, A, B, D, F, H in the panel (A); a=3, b=10, c=15, d=30, e=70, f=100, g=500, h=1000 initial abundances of prey. (Parts (C) and (D) differ from Houdková & Kindlmann (2006) because of printer gen gremlin there.)

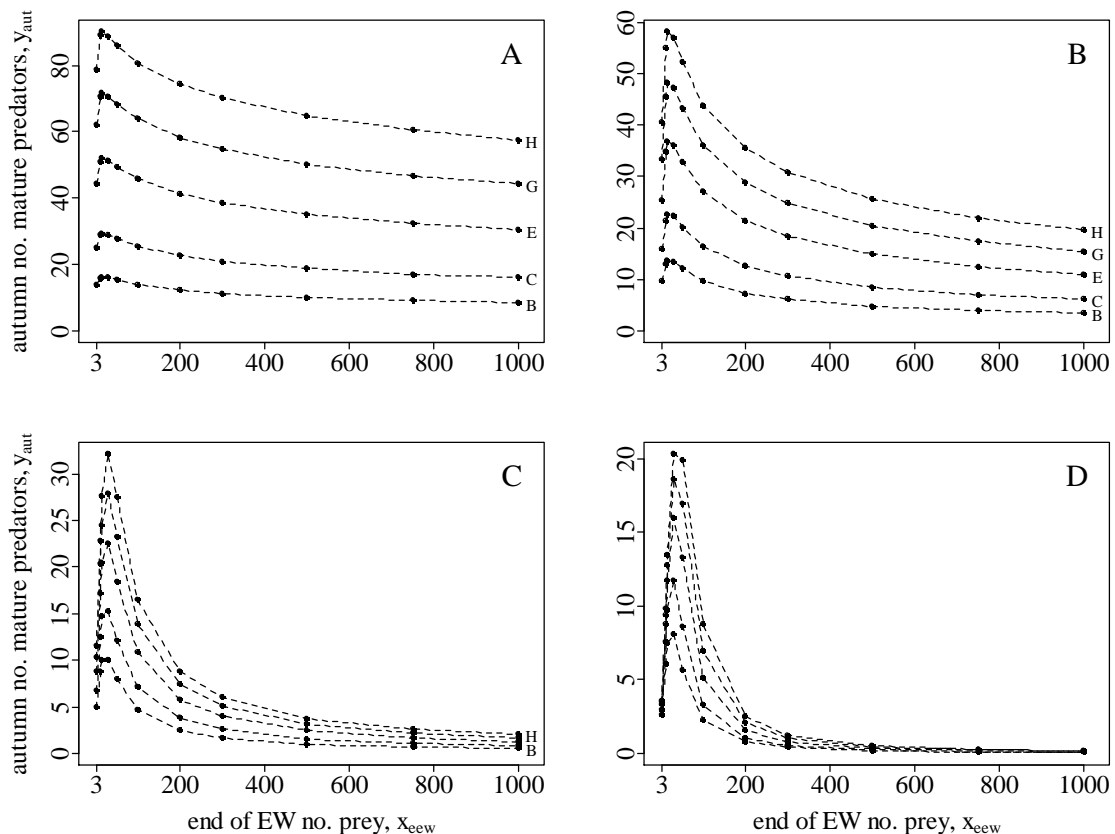


Figure 4. The relationship of autumn predator numbers to the end of EW abundances of prey with respect to the increasing larval voracity: (A) 0.05, (B) 0.10, (C) 0.20, (D) 0.30 according to the equations (1). The initial density of predator eggs $B = 20$, $C = 40$, $E = 80$, $G = 120$, $H = 160$.

abundances of winged prey. Nevertheless, the decrease occurs in dozens or few hundreds of winged prey individuals, i.e., no radical difference.

We then studied the between-season dynamics in a 50-year period, predicted by the model with various parameters of larval voracity and instant of predator departure from patches. The model exerts a rich array of shapes, amplitudes and extremes (fig. 5). In general, prey tends to remain in a stable state (fig. 5 A). This stable prey dynamics is disturbed by the feeding pressure of predators – either by the duration of egg-window when the predator females forage in prey patches (given by the parameter *unsuit* in egg-window dynamics) or by the degree of larval voracity (*vor* in the within-season dynamics). The abundances of predator fluctuate relatively more than those of prey and the fluctuations are the more distinctive, the longer is the egg-window phase (fig. 5 B

vs. 5 D). In an extreme, one or both populations can go extinct (fig. 5 A). However, if the predation pressure of ovipositing females abates, median abundances will increase in the prey as well as predator. Moreover, the risk of extinction will be smaller and the dynamics more stable. A delayed arrival of predators to the system has a similar effect (Houdková & Kindlmann 2006).

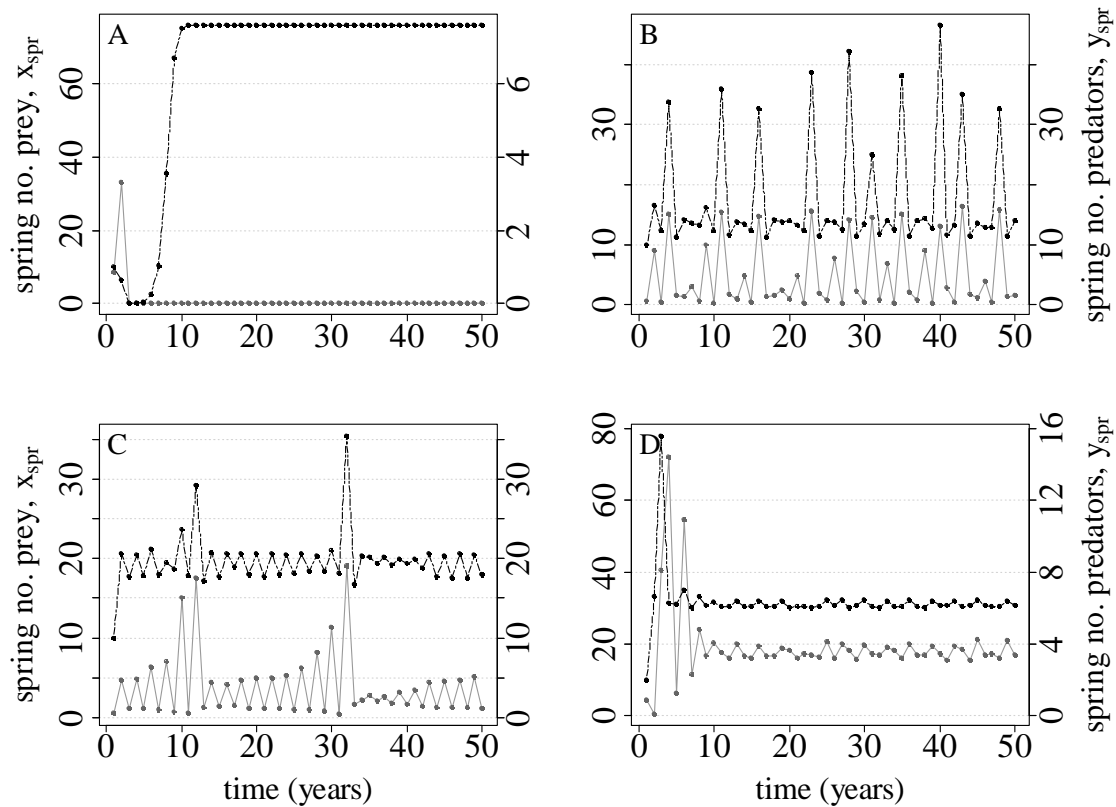


Figure 5. Oscillations in spring abundances of prey (black) and predator (grey) simulated by the model. The larval voracity = 0.20, percentage of unsuitable patches in the instant of predator departure = 100 % (A), 80 % (B), 70 % (C) and 50 % (D). Abundances are in thousands. Great oscillations in first years of panels (A) and (D) are caused by biases in the initial numbers of prey and predator from the overall medians.

The fluctuating abundances most often show three-year and two-year cycles and the number of predators is the driving force of these oscillations. When the predator is less abundant in spring (fig. 6 A, 23rd year), its pressure on the prey is weak, the egg-window phase is long (15 of 15 days), plenty of eggs are laid and

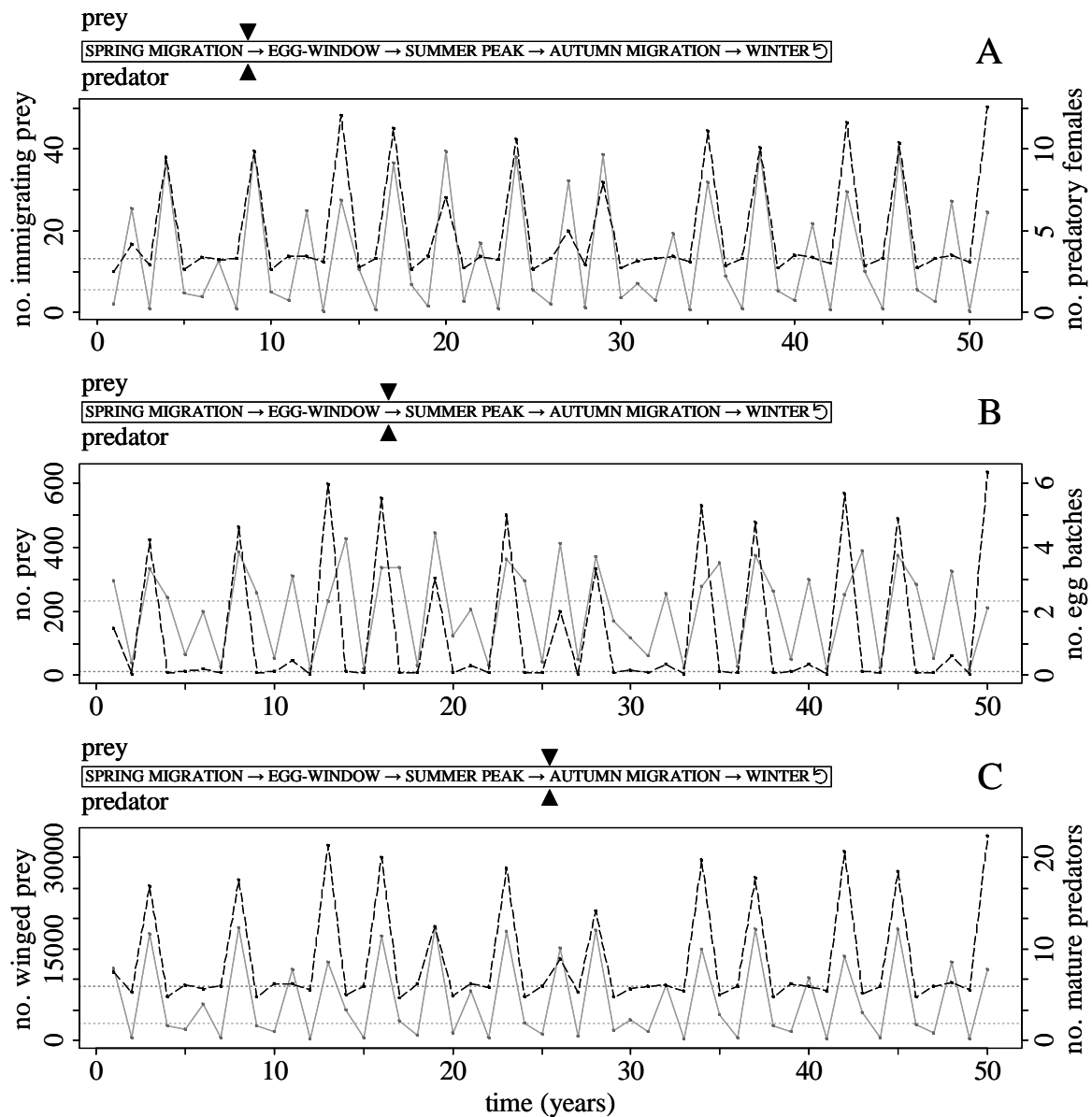


Figure 6. Oscillations in spring (A), end of EW (B), and autumn (C) abundances of prey (black) and predator (grey) simulated by the model. The larval voracity = 0.30, percentage of unsuitable patches in the instant of predator departure = 80 %. Abundances are in thousands.

the prey escalates to an enormous abundance (fig. 6 B, 23rd year). Thus, a lot of predator larvae mature in the profusion of prey (fig. 6 C, 23rd year). In the next season both prey and predator occur in manifold numbers (fig. 6 A, 24th year). As the virtual landscape is finite, predatory females devour a lot of prey and all suitable patches are occupied by egg batches immediately. The egg-window phase

closes in 2 to 3 days and most predatory females do not lay any eggs. Now, every patch either hosts a batch of eggs or is prey-free therefore the predaceous pressure on prey is systematic and its numbers are forced down (fig. 6 B, 24th year). Consequently, a strong competition arises among predatory larvae within one patch and cannibalism plays its role. In abundance of larvae only a median number develops to mature and the prey is suppressed below its median abundances (fig 6 C, 24th year). The next spring, there is a balanced number of predators but the prey is scarce (fig. 6 A, 25th year). Consequently, predatory females intensively forage for food and lay only few egg batches (fig. 6 B, 25th year). As a result, numbers of predators drop next year while the prey does not exceed the median abundance (fig. 6 A, 26th year). This cycle repeats more or less regularly, the random elements in spatial distribution of individuals change the dynamics in detail, but the overall median of abundances or type and intensity of oscillations remain similar for each combination of parameters.

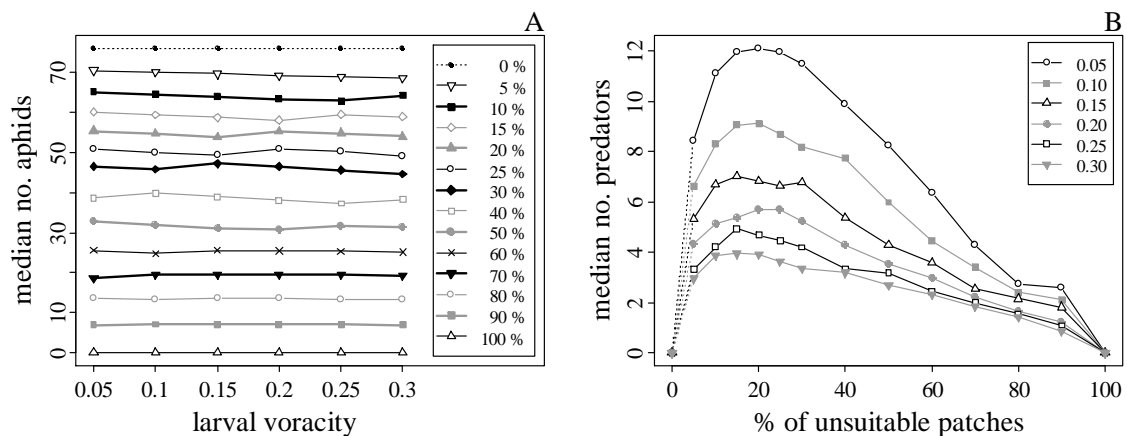


Figure 7. Trends in median abundances of prey and predator. Points represent median of spring abundances in a 50-year period, which is characterized by a combination of parameters of the larval voracity and percentage of suitable patches. Once this number descends below the given proportion (parameter *unsuit*), predators cease ovipositing, leave the system and the egg-window phase closes. (A) Median abundances of aphids (in thousands) do not change with larval voracity (the horizontal axis) but with the duration of the EW phase (legend key). (B) Median numbers of predators (in thousands) change with both, the larval voracity (legend key) and the duration of the EW phase (the horizontal axis).

Trends in medians of spring prey and predator abundances give an idea about the effect of studied parameters on the population dynamics on the long-term scale. The increasing larval voracity lowers the number of matured predators directly (fig. 7 B), but has no impact on the abundance of prey (fig. 7 A). The result is not surprising: the abundance of prey represents a carrying capacity of the landscape for predators and the maximum sustainable amount of predators in the landscape is given by the product of predator's abundance and voracity. The duration of the egg-window phase (parameter *unsuit*) reduces the median abundances of prey: the later the departure of predatory females, the lower the prey abundance (i.e. the longer the EW, the lower the prey abundance, or similarly the greater the parameter *unsuit*, the lower the prey abundance; fig. 7 A). Predator numbers achieve the maximum in departure at 20 % of unsuitable patches (i.e. early departure) then the numbers decline (fig. 7 B).

Looking at the ratio between median abundances of aphids and predators (fig. 8), a well-balanced result appears within a wide range of the instant of departure as well as larval voracity of predators. The prey gains superiority only if predators leave the system very early. At the other end, predators suppress the prey only if they stay for very long. However, this is not advantageous for predators as shown in the figure 7 B.

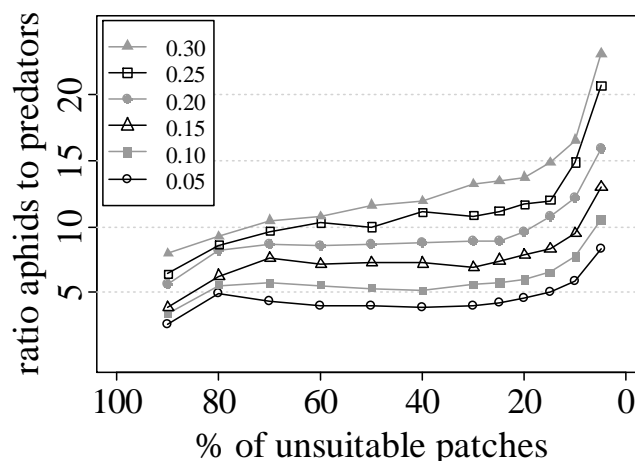


Figure 8. A ratio of prey to predator abundances. Points represent the ratio of medians of spring abundances in the 50 year simulation which is characterized by the combination of parameters of the larval voracity (see the legend key) and percentage of unsuitable patches (the horizontal axis).

Discussion

Despite the necessary simplification, the model results are interesting and comparable with real data on aphid and coccinellid abundances. More than the previous model (Houdková & Kindlmann 2006), this model showed that predators can influence especially the settling period of aphid populations when colonies are small. Consequences for the overall model dynamics are significant. However, the main results of our simulations are somewhat conflicting. In the model, the established population of predators reduces the long-term median abundance of the prey to various extents, depending on the length of the egg-window phase (fig. 7 A). The longer the egg-window phase, the more are the median abundances of the prey suppressed. The long egg-window phase brings also great oscillations in the year-to-year abundances of both, prey and predators. The shape and frequency of oscillations are comparable with oscillations in published long-term data (see below). But, lingering too long within the prey patches suitable for oviposition is not advantageous for the predator. According to the figure 7 B, the optimal instant of predators' departure occurs at about 20 % of unsuitable patches, whereas the oscillations appear if predators depart at about 70 % of unsuitable patches.

The model scenario is constructed for the host-alternating aphid species, especially those on agricultural crops (e.g. wheat, maize, alfalfa), which are specific by two great migrations within a season mixing completely the aphid metapopulations from a wide area and causing high losses of individuals. Long-term abundance records of such species (*Aphis fabae* – Thacker et al. 1997; *Aphis nasturtii*, *Macrosiphum euphorbiae*, *Myzus persicae* – Alyokhin et al. 2005; *Rhopalosiphum padi* – Bommarco et al. 2007, Lankin-Vega et al. 2008) show a range of oscillation patterns found by our simulations including periods of regular two-, three- and four-year cycles, unusual peaks, or several years of stagnation. Searching for mechanisms of these oscillations, significant density-dependent processes in aphid abundances from year to year were proved. Effects of density-independent weather factors were tested as well but the results are not corroborating. The role of natural enemies was not studied at all but there are suggestions that natural enemies contribute to the oscillations of the aphid population dynamics (Thacker et al. 1997; Alyokhin et al. 2005; Bommarco et al.

2007). Several abundance records of tree-dwelling aphid species are also available but as noted by Bommarco et al. (2007) these species are strongly linked to their respective woody hosts and should not be directly compared with the host-alternating species. However, records of deciduous tree-dwelling species (*Phyllaphis fagi* – Turchin & Taylor 1992, Perry et al. 1993; *Myzocallis boernerii* – Sequeira & Dixon 1997, Dixon 2005; *Drepanosiphum platanoides* – Dixon 2005) present much more regular oscillations with mostly two-year cycles. The density-dependent processes were well proved whereas the weather factors were not. The role of natural enemies is discussed without an unequivocal conclusion. On the other hand, Wool (2002) reported neither the density dependent regulation nor any significant correlation with weather factors in an oscillating 20-year sequence of gall abundance of *Baizongia pistaciae* on *Pistacia palaestina* trees in Israel.

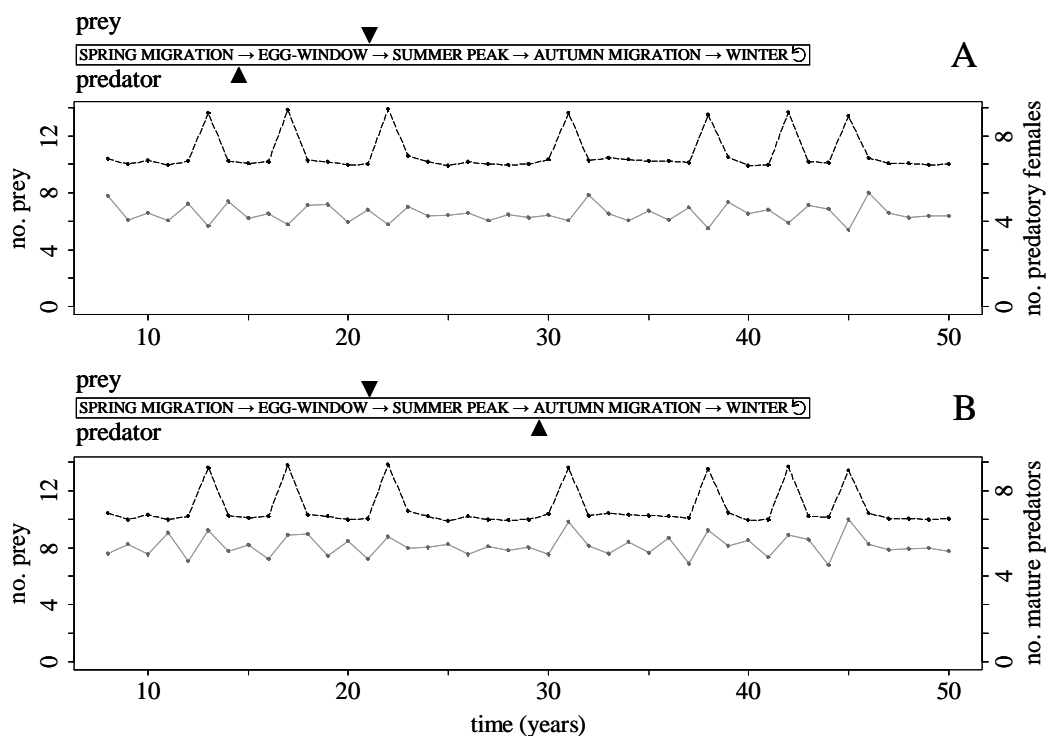


Figure 9. Oscillations in the end of EW abundances of prey (black) and spring (A) numbers of predator (grey), and autumn (B) numbers of predator (grey) simulated by the model. The larval voracity = 0.05, percentage of unsuitable patches in the instant of predator departure = 70 %. Abundances are in thousands. The oscillations are rather indistinct because the combination of parameters sets only weak predatory pressure on prey.

The impact of aphids' natural enemies is intensively studied but the 'quantitative' answer is still not available. The only one found long-term study on parallel oscillations of aphid and coccinellid abundances was provided by Honěk and Martinková (2005). They studied a 27-year record of *Coccinella septempunctata* abundance at a hibernation site in the west of the Czech Republic, and an 18-year record of summer maximum abundances of three aphid species in stands of winter wheat. Annual fluctuations in abundance of *C. septempunctata* have been revealed in the study, similarly to other studies on coccinellids (Honěk and Martinková 2005; Elliott and Kieckhefer 1990; Kieckhefer and Elliott 1990). Further, Honěk and Martinková (2005) found that the spring abundance of a parental coccinellid generation was high only in years when 'June' aphid numbers were low and 'June' aphid numbers were high only in years when the parental coccinellid generation was scarce. This finding agrees well with the results of our simulations (fig. 9).

The cyclical pattern in aphid abundance was described in many aphid species, the random as well as density-dependent processes were described but the underlying mechanisms are still unknown (Thacker et al. 1997; Alyokhin et al. 2005; Bommarco et al. 2007). Dixon (2005) summarizes number of factors which enter the aphid dynamics: besides of weather or abundance and phenology of the host-plant, which are rather easy to measure, aphid cumulative density, intra-specific competition and experience of crowding on the host plant are highly probable to determine the population growth rate of the aphid metapopulations. Three processes have contributed to the oscillations resulting in our simulations: the random distribution of prey among patches in the spring migration, the summer decrease in prey abundance driven by cumulative density of prey in a patch, and optimized oviposition strategy of predatory females. However, the oscillations comparable with empirical ones occur only if predators linger within the virtual landscape for long, until 50 or more percent of patches become unsuitable (fig. 5). Contrary to this result, the unimodal relationship in figure 7 B indicates that the foraging and oviposition strategy of predatory females should tend to only a short stay, not entirely exploiting the patches suitable for oviposition. Then, the oscillations disappear, both populations are abundant and

the system is very stable. In literature, there is some evidence supporting also this result. Mark-recapture studies showed that adult coccinellids often do not remain long in any given location, but appear to move frequently between sites and habitats throughout the breeding season instead (see Evans 2003 for review). Our opposing results could be explained by Frazer's (1988, cited by Evans 2003) conclusion that local areas "are constantly receiving and losing coccinellids regardless of the density of aphids" what he attributed to an innate tendency to disperse even in appetitive flight. Seen from this point of view, the result of figure 7 *B* (the early departure) concurs with the innate tendency to disperse while the oscillations approximating to the empirical censuses indicate that a flow of predators migrating through the landscape and searching for prey to feed and to oviposit might form a sufficient pressure for aphid metapopulations to cause the oscillations.

One more point remains to be discussed: the effect of random disturbances, which occur in the natural environment fairly often. These are also an important source of oscillations. An example of such disturbance is recorded in first years of figure 5 *D*, where unbalanced initial abundances caused enormous increase in aphid numbers and it took four years to dampen the oscillating abundances to the typical median numbers. The probability that another disturbance occurs during these four years is not insignificant. Then, no other driving force is needed to produce oscillations over many years. However, such oscillations would not include any regular pattern similar to that described in figure 6.

Acknowledgement

Supported by the long-term research programmes MSM 0021622416 and by the grant No. LC06073 of the Czech Ministry of Education.

References

- Alyokhin, A., F. A. Drummond, and G. Sewell. 2005. Density-dependent regulation in populations of potato-colonizing aphids. *Population Ecology* 47:257–266.
- Atlihan, R., and M. B. Kaydan. 2000. Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* (Geoffroy) (Homoptera: Aphididae). *Turkish Journal of Agriculture and Forestry* 26:119–124.
- Ba M'Hamed, T., and M. Chemseddine. 2001. Assessment of temperature effects on the development and fecundity of *Pullus mediterraneus* (Col., Coccinellidae) and consumption of *Saissetia oleae* eggs (Hom., Coccoida). *Journal of Applied Entomology* 125:527–531.
- Bazzocchi, G. G., A. Lanzoni, G. Accinelli, and G. Burgio. 2004. Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. *BioControl* 49(3):245–260.
- Bellows, T. S., T. D. Paine, and D. Gerling. 1992. Development, survival, longevity, and fecundity of *Clitostethus arcuatus* (Coleoptera, Coccinellidae) on *Siphoninus phillyreae* (Homoptera, Aleyrodidae) in the laboratory. *Environmental Entomology* 21(3):659–663.
- Blackman, R. L., and V. F. Eastop. 1994. *Aphids on the World's Trees: An Identification and Information Guide*. CABI Publishing, Oxford University Press, New York.
- Bommarco, R., S. Wetterlind, and R. Sigvald. 2007. Cereal aphid populations in non-crop habitats show strong density dependence. *Journal of Applied Ecology* 44:1013–1022.
- Chambers, R. J., P. W. Wellings, and A. F. G. Dixon. 1985. Sycamore aphid numbers and population density. II. Some processes. *Journal of Animal Ecology* 54:425–442.
- Costamagna, A. C., D. A. Landis, and M. J. Brewer. 2008. The role of natural enemy guilds in *Aphis glycines* suppression. *Biological Control* 45:368–379.
- Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). *Environmental Entomology* 35(6):1461–1468.
- Dedryver, C.-A. 1987. *Biologie, écologie et dynamique de population des pucerons des céréales en climat océanique*. Thèse Sciences, Université Paris Sud Orsay.
- Dixon, A. F. G. 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *The Journal of Animal Ecology* 28(2):259–281.
- Dixon, A. F. G. 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the sycamore aphid, *Drepanosiphum platanoides* (Schr.). *Journal of Animal Ecology* 39(3):39–751.
- Dixon, A. F. G. 2000. *Insect Predator-Prey Dynamics: Ladybird beetles & Biological Control*. Cambridge University Press. Cambridge.
- Dixon, A. F. G. 2005. *Insect Herbivore-Host Dynamics: Tree-Dwelling Aphids*. Cambridge University Press. Cambridge.
- Donaldson, J. R., S. W. Myers, and C. Gratton. 2007. Density-dependent responses of soybean aphid (*Aphis glycines* Matsumura) populations to generalist predators in mid to late season soybean fields. *Biological Control* 43:111–118.

- El Habi, M., A. Sekkat, L. El Jadd, and A. Boumezzough. 2000. Biologie d'*Hippodamia variegata* Goeze (Col., Coccinellidae) et possibilités de son utilisation contre *Aphis gossypii* Glov (Hom., Aphididae) sous serres de concombre. *Journal of Applied Entomology* 124:365–374.
- Elliott, N. C., and R.W. Kieckhefer. 1990. Dynamics of aphidophagous coccinellid assemblages in small grain fields in eastern South Dakota. *Environmental Entomology* 19:1320–1329.
- Evans, E. W. 2003. Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *European Journal of Entomology* 100:1–10.
- Frazer, B. D. 1988. Coccinellidae. Pages 231–247 in A. K. Minks, and P. Harrewijn, eds. *Aphids: their Biology, Natural Enemies and Control*. Volume 2B. Elsevier, Amsterdam.
- Gange, A. C. 1995. Aphid performance in an alder (*Alnus*) hybrid zone. *Ecology* 76:2074–2083.
- Girma M., G. Wilde, and J. C. Reese. 1990. Influence of temperature and plant growth stage on development, reproduction, life span and intrinsic rate of increase of the Russian wheat aphid (Homoptera: Aphididae). *Environmental Entomology* 19(5):1438–1442.
- Gosselke, U., H. Triltsch, D. Roßberg, and B. Freier. 2001. GETLAUS01 – the latest version of a model for simulating aphid population dynamics in dependence on antagonists in wheat. *Ecological Modelling* 145:143–157.
- Hassell, M. P. 1987. Detecting Regulation in Patchily Distributed Animal Populations. *Journal of Animal Ecology* 56(2):705–713.
- Hemptinne, J.-L., and A. F. G. Dixon. 2000. Defence, oviposition and sex: semiochemical parsimony in two species of ladybird beetles (Coleoptera, Coccinellidae)? A short review. *European Journal of Entomology* 97:443–447.
- Hemptinne, J.-L., A. F. G. Dixon, and J. Goffin. 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90:238–245.
- Hemptinne, J.-L., A. F. G. Dixon, J.-L. Doucet, and J. E. Petersen. 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *European Journal of Entomology* 90:451–455.
- Hironori, Y., and S. Katsuhiko. 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.
- Honěk, A., and Z. Martinková. 2005. Long term changes in abundance of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in the Czech Republic. *European Journal of Entomology* 102:443–448.
- Houdková, K., and P. Kindlmann. 2006. Scaling up population dynamic processes in a ladybird-aphid system. *Population Ecology* 48(4):323–332.
- Hukusima, S., and M. Kamei. 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Bulletin of the Faculty of Agriculture, Gifu University* 29:53–66.

- Kalushkov, P., and I. Hodek. 2004. The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. *Biocontrol* 49(1):21–32.
- Karley, A. J., W. E. Parker, J. W. Pitchford, and A. E. Douglas. 2004. The mid-season crash in aphid populations: why and how does it occur? *Ecological Entomology* 29:383–388.
- Katsarou, I., J. T. Margaritopoulos, J. A. Tsitsipis, D. Ch. Perdakis, and K. D. Zarpas. 2005. Effect of temperature on development, growth and feeding of *Coccinella septempunctata* and *Hippodamia convergens* reared on the tobacco aphid, *Myzus persicae nicotianae*. *BioControl* 50:565–588.
- Kieckhefer, R. W., and N. C. Elliott. 1990. A 13-year survey of the aphidophagous Coccinellidae in maize fields in eastern South Dakota. *The Canadian Entomologist* 122:579–581.
- Kindlmann, P. 1985. A model of aphid population with age structure. Pages 72–77 in V. Capasso, E. Grosso, and S. L. Paveri-Fontana, eds. *Mathematics in Biology and Medicine. Lecture Notes in Biomathematics*. Springer, Berlin.
- Kindlmann, P., and A. F. G. Dixon. 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., and A. F. G. Dixon. 1999. Generation Time Ratios – Determinants of Prey Abundance in Insect Predator–Prey Interactions. *Biological Control* 16:133–138.
- Kindlmann, P., and A. F. G. Dixon. 2001. When and why top-down regulation fails in arthropod predator-prey systems. *Basic and Applied Ecology* 2:333–340.
- Kindlmann, P., and A. F. G. Dixon. 2003. Insect predator-prey dynamics and the biological control of aphids by ladybirds. Pages 118–124 in R. van Driesche, ed. *Proceedings of the 1st International Symposium on Biological Control of Arthropods*. USDA Forest Service, Honolulu.
- Kindlmann, P., and M. Okrouhlá. 1986. Simulation of the population dynamics of a laboratory aphid-coccinellid system. Pages 357–362 in I. Hodek, ed. *Ecology of Aphidophaga II*. Academia, Praha.
- Kindlmann, P., R. Arditi, and A. F. G. Dixon. 2004. A simple aphid population model. Pages 325–330 in J.-C. Simon, C.-A. Dedryver, C. Rispe, and M. Hulle, eds. *Aphids in a new millennium*. INRA, Paris.
- Kindlmann, P., V. Jarošík, and A. F. G. Dixon. 2007. Population dynamics. Pages 311–329 in H. van Emden, and R. Harrington, eds. *Aphids as crop pests*. CABI, London.
- Kindlmann, P., H. Yasuda, S. Sato, and K. Shinya. 2000. Key life stages of two predatory ladybird species (Coleoptera : Coccinellidae). *European Journal of Entomology* 97:495–499.
- Kindlmann, P., H. Yasuda, Y. Kajita, and A. F. G. Dixon. 2005. Field test of the effectiveness of ladybirds in controlling aphids. Pages 441–447 in M. S. Hoddle, ed. *Proceedings of the 2nd International Symposium on Biological Control of Arthropods*. USDA Forest Service.
- Lankin-Vega, G., S. P. Worner, and D. A. J. Teulon. 2008. An ensemble model for predicting *Rhopalosiphum padi* abundance. *Entomologia Experimentalis et Applicata* 129:308–315.

- Lanzoni, A., G. Accinelli, G. G. Bazzocchi, and G. Burgio. 2004. Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col., Coccinellidae). *Journal of Applied Entomology* 128(4):298–306.
- Mashanova, A., A. C. Gange, and V. A. A. Jansen. 2008. Density-dependent dispersal may explain the mid-season crash in some aphid populations. *Population Ecology* 50(3):285–292.
- Matis, J. H., T. R. Kiffe, T.I. Matis, J. A. Jackman, W. E. Grant, and H. Singh. 2008. On the use of growth rate parameters for projecting population size: application to aphids. *Ecological Modelling* 213:133–142.
- McVean, R. I. K., A. F. G. Dixon, and R. Harrington. 1999. Causes of regional and yearly variation in pea aphid numbers in eastern England. *Journal of Applied Entomology* 123:495–502.
- Michaud, J. P., and J. L. Jyoti. 2007. Use of odours by *Cycloneda sanguinea* to assess patch quality. *European Journal of Entomology* 104:399–405.
- Michels, G. J., and R. V. Flanders. 1992. Larval development, aphid consumption and oviposition for 5 imported coccinellids at constant temperature on Russian wheat aphids and greenbugs. *Southwestern Entomologist* 17(3):233–243.
- Miller, J. C. 1992. Temperature-dependent development of the convergent lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology* 21(1):197–201.
- Miller, J. C., and J. W. Paustian. 1992. Temperature-dependent development of *Eriopis connexa* (Coleoptera, Coccinellidae). *Environmental Entomology* 21(5):1139–1142.
- Mori, K., M. Nozawa, K. Arai, and T. Gotoh. 2005. Life-history traits of the acarophagous lady beetle, *Stethorus japonicus*, at three constant temperatures. *BioControl* 50:35–51.
- Obrycki, J. J., and M. J. Tauber. 1981. Phenology of three coccinellid species: thermal requirements for development. *Annals of the Entomological Society of America* 74(1):31–36.
- Obrycki, J. J., and M. J. Tauber. 1982. Thermal requirements for development of *Hippodamia convergens* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* 75(6):678–683.
- Omkar, and B. E. James. 2004. Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae). *Journal of Applied Entomology* 128:150–157.
- Omkar, and S. Srivastava. 2003. Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. *BioControl* 48:379–393.
- Osawa, N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): Life tables and key factor analysis. *Research on Population Ecology* 35(2):335–348.
- Özder, N., and Ö. Sağlam. 2003. Effects of aphid prey on larval development and mortality of *Adalia bipunctata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* 13(4):449–453.
- Perry, J. N., I. P. Woiwod, and I. Hanski. 1993. Using response-surface methodology to detect chaos in ecological time series. *Oikos* 68(2):329–339.

- Pervez, A., Omkar, and S. K. Singh. 2005. Development and immature survival of two aphidophagous ladybirds, *Coelophora biplagiata* and *Micraspis discolor*. *Insect Science* 12(5):375–379.
- Plantegenest, M., J. S. Pierre, C. A. Dedryver, and P. Kindlmann. 2001. Assessment of the relative impact of different natural enemies on population dynamics of the grain aphid *Sitobion avenae* in the field. *Ecological Entomology* 26(4):404–410.
- R Development Core Team. (2009). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rhains, M., and R. H. Messing. 2005. Spatial and temporal density dependence in a population of melon aphid, *Aphis gossypii* (Homoptera: Aphididae), on established and sentinel taro plants. *Applied Entomology and Zoology* 40(2):273–282.
- Rhains, M., M. Roy, G. Daigle, and J. Brodeur. 2007. Toward management guidelines for the soybean aphid in Quebec. I. Feeding damage in relationship to seasonality of infestation and incidence of native predators. *The Canadian Entomologist* 139:728–741.
- Ro, T. H., and G. E. Long. 1999. GPA-Phenodynamics, a simulation model for the population dynamics and phenology of green peach aphid in potato: formulation, validation, and analysis. *Ecological Modelling* 119:197–209.
- Růžička, Z. 1998. Further evidence of oviposition-deterrence by allomone in chrysopids (Neuroptera: Chrysopidae). *European Journal of Entomology* 95:35–39.
- Růžička, Z. 2001. Oviposition responses of aphidophagous coccinellids to tracks of ladybird (Coleoptera: Coccinellidae) and lacewings (Neuroptera: Chrysopidae) larvae. *European Journal of Entomology* 98:183–188.
- Schmidt, M. H., A. Lauer, T. Purtauf, C. Thies, M. Schaefer, and T. Tschardt. 2003. Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London Series B* 270:1905–1909.
- Sequeira, R., and A. F. G. Dixon. 1997. Population dynamics of tree-dwelling aphids: the importance of seasonality and time scale. *Ecology* 78:2603–2610.
- Siddiqui, W. H., C. A. Barlow, and P. A. Randolph. 1973. Effects of some constant and alternating temperatures on population growth of the pea aphid, *Acyrtosiphon pisum* (Homoptera: Aphididae). *Canadian Entomologist* 105:145–156.
- Skirvin, D. J., J. N. Perry, and R. Harrington. 1997. A model describing the population dynamics of *Sitobion avenae* and *Coccinella septempunctata*. *Ecological Modelling* 96:29–39.
- Snyder, W. E., and A. R. Ives. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84(1):91–107.
- Soares, A. O., D. Coderre, and H. Schanderl. 2004. Dietary self-selection behaviour by the adults of the aphidophagous ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Journal of Animal Ecology* 73:478–486.
- Thacker, J. I., T. Thieme, and A. F. G. Dixon. 1997. Forecasting of periodic fluctuations in annual abundance of the bean aphid: the role of density dependence and weather. *Journal of Applied Entomology* 121:137–145.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* 73:289–305.

- Uygun, N., and R. Atlihan. 2000. The effect of temperature on development and fecundity of *Scymnus levillanti*. *BioControl* 45:453–462.
- Wool, D. 2002. Herbivore abundance is independent of weather? A 20-year study of a galling aphid *Baizongia pistaciae* (Homoptera: Aphidoidea). *Population Ecology* 44:281–291.
- Wyatt, I. J., and S. J. Brown. 1977. The influence of light intensity, day length and temperature on increase rates of four glasshouse aphids. *Journal of Applied Ecology* 14(2):391–399.
- Yasuda, H., and A. F. G. Dixon. 2002. Sexual size dimorphism in the two spot ladybird beetle *Adalia bipunctata* developmental mechanism and its consequences for mating. *Ecological Entomology* 27:493–498.
- Zhou, X., and N. Carter. 1992. Effects of temperature, feeding position and crop growth stage on the population dynamics of the rose grain aphid, *Metopolophium dirhodum* (Homoptera: Aphididae). *Annals of Applied Biology* 121(1):27–37.

Preliminary results

EFFECT OF INCREASING TEMPERATURE ON THE DYNAMICS OF AN APHID–LADYBIRD SYSTEM

VLIV VZRŮSTAJÍCÍ TEPLoty NA DYNAMIKU SYSTÉMU MŠICE–SLUNÉČKO

Kateřina Kintrová

Climate change is occurring (IPCC 2007). Among the measured factors, the increasing temperature is the most important, affecting a wide range of processes. As the insects are poikilothermic, the temperature directly influences their intrinsic processes and behaviour. Existing studies on insect herbivores suggest that direct effects of temperature on the insect dynamics are likely to be larger and more important than those of any other factors (Bale et al. 2002). Here, I simulated population dynamics of an aphid-ladybird system to suggest how the increasing temperature could influence the predator-prey interactions.

I reviewed the available literature on the effects of temperature on the main biological traits of aphids and ladybirds and concluded that:

- a) the dependence of **developmental time of ladybirds** on temperature is nonlinear and is well characterized by a hyperbolic function (Fig. 1) (e.g., Obrycki and Tauber 1981, 1982, Miller 1992);
- b) **larval voracity** of ladybirds is influenced by temperature only weakly (El Habi et al. 2000, Katsarou et al. 2005);
- c) **fecundity** of ladybirds is affected by a range of factors, however, there is no obvious direct relation to the temperature, although an indirect effect of temperature cannot be excluded;
- d) **growth rate of aphids** increases approximately linearly with increasing temperature. The increase spans a range of about 10 thermal degrees, then the aphid growth rate decreases again (Siddiqui et al. 1973, Zhou and Carter 1992, Davis et al. 2006).

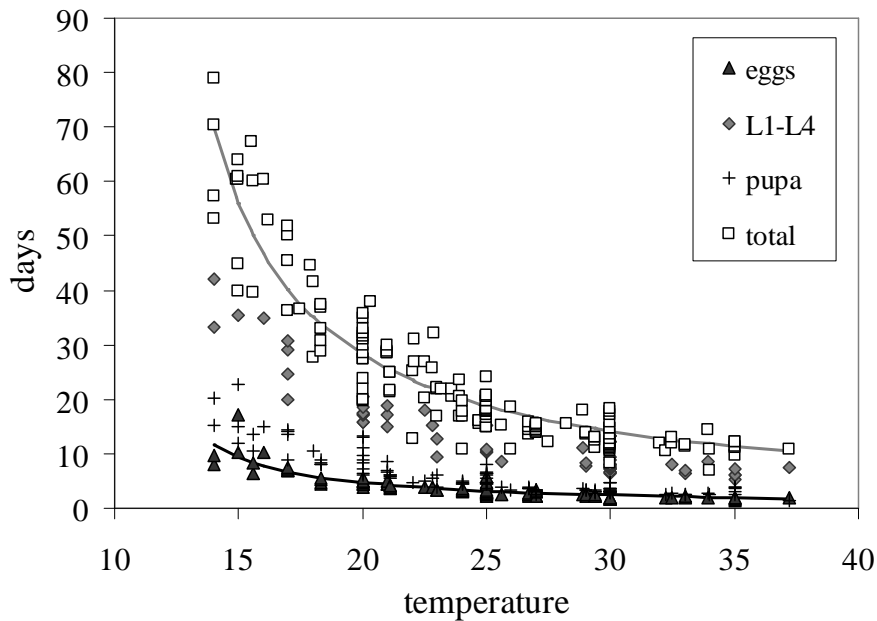


Figure 1. Developmental times in ladybirds (sources cited below) and hyperbolic curves fitted to the data (equations below).

I used the simulation model suggested by Kintrová and Kindlmann (**Paper III**) on assumptions that the rate of increase of aphid populations and the developmental time of ladybirds changes with the increasing temperature. The following equations were derived using the cited data.

- (1) Maximal potential growth rate of prey population:

$$r = 0.25 + (\text{Temperature} - 15) * 0.025,$$

(Siddiqui et al. 1973).

- (2) Time to emergence of adult predators from pupae:

$$T_{\text{emerge}} = 280 / (\text{Temperature} - 10) + 0.1,$$

(Atlihan & Kaydan 2002; Ba M'Hamed & Chemseddine 2001; Bazzocchi et al. 2004; Bellows et al. 1992; Dixon 2000; El Habi et al. 2000; Hodek 1973; Hukusima & Kamei 1970; Katsarou et al. 2005; Lanzoni et al. 2004; Miller 1992; Miller & Paustian 1992; Mori et al. 2005; Obrycki & Tauber 1981, 1982; Özder & Sağlam 2003; Pervez et al. 2005; Uygun & Atlihan 2000; Yasuda & Dixon 2002).

- (3) Time to hatching of first instar predatory larvae from eggs:

$$T_{\text{hatch}} = 46.2 / (\text{Temperature} - 10) + 0.1.$$

Values of these parameters were specified according to the initial setting of the mean temperature (constant within a simulation). The effect of larval voracity of ladybirds on the overall dynamics was studied independently on the temperature.

Preliminary results

Figure 2 represents a relationship between the end of egg-window (EW) abundances of prey and autumn numbers of matured predators as predicted by the equations (1) of the model (**Paper III**). Predator numbers are strongly affected by prey abundances under low temperatures when only a narrow extent of the end of egg-window prey numbers allows predatory larvae to complete their development. The increasing temperature causes an increase in numbers of mature predators because the larval development of predators accelerates and the larvae are able to utilize wider extent of the end of egg-window abundances of prey.

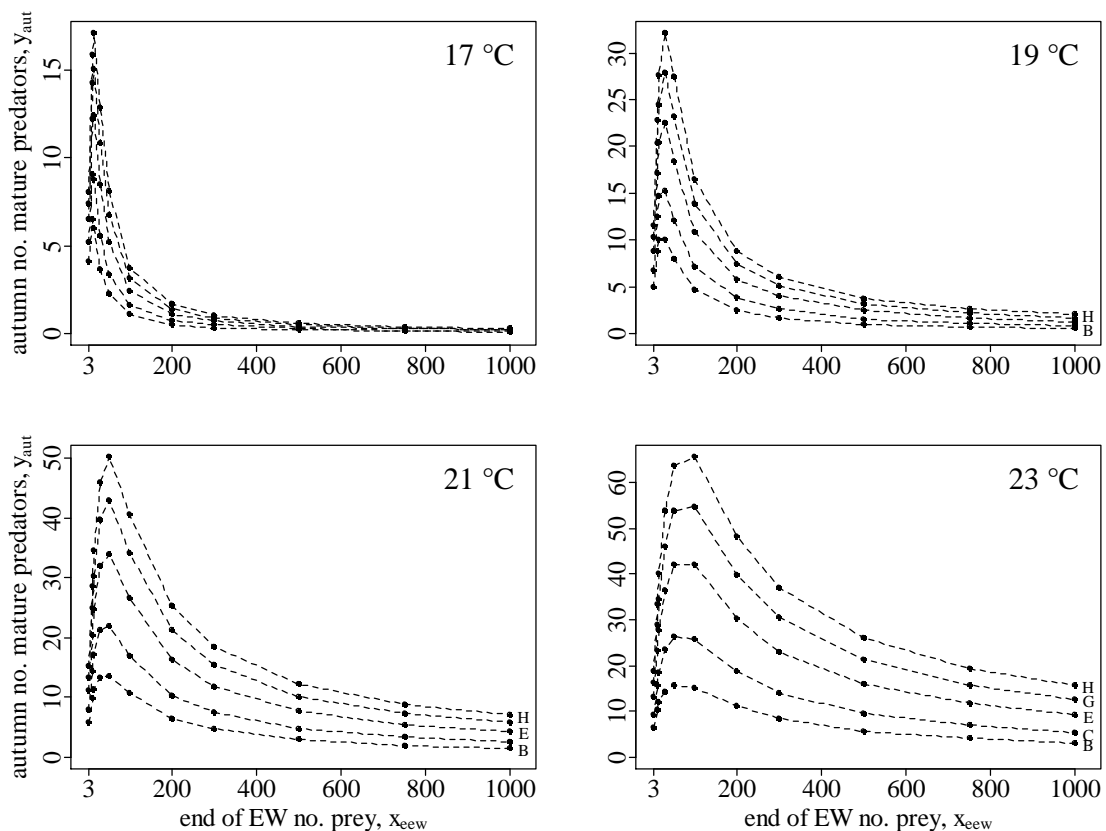


Figure 2. The relationship of autumn predator numbers to the end of EW abundances of prey with respect to the increasing temperature. The larval voracity = 0.20, initial density of predator eggs B = 20, C = 40, E = 80, G = 120, H = 160.

The between-season dynamics in a 50-year period as predicted by the model is shown in figure 3. The median abundances of both prey and predator increase with the increasing temperature. Simultaneously, the amplitudes of oscillations are higher. A mechanism of formation of oscillations is explained in Kintrová and Kindlmann (**Paper III**, fig. 6). Here, an indication arises that occurrence of the extreme insect abundances could be more frequent as temperature will increase (similarly to the weather disturbances).

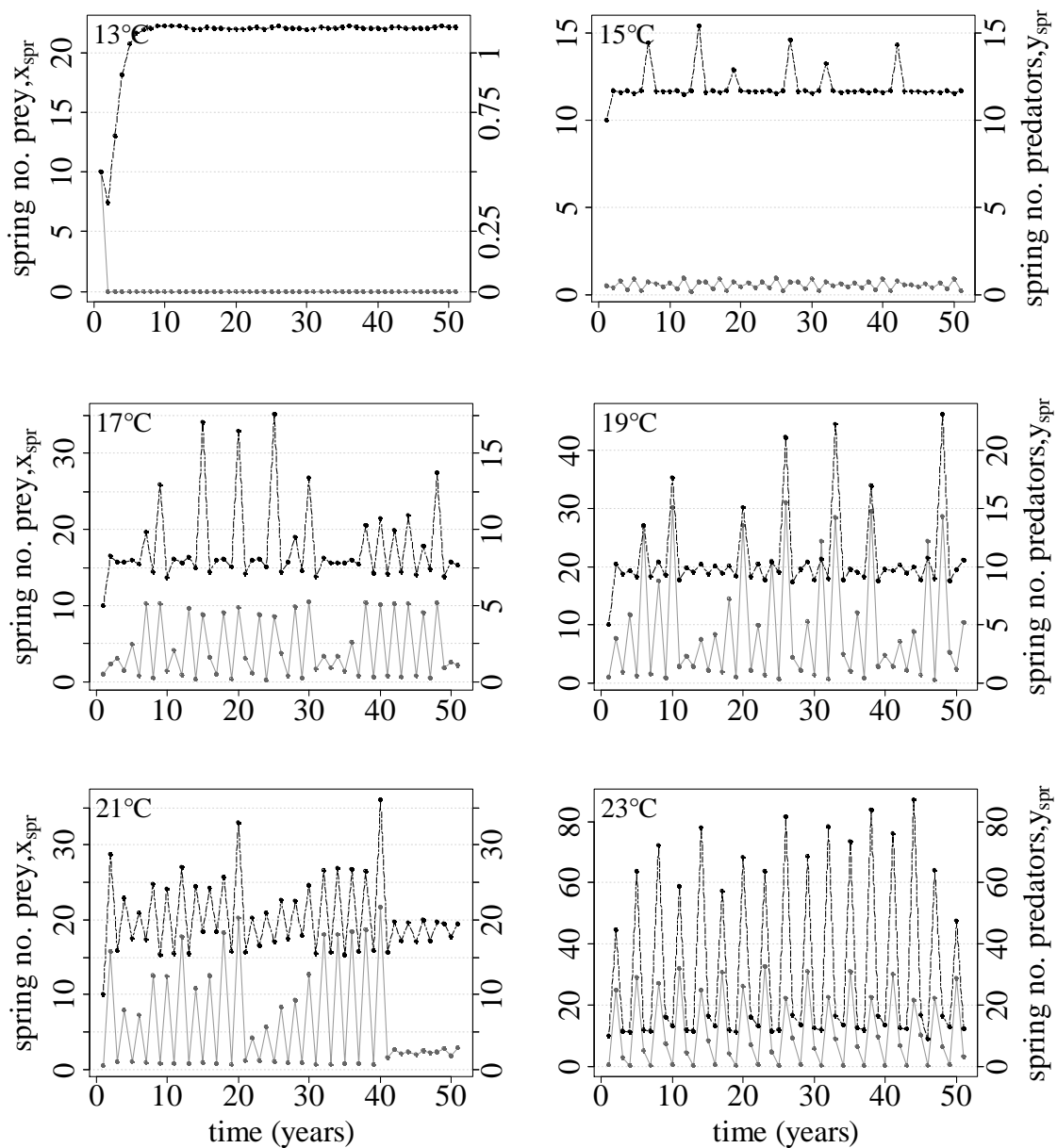


Figure 3. Oscillations in spring abundances of prey (black) and predator (grey) simulated by the model. The larval voracity = 0.25, percentage of unsuitable patches in the instant of predator departure = 70 %. The mean model temperature ranges from 13 °C to 23 °C (indicated in panels). Abundances are in thousands.

With the increasing temperature, both prey and predator attain higher abundances, but only up to a certain optimum value (19–21°C in the model, Fig. 4). Above this temperature the abundances fall down again. The dynamics is more difficult to predict. Under the very cold regime, the population of predator mostly dies out. Then the population of prey attains the maximum abundances under given temperature (about 22 thousands under 13°C). Under temperatures from 15 to 19°C, the voracity of predatory larvae does not influence median abundances of prey (as described in Kintrová and Kindlmann (**Paper III**, fig. 7)). However, larval voracity affected prey abundances under the warmer temperature regimes so that the least voracious predator reduces prey abundances more than the more voracious predator. It has probably two blended reasons: a prey colony maintains more predatory larvae of lower voracity than those of high voracity, and rapidly developing larvae can better exploit prey source under the warm regime (Fig. 2).

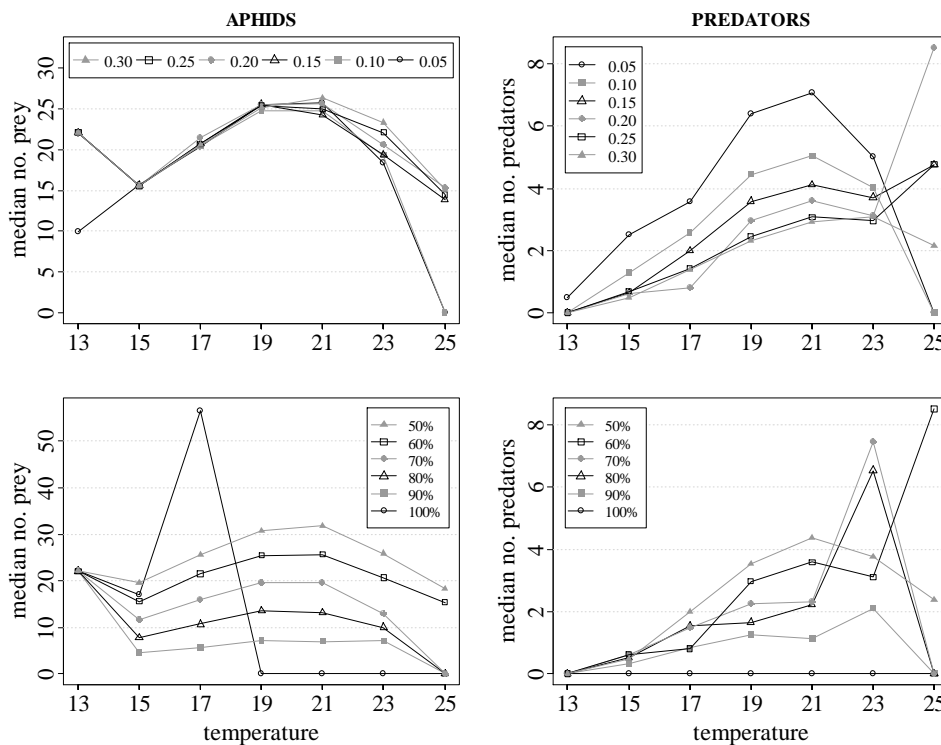


Figure 4. Trends in median abundances of prey and predator. Points represent median of spring abundances in a 50-year period, which is characterized by a combination of temperature, larval voracity and percentage of unsuitable patches. Upper panels show the effect of increasing voracity when the percentage of unsuitable patches equals 60 %. Lower panels show the effect of changing percentage of unsuitable patches when the voracity equals 0.20. The percentage of unsuitable patches (parameter *unsuit*) determines the instant when predators cease ovipositing and leave the system (i.e., the egg-window phase closes). Median abundances are in thousands.

The degree of exploitation of prey colonies by ovipositing predatory females (percentage of colonies unsuitable for oviposition, parameter *unsuit* in the egg-window phase) also influences median abundances of both prey and predator (lower panels of Fig.4). This relation was explained in Kintrová and Kindlmann (**Paper III**, fig. 7) for the temperature regime of 19°C. Here, the patterns in median abundances are more or less regular within the range of 13 to 21°C but they are disrupted above the optimum temperature. Especially the median numbers of predators are besides any expectations.

I suppose that a different rate of contraction of the developmental time with the increasing temperature in aphids and ladybirds could explain these results. Figure 5 presents an approximation of a change in developmental time ratio (predator to prey) with the increasing temperature. It indicates that the generation time ratio (Kindlmann and Dixon 1999) of aphidophagous predators and their aphid prey could scores values similar to that of aphidophagous parasitoids and aphids (~1.2) as temperature increases. In predator-prey systems, where the GTR scores a value about 1, the predator is expected to be able to control abundances of its prey (Kindlmann and Dixon 1999). However, it is not the case of my simulations. I suppose that the discrete character of the simulated seasonal dynamics with the important predator-prey interactions during the egg window may account for the contradiction.

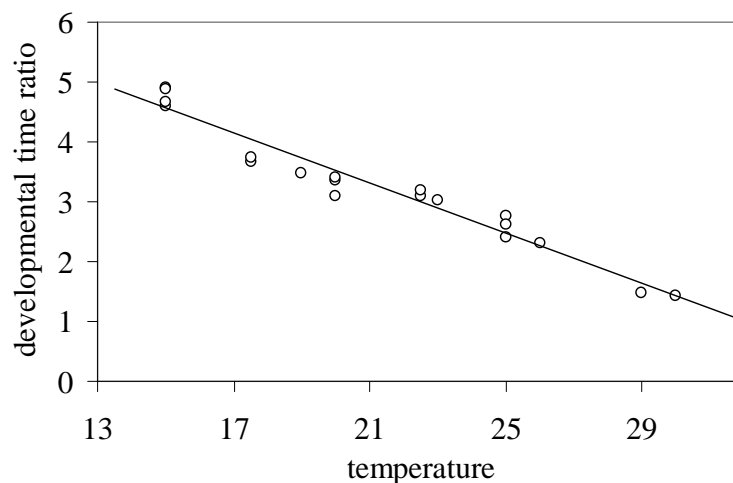


Figure 5. Dependence of the developmental time ratio of predator to prey on temperature. Data on developmental time of aphids (in days) were adopted from Siddiqui et al. (1973), Kieckhefer et al. (1989) and Zhou and Carter (1992). Time from an egg to emergence of an adult in ladybirds were estimated using the equation (3) above. The developmental time ratio approximates an expected decrease in the generation time ratio (Dixon et al.1995, Kindlmann and Dixon 1999). The decreasing trend in developmental time ratio indicates that the ability of ladybirds to suppress the aphid prey may improve with increasing temperature.

References

- Atlihan, R. & Kaydan, M.B. (2000) Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* (Geoffroy) (Homoptera: Aphididae). *Turkish Journal of Agriculture and Forestry* **26**: 119–124.
- Ba M'Hamed, T. & Chemseddine, M. (2001) Assessment of temperature effects on the development and fecundity of *Pullus mediterraneus* (Col., Coccinellidae) and consumption of *Saissetia oleae* eggs (Hom., Coccoidea). *Journal of Applied Entomology* **125**: 527–531.
- Bale, J.S. et al. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**: 1–16.
- Bazzocchi, G.G., Lanzoni, A., Accinelli, G. & Burgio, G. (2004) Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. *BioControl* **49**(3): 245–260.
- Bellows, T.S., Paine, T.D. & Gerling, D. (1992) Development, survival, longevity, and fecundity of *Clitostethus arcuatus* (Coleoptera, Coccinellidae) on *Siphoninus phillyreae* (Homoptera, Aleyrodidae) in the laboratory. *Environmental Entomology* **21**(3): 659–663.
- Davis, J.A., Radcliffe, E.B. & Ragsdale, D.W. (2006) Effects of high and fluctuating temperatures on *Myzus persicae* (Homoptera: Aphididae). *Environmental Entomology* **35**(6): 1461–1468.
- Dixon, A.F.G. (2000) *Insect Predator-Prey Dynamics: Ladybird beetles and Biological Control*. Cambridge University Press. Cambridge.
- Dixon, A.F.G., Hemptinne, J.-L. & Kindlmann, P. (1995) The ladybird fantasy – prospects and limits to their use in the biological control of aphids. *Züchtungsforschung* **1**: 395–397.
- El Habi, M., Sekkat, A., El Jadd, L. & Boumezzough, A. (2000) Biologie d'*Hippodamia variegata* Goeze (Col., Coccinellidae) et possibilités de son utilisation contre *Aphis gossypii* Glov (Hom., Aphididae) sous serres de concombre. *Journal of Applied Entomology* **124**: 365–374.
- Hemptinne, J.-L., Dixon, A.F.G., Doucet, J.-L. & Petersen, J.E. (1993) Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *European Journal of Entomology* **90**: 451–455.
- Hodek, I. (1973) *Biology of Coccinellidae*. Academia, Prague.
- Hokusima, S. & Kamei, M. (1970) Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Bulletin of the Faculty of Agriculture, Gifu University* **29**: 53–66.
- IPCC, Intergovernmental Panel on Climate Change (2007) Climate change 2007: Synthesis report.
Available at: http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf
- Katsarou, I., Margaritopoulos, J.T., Tsitsipis, J.A., Perdikis, D.Ch. & Zarpas, K.D. (2005) Effect of temperature on development, growth and feeding of *Coccinella septempunctata* and *Hippodamia convergens* reared on the tobacco aphid, *Myzus persicae nicotianae*. *BioControl* **50**: 565–588.
- Kindlmann, P. & Dixon, A.F.G. (1999) Generation time ratios – determinants of prey abundance in insect predator–prey interactions. *Biological Control* **16**: 133–138.

- Kintrová, K. & Kindlmann, P. (**Paper III**, submitted) Modelling of metapopulation dynamics in an aphid-coccinellid system on a long-term scale.
- Lanzoni, A., Accinelli, G., Bazzocchi, G.G. & Burgio, G. (2004) Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col., Coccinellidae). *Journal of Applied Entomology* **128**(4): 298–306.
- Miller, J.C. (1992) Temperature-dependent development of the convergent lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology* **21**(1): 197–201.
- Miller, J.C. & Paustian, J.W. (1992) Temperature-dependent development of *Eriopis connexa* (Coleoptera, Coccinellidae). *Environmental Entomology* **21**(5): 1139–1142.
- Mori, K., Nozawa, M., Arai, K. & Gotoh, T. (2005) Life-history traits of the acarophagous lady beetle, *Stethorus japonicus*, at three constant temperatures. *BioControl* **50**: 35–51.
- Obrycki, J.J. & Tauber, M.J. (1981) Phenology of three coccinellid species: thermal requirements for development. *Annals of the Entomological Society of America* **74**(1): 31–36.
- Obrycki, J.J. & Tauber, M.J. (1982) Thermal requirements for development of *Hippodamia convergens* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* **75**(6): 678–683.
- Özder, N. & Sağlam, Ö. (2003) Effects of aphid prey on larval development and mortality of *Adalia bipunctata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* **13**(4): 449–453.
- Pervez, A., Omkar & Singh, S.K. (2005) Development and immature survival of two aphidophagous ladybirds, *Coelophora biplagiata* and *Micraspis discolor*. *Insect Science* **12**(5): 375–379.
- Siddiqui, W.H., Barlow, C.A. & Randolph, P.A. (1973) Effects of some constant and alternating temperatures on population growth of the pea aphid, *Acyrtosiphon pisum* (Homoptera: Aphididae). *Canadian Entomologist* **105**: 145–156.
- Uygun, N. & Atlihan, R. (2000) The effect of temperature on development and fecundity of *Scymnus levaillanti*. *BioControl* **45**: 453–462.
- Yasuda, H. & Dixon, A.F.G. (2002) Sexual size dimorphism in the two spot ladybird beetle *Adalia bipunctata* developmental mechanism and its consequences for mating. *Ecological Entomology* **27**: 493–498.
- Zhou, X. & Carter, N. (1992) Effects of temperature, feeding position and crop growth stage on the population dynamics of the rose grain aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). *Annals of Applied Biology* **121**(1): 27–37.

Summary of results and conclusions

Scaling up population dynamics of the aphid–ladybird system from a single prey colony to the metapopulation level (**Paper I**) resulted in patterns similar to those in a small-scale model by Kindlmann and Dixon (2003). When the predator was present, abundances of both prey and predator oscillated with an approximately two-year period. The character of oscillations was determined mainly by activity of predators during the egg-window phase: the later the predator arrived into the model system, the smaller was the amplitude of oscillations, and the higher were the long-term (across many years) average abundances of both prey and predator. It has been shown on a colony level that top-down regulation fails in aphidophagous predator-aphid systems (Kindlmann and Dixon 2001). On the metapopulation level, the impact of predators on the prey metapopulation was relatively low as well.

Extension of the model by Houdková and Kindlmann (2006) (**Paper III**) is novel in that the numbers of prey and predators in colonies were simulated individually (extra in each colony) and the basis of the prey metapopulation in the next spring was derived from a number of winged aphids emigrating from summer colonies. Oscillations with two and three-year cycles occurred in abundances of both prey and predator. The pattern in oscillations is comparable with empirical data (Thacker et al. 1997, Alyokhin et al. 2005, Honěk and Martinková 2005, Bommarco et al. 2007, Lankin-Vega et al. 2008). However, the oscillations occurred only when predators lingered for long within prey colonies. Other result showed that predators maximized their fitness on a long-term scale, when only 20 % of colonies suitable for oviposition were exploited. This result corresponds with mark-recapture studies showing that adult coccinellids often do not remain long in any given location, but appear to move frequently between sites and habitats throughout the breeding season instead (Evans 2003). A possible explanation of contradiction in our results was offered by Frazer's conclusion (1988) that local areas “are constantly receiving and losing coccinellids regardless of the density of aphids” what he attributed to an innate tendency to disperse even in appetitive flight. Then the prediction of early departure of predators from the system concurs with the innate tendency of predators to disperse while oscillations produced by prolonged predators' activity during the egg window indicate that a flow of predators migrating through the landscape, foraging on prey and ovipositing might form a sufficient pressure on an aphid metapopulation to cause the oscillations.

Preliminary results of modelling the effect of the increasing temperature on the predator-prey dynamics indicate that more pronounced oscillations of abundances might be expected in long-term dynamics of insect systems. In the model, more predators matured as the temperature increased. Within the studied range of temperature, prey as well as predator attained the highest median spring abundances under the regime of 19 – 21°C. Under thermal regimes below the optimum temperature, effects of larval voracity and duration of the egg-window phase (parameter *unsuit*) on the median abundances corresponded with the trends described in the Paper III, i.e., the increasing larval voracity reduced the number of matured predators but had no impact on the median abundance of prey, and the median abundances increased with decreasing duration of the egg-window phase. On the other end of the studied range of temperatures, these relations did not apply. Predators with less voracious larvae were able to reduce the median prey abundances to small extent. The relationship between median abundances and duration of the egg-window phase was disrupted by either extreme in predator's abundance or collapse of both populations. I hypothesize that a reason of the breaks in trends might be related to decrease in a ratio of the generation time of predator to that of its prey (Kindlmann and Dixon 1999) in combination with the discrete character of the simulated seasonal dynamics regulated by the important predator-prey interactions during the egg window.

To contribute to the discussion on the often studied question of frequency of intraguild predation within aphidophagous predatory guild, we constructed a model for two predators (**Paper II**). We assumed that n aphid colonies are attacked at random by p_A (p_B) individuals of predatory species A (B) and that the attacks are independent of each other both intra- and interspecifically. The resulting frequency of random encounters of predators A and B in one aphid colony was low. The simple simulation of population dynamics of species A and B with respect to the intraguild predation revealed that the decisive factor of predator's fitness is growth rate, rather than competitive ability. A comparison of frequency of intraguild encounters estimated from our empirical data indicated that, in most cases, it is even lower than expected just by random distribution of both species. This fact could be explained by existence of the optimal oviposition strategy decreasing the risk of cannibalism and/or intraguild predation in aphidophagous predators (Hemptinne et al. 1992, 1993). The generality of this conclusion should be verified on a larger scale.

In conclusion, modelling approach to study of insect population dynamics involves many instruments and techniques. I have used only some of them. I found this way interesting, thoughts provoking and

flexible in answering questions. The answer is usually as good as was the question. However, every prediction made by a model needs further verification on empirical data. This is especially difficult in the case of predictions of population dynamics in the aphid–ladybird system. Let take it as a challenge! I believe that the model is now prepared to answer more focused questions than those I have asked at the beginning.

Tony Dixon said that aphids make ideal models for studying the current fashionable aspects of biology and that our task is to convince other scientists about that. And I would like to append that modelling is a play and scientists are created to play!

Cited literature

- Alyokhin, A., Drummond, F.A. & Sewell, G. (2005) Density-dependent regulation in populations of potato-colonizing aphids. *Population Ecology* **47**: 257–266.
- Bommarco, R., Wetterlind, S. & Sigvald, R. (2007) Cereal aphid populations in non-crop habitats show strong density dependence. *Journal of Applied Ecology* **44**: 1013–1022.
- Evans, E.W. (2003) Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *European Journal of Entomology* **100**: 1–10.
- Frazer, B.D. (1988) *Coccinellidae*. Pages 231–247 in A. K. Minks, and P. Harrewijn, eds. *Aphids: their Biology, Natural Enemies and Control*. Volume 2B. Elsevier, Amsterdam.
- Hemptinne, J.-L., Dixon, A.F.G. & Goffin, J. (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* **90**: 238–245.
- Hemptinne, J.-L., Dixon, A.F.G., Doucet, J.L. & Petersen, J.E. (1993) Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *European Journal of Entomology* **90**(4): 451–455.
- Honěk, A., & Martinková, Z. (2005) Long term changes in abundance of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in the Czech Republic. *European Journal of Entomology* **102**: 443–448.
- Houdková, K. & Kindlmann, P. (2006) Scaling up population dynamic processes in a ladybird-aphid system. *Population Ecology* **48**: 323–332.
- Kindlmann, P. & Dixon, A.F.G. (1999) Generation time ratios – determinants of prey abundance in insect predator–prey interactions. *Biological Control* **16**: 133–138.
- Kindlmann, P. & Dixon, A.F.G. (2001) When and why top-down regulation fails in arthropod predator-prey systems. *Basic and Applied Ecology* **2**: 333–340.
- Kindlmann, P. & Dixon, A.F.G. (2003) Insect predator-prey dynamics and the biological control of aphids by ladybirds. Pages 118–124 in R. van Driesche, ed. *Proceedings of the 1st International Symposium on Biological Control of Arthropods*. USDA Forest Service, Honolulu.
- Lankin-Vega, G., Worner, S.P. & Teulon, D.A.J. (2008) An ensemble model for predicting *Rhopalosiphum padi* abundance. *Entomologia Experimentalis et Applicata* **129**: 308–315.
- Thacker, J.I., Thieme, T. & Dixon, A.F.G. (1997) Forecasting of periodic fluctuations in annual abundance of the bean aphid: the role of density dependence and weather. *Journal of Applied Entomology* **121**: 137–145.

Shrnutí práce

V této práci se zabývám modelováním populační dynamiky systému mšice–slunéčko. Popsaný model je rozšířením již publikovaného modelu, který je založený na mechanismu negativní odpovědi vnitřní dynamiky mšic na jejich kumulativní hustotu (Kindlmann 1985, Kindlmann a Okrouhlá 1986, Kindlmann a Dixon 1996, Kindlmann a Dixon 2003, Kindlmann et al. 2004). Mým cílem bylo rozšířit rozsah simulací z jedné kolonie na celou metapopulaci, nasimulovat optimalizační strategii v rozmisťování vajíček popsanou u mšicožravých predátorů a studovat vliv vybraných parametrů na celkovou dynamiku systému. Simulaci pro jednu vegetační sezónu jsem propojila do dlouhodobého cyklu a studovala jsem také meziroční oscilace v početnosti populací.

Model je postaven na těchto předpokladech:

- (a) Životní cyklus mšice zahrnuje střídání letní a zimní hostitelské rostliny a podzimní generaci s pohlavním rozmnožováním. Přezimují vajíčka na zimní hostitelské rostlině.
- (b) Hlavním řídicím faktorem v dynamice mšice je její kumulativní hustota, tj. početnost vrámci jedné kolonie (Kindlmann a Okrouhlá 1986, Kindlmann et al. 2004, Dixon 2005).
- (c) Mšicožravý predátor má jednu generaci během vegetační sezóny (Hagen 1962, Honěk 1989). Larvy predátora žijí pouze v koloniích mšic a jsou kanibalistické (Gagné et al. 2002, Osawa 2002, Sato et al. 2003). Při kladení vajíček se samičky řídí optimalizační strategií, která minimalizuje riziko predace a hladovění pro nakladená vajíčka i vylíhnuté larvy (Hempton et al. 1992, 1993, Hironori a Katsuhiko 1997, Kindlmann et al. 2000). Podle této strategie existuje v životnosti kolonie kořisti období vhodné pro kladení vajíček, tzv. „ovipoziční okénko“ (Hempton et al. 1993, Hempton a Dixon 2000). Vajíčka nakladená později budou nejspíše sežraná staršími larvami predátorů nebo larvy vylíhnuté z těchto vajíček pojdou hladu.
- (d) Na podzim predátoři migrují na zimoviště a na jaře se zase vrací (Hagen 1962, Hodek 1973, Honěk 1989).

V modelu jsou použity mechanistické i analytické přístupy pro modelování dynamiky a do procesů je zahrnutá také jistá míra náhodnosti. Model se skládá ze tří částí:

- 1. Dynamika „ovipozičního okénka“**, kterou modelujeme mechanisticky s prvky náhodnosti, tj. v každém kroku sledujeme jednotlivé samičky predátora, které optimalizují své chování podle řady parametrů.
- 2. Dynamika vegetační sezóny**, kdy již jednotlivec nehraje tak důležitou roli a je tedy možné použít obecnější diferenciální rovnice.
- 3. Meziroční dynamika**, která zahrnuje velmi zjednodušenou simulaci úmrtnosti při podzimní migraci a přezimování kořisti i predátora.

STUDOVANÉ OTÁZKY

S využitím modelu jsme hledali odpovědi na následující otázky.

Jak se změní dynamika systému, jestliže rozšíříme rozsah simulací z jedné kolonie kořisti na celou metapopulaci? V modelu jedné kolonie predátoři nedokázali účinně snížit početnost kořisti (Kindlmann a Dixon 2003). Změní se jejich účinnost na metapopulační úrovni? Pokud ano, ve které fázi ročního cyklu mají predátoři na kořist největší vliv? (**Práce I**)

Cyklické oscilace početnosti v dlouhodobých pozorováních byly popsány u několika druhů mšic (např., Sequeira a Dixon 1997, Thacker et al. 1997, Alyokhin et al. 2005, Dixon 2005, Bommarco et al. 2007, Lankin-Vega et al. 2008). Byly publikovány studie náhodných i hustotnězávislých procesů, ale základní mechanismus oscilací stále neznáme (Thacker et al. 1997, Alyokhin et al. 2005, Bommarco et al. 2007). Presentovaný simulační model predikuje řadu oscilací v početnosti kořisti i predátora, které jsou charakterizovány mediánem početnosti, amplitudou a délkou cyklu. Jsou tyto oscilace srovnatelné s oscilacemi popsány v literatuře? Který mechanismus vyvolává oscilace za zjednodušených modelových podmínek? (**Práce III**)

Změna klimatu přitahuje v poslední dekádě pozornost mnoha vědců. Velmi důležitým se zdá být vliv oteplování na populační dynamiku hmyzu, zvláště u druhů škodících v zemědělství a druhů přenášejících nakažlivé nemoci. Publikované studie napovídají, že přímý vliv teploty na herbivorní hmyz je pravděpodobně větší a důležitější než vliv jiných faktorů (Bale et al. 2002). V našem modelu jsou teplotou přímo ovlivněny dva klíčové parametry: růstová rychlost mšic a vývojová doba sluníček. Jaký vliv bude mít vzrůstající teplota na interakce kořisti a predátora? (**Předběžné výsledky**)

Predace uvnitř společenstva predátorů se stala hlavním tématem ve výzkumu biologické kontroly hmyzu. Z teoretických pokusů vyplývá, že predace uvnitř společenstva predátorů má shodně negativní vliv na schopnosti predátorů potlačit populace herbivorů v zemědělství v rámci biologické kontroly (Rosenheim a Harmon 2006). Interakce uvnitř společenstva jsou pravděpodobně velmi rozšířené v systémech mšice–parasitoid a mšice–parasitoid–predátor a pro parasitoidy jsou většinou zničující (Brodeur a Rosenheim 2000, Colfer a Rosenheim 2001). Jak často se ale vyskutují interakce uvnitř společenstva samotných predátorů na otevřených stanovištích? (**Práce II**)

SHRNUTÍ VÝSLEDKŮ

Rozšířením škály populační dynamiky systému mšice-slunéčko z jedné kolonie kořisti na celou metapopulaci (**Práce I**) jsme získali výsledky podobné výsledkům simulovaným na malé škále (Kindlmann a Dixon 2003). Za přítomnosti predátora oscilují početnosti obou aktérů s přibližně dvouletou periodou. Charakter výsledných oscilací určuje především aktivita predátora během „ovipozičního okénka“: čím později predátor do systému přiletí, tím je amplituda oscilací menší a dlouhodobé průměry početností kořisti i predátora jsou vyšší. Kindlmann a Dixon (2001) ukázali, že regulační mechanismy „shora-dolů“ v systému mšice-slunéčko na úrovni jedné kolonie selhávají. Na metapopulační úrovni je vliv predátora na kořist také relativně malý.

Model prezentovaný v **práci III** je nový ve dvou bodech: počty kořisti a predátorů během vegetační sezóny jsou simulovány pomocí iterací diferenciálních rovnic jednotlivě v každé kolonii kořisti a početnost metapopulace kořisti v nové sezóně je odvozena z počtu okřídlených mšic odlétajících z letních kolonií. Oscilace s dvou a tříletým cyklem se objevují v abundancích kořisti i predátora. Charakter oscilací je srovnatelný s empirickými daty (Thacker et al. 1997, Alyokhin et al. 2005, Honěk a Martinková 2005, Bommarco et al. 2007, Lankin-Vega et al. 2008). Oscilace ovšem vznikají jen tehdy, když samičky predátorů žeroucí mšice a kladoucí vajíčka do vhodných kolonií kořisti zůstávají v systému během „ovipozičního okénka“ dlouho. V protikladu stojí jiný výsledek, který v dlouhodobém měřítku predikuje maximální biologickou úspěšnost těm samičkám, které ke kladení vajíček využijí jen 20 % vhodných kolonií a potom odletí. Tento výsledek se shoduje se studiemi, které naznačují, že během rozmnožovacího období dospělá slunéčka často migrují mezi stanovišti a habitaty a nikde se nezdržují dlouho (Evans 2003). Jedno z možných vysvětlení rozporu v našich výsledcích nabízí Frazer (1988), když popisuje situaci v habitatech jako stálý „tok slunéček“ bez ohledu na hustotu mšic v daném místě. Neustálou migraci slunéček přitom přisuzuje vrozené tendenci

rozptylovat se, i když je jedinec hladový. Potom naše předpověď, že slunéčka by měla opustit systém po relativně krátké době, souhlasí s přirozeným sklonem k disperzi, zatímco vznik oscilací podmíněný déle trvající aktivitou slunéček v systému odpovídá stálému „toku slunéček“ krajinou. To by ovšem znamenalo, že početná populace slunéčka dokáže snížit abundanci mšic v krajině, přestože účinnost jednotlivých jedinců je zanedbatelná. Tím také podporuje vznik oscilací v dlouhodobé početnosti obou druhů.

Předběžné výsledky modelování vlivu vzrůstající teploty na dynamiku systému predátor–kořist naznačují, že můžeme očekávat výrazné výkyvy v dlouhodobé početnosti hmyzích populací. Za modelových podmínek se počet predátorů, kteří úspěšně dokončí metamorfózu, zvyšuje se vzrůstající teplotou. V rozmezí studovaných hodnot existuje optimální teplota (19 – 21 °C), při které kořist i predátor dosahují nejvyšších mediánů v jarní abundanci. Při teplotách pod tímto optimem odpovídá vliv žravosti larev i vztah mezi dobou trvání „ovipozičního okénka“ a mediánem početnosti trendům popsaným v práci III, to znamená, že vyšší žravost snižuje počet dospělých predátorů, ale nemá žádný vliv na medián početnosti kořisti, a délka „ovipozičního okénka“ nepřímo úměrně ovlivňuje oba mediány. Na druhém konci studovaného teplotního rozmezí ovšem tyto vztahy přestávají platit. Predátorům s méně žravými larvami se daří poněkud snížit medián početnosti mšic. Závislost mezi délkou „ovipozičního okénka“ a mediánem početnosti je narušen buď extrémem v početnosti predátora nebo zhroucením obou populací. Domnívám se, že narušení trendů může souviset s poklesem hodnoty poměru generační doby predátora ku generační době kořisti (Kindlmann a Dixon 1999) v kombinaci s přerušovanou dynamikou systému mšice–slunéčko, kde zejména vztahy během „ovipozičního okénka“ ovlivňují následnou dynamiku.

Jako příspěvek do diskuze na téma ‘skutečná frekvence predace uvnitř společenstva predátorů’ jsme sestrojili jednoduchý model pro dva predátory (**Práce II**). Mezi 100 kolonií kořisti jsme náhodně rozmístili p_A (p_B) predátorů druhu A, případně B, bez ohledu na vnitro– nebo mezidruhové interakce. V tomto rozsahu je frekvence náhodného setkání predátora druhu A s predátorem druhu B v jedné kolonii kořisti malá. Jednoduchý model populační dynamiky pro dva druhy predátorů s ohledem na predaci mezi nimi ukazuje, že rozhodujícím faktorem biologické úspěšnosti predátora je spíše růstová rychlost než schopnost kompetice. Frekvence setkávání predátorů v jedné kolonii mšic v nechráněném polním experimentu byly většinou ještě nižší, než frekvence očekávané v náhodném modelu. Toto vysvětlujeme tím, že podle teorie optimálního kladení rozmisťují samičky svá vajíčka tak, aby snížily riziko kanibalismu a střetu s jiným predátorem pro své potomstvo (Hemptinne et al. 1993, Růžička 1998, 2000). Platnost tohoto závěru je třeba ověřit také na širší škále.

Citovaná literatura

- Alyokhin, A., Drummond, F.A. & Sewell, G. (2005) Density-dependent regulation in populations of potato-colonizing aphids. *Population Ecology* **47**: 257–266.
- Bale, J.S. *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**: 1–16.
- Bommarco, R., Wetterlind, S. & Sigvald, R. (2007) Cereal aphid populations in non-crop habitats show strong density dependence. *Journal of Applied Ecology* **44**: 1013–1022.
- Brodeur, J. & Rosenheim, J.A. (2000) Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* **97**: 93–108.
- Colfer, R.G. & Rosenheim, J.A. (2001) Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* **126**: 292–304.
- Dixon, A.F.G. (2005) *Insect herbivore-host dynamics: Tree-dwelling aphids*. Cambridge University Press, Cambridge.
- Evans, E.W. (2003) Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *European Journal of Entomology* **100**: 1–10.
- Frazer, B.D. (1988) *Coccinellidae*. Pages 231–247 in A. K. Minks, and P. Harrewijn, eds. *Aphids: their Biology, Natural Enemies and Control*. Volume 2B. Elsevier, Amsterdam.
- Gagné, I., Coderre, D. & Mauffette, Y. (2002) Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecological Entomology* **27**: 285–291.
- Hagen, K.S. (1962) Biology and Ecology of Predaceous Coccinellidae. *Annual Review of Entomology* **7**: 289–326.
- Hemptinne, J.-L. & Dixon, A.F.G. (2000) Defence, oviposition and sex: semiochemical parsimony in two species of ladybird beetles (Coleoptera, Coccinellidae)? A short review. *European Journal of Entomology* **97**(4): 443–447.
- Hemptinne, J.-L., Dixon, A.F.G. & Goffin, J. (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* **90**: 238–245.
- Hemptinne, J.-L., Dixon, A.F.G., Doucet, J.L. & Petersen, J.E. (1993) Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *European Journal of Entomology* **90**(4): 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.
- Honěk, A. (1989) Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). *Acta Entomologica Bohemoslovaca* **86**: 179–192.
- Honěk, A., & Martinková, Z. (2005) Long term changes in abundance of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in the Czech Republic. *European Journal of Entomology* **102**: 443–448.
- Houdková, K. & Kindlmann, P. (2006) Scaling up population dynamic processes in a ladybird–aphid system. *Population Ecology* **48**: 323–332.

- Kindlmann, P. (1985) A model of aphid population with age structure. In: *Mathematics in Biology and Medicine*. Capasso, V., Grosso, E. & Paveri-Fontana, S.L. (eds.). Series: Lecture Notes in Biomathematics **57** Springer, Berlin, pp. 72–77.
- Kindlmann, P. & Dixon, A.F.G. (1996) Population dynamics of tree-dwelling aphids: from individual to population. *Ecological Modelling* **89**: 23–30.
- Kindlmann, P. & Dixon, A.F.G. (1999) Generation time ratios – determinants of prey abundance in insect predator–prey interactions. *Biological Control* **16**: 133–138.
- Kindlmann, P. & Dixon, A.F.G. (2001) When and why top-down regulation fails in arthropod predator–prey systems. *Basic and Applied Ecology* **2**: 333–340.
- Kindlmann, P. & Dixon, A.F.G. (2003) Insect predator-prey dynamics and the biological control of aphids by ladybirds. In: *Proceedings of the 1st International Symposium on Biological Control of Arthropods*. USDA, Forest Service, Honolulu/Morgantown, pp 118–124.
- Kindlmann, P. & Okrouhlá, M. (1986) Simulation of the population dynamics of a laboratory aphid coccinellid system. In: *Ecology of Aphidophaga II*. Hodek, I. (ed.), Academia, Praha, pp. 357–362.
- Kindlmann, P., Yasuda, H., Sato, S. & Shinya, K. (2000) Key life stages of two predatory ladybird species (Coleoptera: Coccinellidae). *European Journal of Entomology* **97**: 495–499.
- Kindlmann, P., Arditi, R. & Dixon, A.F.G. (2004) A simple aphid population model. In: *Aphids in a new millennium*. Simon, J.C., Dedryver, C.A., Rispe, C. & Hullé, M. (eds.), INRA, Paris, pp. 325–330.
- Lankin-Vega, G., Worner, S.P. & Teulon, D.A.J. (2008) An ensemble model for predicting *Rhopalosiphum padi* abundance. *Entomologia Experimentalis et Applicata* **129**: 308–315.
- Osawa, N. (2002) Sex dependent effects of sibling cannibalism on life history traits of the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Journal of the Linnean Society* **76**: 349–360.
- Rosenheim, J.A. & Harmon, J.P. (2006) The influence of intraguild predation on the suppression of a shared prey population: an empirical reassessment. In: *Trophic and Guild Interactions in Biological Control*. Brodeur, J. & Boivin, G. (eds.), Springer, Dordrecht, pp. 1–20.
- Růžicka, Z. (1998) Further evidence of oviposition-detering allomone in chrysopids (Neuroptera: Chrysopidae). *European Journal of Entomology* **95**(1): 35–39.
- Růžicka, Z. (2001) Oviposition responses of aphidophagous coccinellids to tracks of ladybird (Coleoptera: Coccinellidae) and lacewings (Neuroptera: Chrysopidae) larvae. *European Journal of Entomology* **98**(2): 183–188.
- Sato, S., Dixon, A.F.G. & Yasuda, H. (2003) Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecological Entomology* **28**: 628–633.
- Sequeira, R. & Dixon, A.F.G. (1997) Population dynamics of tree-dwelling aphids: the importance of seasonality and time scale. *Ecology* **78**: 2603–2610.
- Thacker, J.I., Thieme, T. & Dixon, A.F.G. (1997) Forecasting of periodic fluctuations in annual abundance of the bean aphid: the role of density dependence and weather. *Journal of Applied Entomology* **121**: 137–145.