Population biology of periodic Xestia moths

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Academic dissertation

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Helsinki 2003
“Even the steadiest wind raises waves on the surface of a lake”

Antti Huttunen
Population biology of periodic *Xestia* moths

Gergely Várkonyi

The thesis is based on the following articles and manuscripts:


These are referred to by their Roman numerals in the text.
Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

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<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
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In addition to the authors, Ilkka Hanski had a major contribution in article IV (Original idea, Analyses). Other contributors are acknowledged in the relevant articles or manuscripts.

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Contents

0 Summary ................................................................................................................................. 9
   Introduction .......................................................................................................................... 9
   Evolution of periodicity ................................................................................................. 10
   Hypotheses to explain periodic occurrence in insects .................................................. 11
   Aims of this thesis ........................................................................................................... 13
   Natural history of Xestia moths ...................................................................................... 13
   Distribution and life cycle evolution .............................................................................. 13
   Patterns of periodic occurrence ...................................................................................... 14
   Length of life cycle, revisited ......................................................................................... 15
   Immature biology ............................................................................................................ 15
   The problem of periodic occurrence in Xestia .............................................................. 17
   Interaction with Ophion luteus ....................................................................................... 18
   Other parasitoids ............................................................................................................. 19
   Predators and pathogens ................................................................................................. 21
   Movements of Xestia and Ophion luteus ...................................................................... 21
   Movement behaviour of Xestia fennica and X. speciosa ............................................. 21
   Mobility of Ophion luteus ............................................................................................... 23
   Spatial dynamics of Xestia moths .................................................................................... 23
   Population genetics of Xestia tecta ................................................................................. 25
   Conclusions and open questions ..................................................................................... 26
   References ......................................................................................................................... 28

I Host-parasitoid dynamics in periodic boreal moths. ......................................................... 35
   Sampling methods and data analysis .............................................................................. 36
   Biology of Xestia moths and the ichneumonid Ophion luteus ..................................... 37
   Results ............................................................................................................................... 37
   Host-parasitoid model ....................................................................................................... 39
   Insectivorous shrews ......................................................................................................... 41
   Discussion .......................................................................................................................... 42
   References ......................................................................................................................... 43

II Population densities and movement ranges of Xestia moths and the parasitoid Ophion luteus ......................................................................................................................... 47
   Material and methods ....................................................................................................... 48
   Study area .......................................................................................................................... 48
   Density estimates of Xestia larvae .................................................................................. 49
   Mark-release-recapture experiment on Ophion luteus .................................................... 50
   Results ............................................................................................................................... 52
   Density estimates of Xestia larvae .................................................................................. 52
   Density of Ophion luteus ................................................................................................. 54
   Mobility of Ophion luteus ............................................................................................... 55
   Discussion .......................................................................................................................... 56
   Population density of Xestia moths .................................................................................. 56
   Xestia-Ophion interaction ............................................................................................... 58
   References ......................................................................................................................... 59
III  Spatial dynamics of periodic *Xestia* moths in Finnish Lapland .......................... 63
   Material and methods ......................................................................................... 65
   Spatial dynamics of *Xestia* and their interaction with *Ophion luteus* .......... 65
   Analysis of landscape data ................................................................................. 66
   Results .................................................................................................................. 67
   Spatial dynamics of *Xestia* and their interaction with *Ophion luteus* .......... 67
   Analysis of landscape data ................................................................................. 69
   Discussion ............................................................................................................. 70
   Spatial dynamics .................................................................................................. 70
   Interaction with *Ophion luteus* ...................................................................... 71
   Landscape structure .............................................................................................. 72
   References ............................................................................................................ 74

IV  Use of forest corridors by boreal *Xestia* moths .............................................. 79
   Introduction .......................................................................................................... 79
   Materials and method ......................................................................................... 80
   Study area ............................................................................................................ 80
   The species .......................................................................................................... 81
   Study system ......................................................................................................... 82
   Analysis of recapture data .................................................................................. 82
   Results .................................................................................................................. 83
   Recapture rates ................................................................................................... 83
   Movement behaviour ............................................................................................ 84
   Discussion ............................................................................................................. 86
   Use of corridors ................................................................................................... 87
   References ............................................................................................................ 89

V  Genetic differentiation between alternate-year cohorts of *Xestia tecta*  
   (Lepidoptera, Noctuidae) in Finnish Lapland ....................................................... 93
   Material and methods ......................................................................................... 95
   Samples ................................................................................................................ 95
   Allozymes ........................................................................................................... 95
   Mitochondrial DNA .............................................................................................. 95
   Analysis ................................................................................................................ 96
   Results .................................................................................................................. 96
   Allozymes ........................................................................................................... 96
   Mitochondrial DNA .............................................................................................. 96
   Discussion ............................................................................................................. 96
   Allozymes ........................................................................................................... 97
   Mitochondrial DNA .............................................................................................. 98
   Hypotheses to explain the low levels of genetic differentiation ....................... 98
   Gene flow ............................................................................................................. 98
   The recent common ancestor hypothesis ......................................................... 99
   References ............................................................................................................ 99
Population biology of periodic *Xestia* moths

**Summary**

**Introduction**

Populations of living organisms are unevenly distributed both in space and time. Population biology is the branch of science investigating the patterns of these distributions and the evolutionary, genetical and ecological reasons leading to them. Temporally stable spatial pattern formation of populations may occur due to spatial heterogeneity of the environment but also due to population dynamic interactions between species in virtually homogeneous space (e.g. Harrison 2000). On the other hand, spatially stable temporal patterns have been reported e.g. for cyclic herbivores, such as small rodents (Hansson and Henryton 1985, Hanski et al. 1991, Sundell 2002) and moths (Haukojoja et al. 1988, Roland 1993), and for many periodic insects. In the longer course of time, patterns of species abundances are likely to change both in space and time.

Unlike classical population cycles, periodic occurrence is restricted to animal species possessing a fixed multiannual life cycle in extratropical regions (there are also examples of host-parasitoid interaction from the tropics, where discrete cycles may emerge if the host has a twice as long life cycle than its parasitoid; Godfray and Hassell 1987, 1989). Animal populations with a fixed k-year life cycle can be divided to as many as k temporally discrete broods or cohorts (Heliövaara et al. 1994). Due to the invariable length of the life cycle, members of a(ny) cohort maturate synchronously, and subsequently reproduce and die within a short period (Heliövaara et al. 1994). One of the prerequisites for periodic occurrence is that only a single cohort is abundant and the other(s) permanently rare or extinct. Hence, a species with periodic dynamics occurs as adults in large numbers every k\textsuperscript{th} year but remains scarce in the intervening years (Bulmer 1977). A survey of the literature shows that most periodic animals are insects, but the phenomenon is also reported from the Pacific pink salmon (e.g. Aspinwall 1974, pp. 293-297 in Royama 1992). Periodic insect life cycles vary from 2 to 17 years (for a list of examples see Heliövaara et al. 1994), but most species are biennial with alternate-year occurrence. Periodicity has been reported from a range of insect orders, including Ephemeroidea (Hexagenia limbata: Riklik and Momot 1982), Hemiptera (Magicicada spp.: e.g. Lloyd and Dybas 1966a, b, Aradus cinnamomeus: Heliövaara and Väisänen 1984, 1987, 1988a), Lepidoptera (e.g. Xestia spp.: Valle 1933, Kettlewell in Ford 1955, Mikkola 1976, Imby and Palmqvist 1978, Suomalainen 1983, Lafontaine et al. 1987, Pulliainen and Itämites 1988, Mikkola and Kononenko 1989, Rost et al. 2001, I, Psodos (=Glacies) coracina: Kettlewell in Ford 1955, Lasiocampa quercus: Kettlewell 1973, Erebia spp.: Suomalainen 1937, Douwes 1980, Wipking and Mengelkoch 1994, Oeneis jutta: Douwes 1980, Cosmotriche lobulina: Saarenmaa 1982, Retinia resienna: Heliövaara and Väisänen 1988b, Korscheltellus gracilis: Leonard and Parker 1994), Diptera (Chironomus anthracinus: Jónasson 1971), Hymenoptera (Neodiapion setifer: Pschorn-Walcher 1970, Saarenmaa 1989) and Coleoptera (e.g. Melolontha spp.: Bulmer 1977) (names of the insect orders according to Rasnitsyn and Quicke 2002). The vast majority of recognized periodic species belongs to Lepidoptera (I).

Though many insects with fixed multiannual life cycle exhibit a periodic occurrence, there are also well-documented exceptions (Imby and Palmqvist 1978, Douwes 1980, Whittaker 1985, Butler and
McMillan 1990, see also I). The reason for why some taxa with fixed biennial life cycle are periodic and others are not seems to lie in population dynamics rather than in evolutionary history, as separate populations of certain species may emerge either every year or predominantly in alternate years (e.g. Imby and Palmqvist 1978, Douwes 1980, N. Hydén personal communication). In fact, the problem about the evolution and ecology of periodicity may be divided into several questions. How and in what circumstances individual development will be prolonged?

How multiannual life cycle will be fixed in a population? What processes lead to periodic dynamics in populations with a rigid multiannual life span?

Evolution of periodicity

Long life cycle in insects is related to large body size, cool or unpredictable environment and nutrient-poor diet (Danks 1992). A combination of these intrinsic and extrinsic factors tends to further lengthen life cycles. Cold seasonal climate (a predictable extrinsic constraint) reduces the number of days per year when physiological processes, including development, can take place, hence prolonging development time. There are many examples of insects with different geographical races or subspecies possessing either a one- or a two-year life span (Kettlewell 1973, Saarenmaa 1982, Pschorn-Walcher 1970, Saarenmaa 1989).

In all these cases, the biennial clade occurs in a cooler climate than the univoltine one, which suggests that two-year life span of these insects has developed via adaptation to low temperatures. The pine bark bug Aradus cinnamomeus and the pine resin gall moth Retinia resinella both have a 2-year life cycle in southern parts of Fennoscandia, but north of the long-term 21°C July isotherm they develop in three years (Heliovaara et al. 1994). A similar pattern, but intriguingly as a result of a reverse process, is reported from the North American periodic cicadas (Magicicada). Altogether seven species (Marshall and Cooley 2000) have been recognized with a strict 13- or 17-year periodicity. Species with a 13-year life span have originated from species with a 17-year period by four-year acceleration of development (Martin and Simon 1988). These incipient 'species' are all distributed in the warmer southern parts of the geographical range of Magicicada (e.g. Simon et al. 2000). Simple environmental factors such as temperature and photoperiod coupled with intrinsic (genetical and physiological) constraints may give rise to very complex life cycle pathways (Danks 1991).

While adverse seasonal conditions may lengthen the life span of populations, unpredictable environment tends to increase variation in the length of development within populations (Danks 1992, Heliovaara et al. 1994). This is due to a trade-off between the mean and variance of fitness of individuals, such that phenotypes with reduced mean fitness may be at a selective advantage under certain conditions (Philippi and Seger 1989). This phenomenon is called evolutionary risk-spreading (Hopper 1999) or bet-hedging (Slatkin 1974). Since unpredictable environmental catastrophes may cause heavy mortality in populations, in regions with unstable environment there may occur strong selection for increasing the variation in the length of dormancy, hence the risk of local extinction by accidental disastrous events will be diminished. This is because genetic lineages with variation in the duration of immature development will survive more likely, and in the longer course of time these lineages will become prevalent in the population.

As explained above, the length of life cycle in an entire insect population may have become longer or shorter due to adaptations to climatic conditions. Temporal risk-spreading is another way that may have given rise to populations with a multiannual life cycle and/or periodic occurrence (Heliovaara et al. 1994, Hopper 1999). Martin and Simon (1990b) and Williams and Simon (1995) have hypothesized the evolutionary steps resulting in the unique periodicity in Magicicada. In populations with variability in the duration of life cycle, individuals with a longer life span may have
become larger and gained elevated fecundity (Karban 1986). *Magicicada* populations have experienced a population bottleneck in the eastern parts of North America during the Pleistocene (Cox and Carlton 1988, Martin and Simon 1990a, Cox 1992, Yoshimura 1997, Cox and Carlton 1998). Cox and Carlton (1988) presented a paleoclimatic model, which predicts increased survivorship for cicada broods with longer life cycles. Lloyd and Dybas (1966b) assumed that ancestors of *Magicicada* had a 7-year life cycle. Long life cycle in these cicadas has been attributed to xylem feeding. Due to variable weather conditions one of the broods may have grown in number while other broods not. Interaction with natural enemies would have regulated the minor broods that emerge after peak years and decreased variability in the life span of the major brood. This interaction yielded a protoperiodic condition, in which there is a substantial abundance difference among broods. Selection favoured even longer life cycles and synchronized emergence in these populations, while synchronized cicada emergence satiated predators and hence increased survivorship in the periodic cicada populations (Lloyd and Dybas 1966b, Martin and Simon 1990b). High density in *Magicicada* populations increased interference competition between broods at the nymphal stage and improved both adult survivorship and mating success in the major brood (Williams and Simon 1995).

Hypotheses to explain periodic occurrence in insects

The evolution of *Magicicada* seems to involve a wide range of interconnected events that together have eventually yielded a unique phenomenon. Other periodic insects have a much shorter life cycle (mostly two years; see Heliovaara et al. 1994) and probably simpler life cycle evolution. Several hypotheses have been put forward to explain periodicity in insects, all of which seem to have contributed to the evolution of periodicity in *Magicicada*. Valle (1933) explained the absence of even-year-emerging cohort of biennial *Xestia* moths in eastern Finnish Lapland by a hypothetical weather catastrophe, which would have eliminated the entire cohort. As pointed out by Mikkola (1976), this hypothesis is implausible, since a single catastrophe is very unlikely to completely destroy a cohort over large areas, and scarce cohorts would have grown in numbers back to the carrying capacity. A further argument against an abiotic catastrophe is that different moth species in Finnish Lapland do not share common spatial domains of predominantly odd- or even-year adult emergence. For instance, most *Xestia* moths emerge in eastern Lapland in odd years and in western Lapland in even years (Mikkola 1976, Rost et al. 2001, I, III), while the moth *Cosmotriche lobulina* flies only in even years in Finnish Lapland (Saarenmaa 1982).

The two plausible hypotheses to explain how periodic occurrence is maintained in many periodic insects are inter-cohort competition and interaction with natural enemies. Competition between year-classes may take place when larvae of different age or larvae and adults feed on the same resource. There are three ways how such competition may operate. First, interference competition, such as killing members of the other cohort(s) and cannibalism, may be apparent in years when the abundant cohort is at late instars or has reached the adult stage. Such interference competition has been reported for the May beetle *Melolontha melolontha* (see Bulmer 1977) and it has been suggested to operate in *Magicicada* nymphs (Bulmer 1977, Simon et al. 1981). The common feature in these examples is root feeding by different cohorts in limited space. Second, competition for resources is also likely to take place in May beetles and periodic cicadas (Bulmer 1977). However, the only well-documented example of such exploitation competition comes from the pine bark bug *Aradus cinnamomeus*, which is a sap-feeder on pine trunks both at the larval and the adult stage. In an experimental study, deeper-penetrating young larvae were found to be better exploitation competitors than older
larvae and adults (Heliövaara and Väisänen 1986), which may explain the parapatric distribution of the bug cohorts in Fennoscandia. In the third type of competition, the major cohort of a periodic herbivore induces chemical defence in the host plant, hence the survivorship of the cohort to emerge in the subsequent year will be reduced. There are no good examples for this kind of interaction, but such mechanism has been postulated to operate in the moths Retinia resinella (Heliövaara and Väisänen 1988) and Xestia (Mikkola and Kononenko 1989). Resource-mediated intraspecific competition is in fact not real competition in the narrow sense of the term but rather analogous to apparent competition (Holt 1977). On the other hand, it shares an important common element with the second major mechanism that has been suggested to explain periodic occurrence, namely interaction with natural enemies. In both cases, the major cohort induces delayed negative feedback (chemical response in the host plant and numerical response in natural enemies), which is directed against the minor cohort in the subsequent year. It is important to notice that this type of interaction may operate only if the time lag in the response is half as long as the life cycle of the herbivore. This is the case in some host-parasitoid interactions in both the tropics (Godfray and Hassell 1987, 1989) and in boreal forests (Mikkola 1976, Rost et al. 2001, I).

Interaction with natural enemies is a plausible general explanation for periodicity in holometabolous biennial insects, where the year-classes feed mostly in different habitats, and where there is hence only a short or non-existent time window for intraspecific inter-cohort competition to occur (Mikkola and Kononenko 1989, I). Biennial life cycle in the prey/host is a prerequisite for an appropriate numerical response (with one-year lag) in the predator or the parasitoid. The temporary increase in the density of the natural enemy every second year may potentially keep the minor cohort scarce through time. Another necessary condition for this interaction is that the predator or parasitoid is at least locally specialized to the prey species. An alternative prey or host in the off-years would increase pressure against the major cohort and hence relax the regulation of the minor cohort.

Although interaction with natural enemies is possibly the most widespread mechanism (in terms of the number of periodic species) maintaining periodic occurrence in insects, only limited evidence has accumulated to support this hypothesis. Kettlewell (in Ford 1955) suggested that a univoltine parasitoid would switch between the biennial periodic noctuid moths Psodos coracina and Xestia alpicola that have alternate peak years in Scotland. This scenario is implausible, however, since such a parasitoid could not regulate any of the minor cohorts in the presence of an abundant alternative host (I). This mechanism could only work in the most unlikely case that the minor cohorts of both species would have gone extinct. Kettlewell (1973) proposed that a parasitoid attacking the univoltine moth Saturnia pavoniae might regulate the minor cohort of the biennial periodic moth Lasiocampa quercus. This hypothesis is plausible only if the univoltine host is little used by the parasitoid (I).

Mikkola (1976) put forward a natural enemy hypothesis according to which specialist predators, parasitoids and pathogens regulate the minor cohorts of several coexisting species in Xestia moths. Multiple evidence from eastern Finnish Lapland now support this hypothesis (I, see below), including knowledge of the biology of the moth species and the potential parasitoids, analysis of a long time series of Xestia, the parasitoid wasp Ophion luteus and Sorex shrews as well as modelling. Leonard and Parker (1994) studied periodic occurrence in the hepialid moth Korscheltellus gracilis in eastern parts of North America. They found that interaction with insect parasitoids, nematode parasites and pathogenic fungi may explain periodicity in the moth, although they did not present sufficient data to critically test this hypothesis. However, they could exclude the alternative hypotheses of cryptic species, recent colonization, abiotic catastrophes and exploitative competition, while the hypothesis
of interference competition remained untested due to limited and inconclusive data. Wipking and Mengelkoch (1994) have presented evidence of significantly higher rate of parasitism in the early instar larvae of biennial Erebia butterflies in low than in peak years of the occurrence. This result is consistent with the natural enemy hypothesis. Similar evidence has been presented for the interaction between the early instar larvae of Xestia tecta and its ichneumonid parasitoid Meloboris collector (I).

Alternate-year occurrence of many lepidopteran species has probably evolved in two separate steps. First, univoltine species overcome the cold climate in northern and alpine environments by prolonging their life span to two years. Second, interaction with natural enemies may have led to alternate-year occurrence. A weather catastrophe is not only implausible but not even needed for initiating such a dynamic interaction, as demonstrated by our modelling results (I). According to these results, interaction with a parasitoid with an appropriate life history leads to periodic dynamics with major and minor host cohorts from all initial conditions.

Competition may reinforce periodicity in biennial holometabolous insects, such as moths and butterflies, but it may have a more important role in hemimetabolous insects and in holometabolous insects with long larval development (>2 years; e.g. Melolontha beetles). On the other hand, interaction with natural enemies may be a complementary explanation for periodicity in hemimetabolous insects (e.g. Aradus cinnamomeus; Heliövaara and Väisänen 1984).

Aims of this thesis

This thesis is focused on the problem of alternate-year occurrence of biennial Xestia moths in Finland. In the first article (I), we present a general review of the periodic dynamics in Xestia and discuss multiple evidence, including both empirical and modelling results, supporting Mikkola's (1976) natural enemy hypothesis. In the second article (II) I demonstrate that the ratio of empirically measured densities of Xestia and Ophion is similar to the respective ratio in the long-term time series data analysed in article I. These density estimates are also consistent with predictions of the host-parasitoid model that has been constructed for the Xestia-Ophion interaction (I). Articles IV and II include analyses of dispersal distances in the host and the parasitoid, respectively, which information is essential for understanding the link between local and regional dynamics in the host-parasitoid interaction. In article III, I study the Xestia-Ophion interaction along a long transect stretching across the two major spatial domains with opposite-phase Xestia dynamics in Finnish Lapland. A further goal of this study was to identify the spatial scale at which Xestia moths respond to the area of suitable habitat. Finally, I analyse the landscape structure in central Finnish Lapland to test the theoretical prediction by Rost et al. (2001) that the boundary between Xestia domains becomes fixed in areas of low environmental carrying capacity. In the final article of this thesis (V) we study whether genetic data indicate spatial and/or temporal isolation of the Xestia tecta cohorts.

Below, I first summarize what is known about the natural history of biennial Xestia moths. I then discuss results that are relevant to the problem of periodic occurrence in Xestia (I, II, III). Next I summarize the results on movements of Xestia and Ophion (IV, II) and results on spatial dynamics of Xestia (III). Finally, I summarize what has been found about genetic differentiation of the different cohorts of X. tecta (V).

Natural history of Xestia moths

Distribution and life cycle evolution

Owlet moths in the subgenus Pachnobia s.l. (including former subgenera Anomogyna, Pachnobia s.str. and Schonenia, Kullberg et al. 2001) of genus Xestia (Lepidoptera,
Noctuidae) are distributed to boreal forests, subarctic tundra and, at more southern latitudes, to alpine habitats of the Northern Hemisphere (Mikkola 1976, Mikkola and Jalas 1977, Lafontaine et al. 1987, Mikkola and Kononenko 1989, Skou 1991). All species that have been studied seem to share a fixed two-year development (Mikkola and Jalas 1977, Lafontaine et al. 1987, Skou 1991), though it has been suggested that in Central European mountains development would be completed in one year (Lafontaine et al. 1987, Mikkola and Kononenko 1989). However, there is no evidence whatsoever for such acceleration of the life cycle in alpine habitats. Other periodic insects with both alpine and boreal populations do not seem to have shorter life span in the alpine environments (Pschorn-Walcher 1970, Wipking and Mengelkoch 1994).

Biennial life span in *Xestia* seems to have evolved only once, and subsequent radiation has resulted in ca. 40 species (see Mikkola et al. 1991, Mikkola et al. 1994, Kononenko et al. 1996) in Eurasia and North America. Mikkola et al. (1991) suggested that during the Miocene, the common ancestors of extant species of *Pachnobia* s.l. lived in the mountains or steppes of inner Asia. Speciation of extant species has been dated to the upper Pleistocene, for instance speciation to the Holarctic species *Xestia speciosa* and its Nearctic vicarian sibling *X. mixta* probably took place before the Wisconsinan glaciation (Mikkola et al. 1991).

**Patterns of periodic occurrence**

In most areas, *Xestia* (*Pachnobia* s.l.) species have a clearly periodic occurrence with alternate-year emergence of the vast majority of adults (Mikkola 1976, Imby and Palmqvist 1978, Lafontaine et al. 1987, I, III). There is evidence for periodicity in at least 20 *Xestia* species (for a list of 19 species see Heliovaara et al. 1994; in addition *X. lyngei* emerges predominantly in odd years: Skou 1991). Coexisting periodic *Xestia* species typically (Mikkola 1976, Lafontaine et al. 1987, Pulliainen and Itäemies 1988, Rost et al. 2001, I) but not always (Imby and Palmqvist 1978, N. Hydén personal communication) share common years of adult emergence. Periodic occurrence is not spatially uniform but there are domains with adult emergence mostly in odd or even years as well as areas with equal cohort densities (Mikkola 1976, Imby and Palmqvist 1978, Rost et al. 2001, I, III). Spatial domains are typically large, of the order of thousands of square kilometres or larger. Odd-flight-year dominance has been reported from eastern Fennoscandia, northern Siberia and western parts of North America, while the opposite even-flight-year dominance seems to occur in western Fennoscandia, the Scottish Highlands and eastern North America (Mikkola 1976, Imby and Palmqvist 1978, Itäemies et al. 1982, Lafontaine et al. 1987, Pulliainen and Itäemies 1988, Mikkola and Kononenko 1989, Rost et al. 2001, I, III). Mikkola and Kononenko (1989) and Mikkola et al. (1991) suggested that the huge area stretching from Finland via Siberia and the Beringian Isthmus to Canada west of the Hudson Bay would represent a single domain, reflecting the glacial history of the subgenus. Although there is no evidence for opposite-phase domains of *Xestia* in this area, the existing positive evidence is rather limited and inconclusive.

Periodic occurrence in *Xestia* has been studied in detail in Fennoscandia (e.g. Mikkola 1976 and references therein, Imby and Palmqvist 1978, Itäemies et al. 1982, Suomalainen 1983, Pulliainen and Itäemies 1988, Salokannel and Mattila 2000, Rost et al. 2001, I, III), which is perhaps equally due to the relatively large number of periodic *Xestia* species in the region (>10, uncertainty due to limited data of *X. brunneopicta* and *X. atrata*) and the high density and enthusiasm of lepidopterists. Finland is one of the most interesting areas within the geographic range of *Xestia*, since a major boundary between opposite-phase domains stretches across the country (Mikkola 1976, Rost et al. 2001, I, III, see also fig. 1 in V).
Length of life cycle, revisited

Fixed two-year life cycle in *Xestia* is based on two obligatory winter diapauses (Mikkola and Jalas 1977, Lafontaine et al. 1987, Skou 1991, Várkonyi and Ahola 2001, I, II). The first diapause takes place in the first to fourth larval instar (Várkonyi and Ahola 2001), while most species spend their second winter in the final (5th) instar. Species in the former subgenus *Schoyenia* seem to overwinter the second time as pupae (Mikkola and Jalas 1977, Skou 1991). That all periodic species overwinter first as early or mid-instar larvae is probably not genetically controlled, but is rather due to the short growing season. Evidence for this hypothesis comes from indoor rearings, where at sufficiently high temperatures and artificially prolonged day length larvae develop steadily to the final instar (M. Ahola personal communication). On the other hand, the second winter diapause in the former subgenera *Anomogyna* and *Pachnobia* s.str. seems to be crucial for successful pupation during the subsequent summer (Lafontaine et al. 1987, I). Thus larvae that were forced to skip the first diapause by providing appropriate conditions fail to pupate if not allowed to enter and stay in a long diapause at low temperatures (M. Ahola personal communication). Hence, the only theoretical source for variability in the length of the life cycle is prolongation by a year or a few years. In very dense *ex ovo* rearings (300–800 times natural densities) of *Xestia alpicola* and *X. speciosa*, a small fraction of the individuals failed to reach the full-grown larval stage before the second winter, and these larvae successfully developed to the fifth instar during the subsequent summer (I). Unfortunately, these larvae never pupated but died prior to metamorphosis, hence there is no evidence for plasticity to prolong the life cycle even under exceptionally poor conditions.

Repeated sampling of *Xestia* larvae in nature shows that larvae have unequal growth rates (personal observation), apparently due to variability in the exposition of the habitat (e.g. duration of the snow cover in early summer) and other environmental factors. Variability in the developmental rate of larvae (with synchronized adult emergence) is also found in root-feeding nymphs of *Magicicada* (Lloyd and Dybas 1966b) and in aquatic larvae of the leptophlebiid mayfly *Habrophlebia vibrans* (Lauzon and Harper 1986) and the chironomid *Chironomus cucini* (Butler and McMillan 1990). Martin and Simon (1990) suggested that prolonging the life cycle of protoperiodic *Magicicada* was a response to selection for perfect periodicity in terms of allowing the slowly developing nymphs to 'catch up' and emerge synchronously with the rest of the brood. *Xestia* larvae—even in those species that overwinter the first time in the first larval instar—usually complete their development clearly before the end of the second summer, and fully-grown larvae of some species even fall to a quiescent stage for the rest of the summer (Várkonyi and Ahola 2001). This behaviour coupled with rapid development might be an adaptation to overcome the developmental constraints in the harsh northern environment, and is therefore analogous to the waiting period of fully-grown but not fully-aged nymphs of *Magicicada*.

As *Xestia* larvae apparently do not have a problem to reach the final instar in nature before the second winter diapause, the hypothesis of fixed two-year life cycle seems to be well grounded. Hence, the hypothesis according to which the minor cohort is an assemblage of descendants of the major cohort with delayed development rather than an independent cohort with two-year life span (Mikkola 1976, Hanski 1988) seems implausible.

**Im mature biology**

In northern Finland, mated female *Xestia* lay up to ca. 300 eggs (II) to the ground vegetation in late July and early August (for a scheme of the entire life cycle in eastern Lapland see fig. 1 in I or fig. 2 in V). In laboratory conditions, eggs are laid in batches of 10–30 eggs (*Xestia*
tecta) or laid either individually or in small batches of <10 eggs (X. speciosa, X. alpicola and X. fennica; own observations). Larvae hatch in indoor rearings within a week while in outdoor rearings in two to three weeks. The small larvae feed on species of Ericaceae (most importantly on Vaccinium myrtillus and V. uliginosum) and Empetraceae (Empetrum nigrum ssp. hermaphroditum). Other recorded host plants in Europe include Vaccinium vitis-idaea, Arctostaphylos uva-ursi, Calluna vulgaris (Ericaceae), Betula nana, Betula pubescens ssp. tortuosa (Betulaceae), Ribes spicatum (Grossulariaceae), Lonicera nigra (Caprifoliaceae), Rubus chamaemorus, Alchemilla sp., (Rosaceae), Solidago virgaurea and Hieracium sp. (Asteraceae) (Valle 1940, Forster and Wohlfahrt 1964, Mikkola and Jalan 1977, Skou 1991, M. Ahola personal communication). After the first winter diapause spent in the moss layer some species (Xestia sincera, X. borealis and X. brumneopicta) switch their habitat and start feeding on young needles of Norway spruce Picea abies (e.g. Mikkola and Jalan 1977, Skou 1991, Itämis et al. 1996, Värkonyi and Ahola 2001). It appears that habitat switching in X. sincera does not happen immediately after the snowcover has melted but once-overwintered larvae feed first on bilberry V. myrtillus (own observations) and penultimate instar larvae climb up to spruce trees. In captivity, larvae accept many other plants for food, suggesting that most species are host plant generalists.

Larvae overwinter the second time in the final (5th) instar (see previous section). After the second hibernation, which typically takes place deep in the moss layer, some larvae climb up to feed before pupation. Because many of these larvae are parasitized by ichneumonid wasps (own unpublished data, see section ‘Other parasitoids’), the importance of feeding prior pupation remains poorly understood. Pupation takes 3–4 weeks in Lapland, and adult moths emerge from late June to August, depending on species (own observations).

Xestia larvae feed typically during the night, but at least in mid-summer at northern latitudes when nights are light, some species keep feeding also at daylight. In a sweepnetting study conducted on 22–23 June 1998 in the Värriö region (Fig. 1), eastern Finnish Lapland, the average numbers of 2nd to 3rd instar Xestia tecta larvae in ten-sweeping samples collected within the same habitat patch at day and night were 19.8 and 32.8, respectively (N=5 in both). Feeding activity at day and night differed significantly (t-test: t=-2.75, df=8, P=0.025). The difference in feeding activity of 4th to 5th instar X. tecta larvae one month later (23 July 1998) was even more pronounced (average numbers of larvae in 14 and 11 ten-sweeping samples collected at day and night were 0.2 and 3.3; Mann-Whitney test: U=12, Ntotal=25, P<0.001). This result suggests that crepuscular-nocturnal activity in X. tecta larvae becomes gradually more distinct with larval development. This pattern holds also in larvae before the first and after the second winter diapause: young larvae are clearly active at daylight while twice-overwintered larvae can never be found feeding during the day. Other common biennial Xestia species seem to be more strictly nocturnal during their entire larval stage. An interesting feature in the behaviour of many noctuids including Xestia is that fully-grown larvae tend to gather beneath light traps. This behaviour has been little utilized in research, but it is a potential method to census large larvae.

Absolute population density of once-overwintered 2nd to 3rd instar Xestia larvae in Värriö has been estimated using the removal method (Greenwood 1996, Southwood and Henderson 2000) (II). Pooled densities of Xestia, mainly consisting of the dominant species X. tecta and X. alpicola, ranged between 4 and 10 individuals/m² in different forest types. Xestia tecta was most abundant (7.4 larvae/m²) in Uliginosum-Empetrum-Myrtillus type forests (UEMT; Kalliola 1973) (II). Larval densities became substantially reduced within one month due to predation and the emergence of the early larval parasitoid guild (II, see below), and the densities of 4th to 5th instar larvae were only 10 (X. tecta and X.
speciosa) to 26% (X. alpicola) of the respective densities of the 2nd to 3rd instar larvae (II). A similarly rapid decrease in X. tecta density was found in the independent data set on feeding activity (see above): the density of night-swept larvae decreased in 30 days from 32.8 to 3.3. The pooled larval density of Xestia shortly before the second winter diapause was only ca. 2 individuals/m² (0.8 for X. tecta alone) (II). In an emergence-trap study conducted in Värriö, the pooled density of emerging Xestia adults was estimated to be 0.027 moths/m², which is possibly an underestimate of the true average density (II).

The problem of periodic occurrence in Xestia

The most likely explanation for periodicity in biennial Xestia populations is interaction with
natural enemies. In this chapter I first shortly discuss why the other plausible hypothesis, namely inter-cohort competition, is unlikely to explain periodic occurrence in *Xestia*. Then I turn to the evidence for the natural enemy hypothesis, including modelling results.

Why is periodicity in *Xestia* unlikely to be maintained by inter-cohort competition? First of all, interference competition such as fighting behaviour or cannibalism has been never observed in nature nor in rearings (Mikkola and Kononenko 1989, I). Second, exploitative competition between larvae is implausible, since the distribution of larvae is aggregated (own observations), and because the host plants of the polyphagous larvae are very abundant almost everywhere in the boreal forest zone (Mikkola and Kononenko 1989, I). Finally, resource-mediated competition is also improbable, because *Xestia* larvae, unlike larvae of the Autumnal moth *Epirrita autumnata* (own observations), do not cause visible damage in the ground vegetation even in peak years (I).

**Interaction with Ophion luteus**

In a long-term light-trap material collected with 11 permanent light traps at the Värriö Subarctic Research Station of the University of Helsinki (Fig. 1) from 1978 onwards (Itäemies et al. 1982, Pulliainen and Itäemies 1988, I), *Xestia* moths and the ichneumonid parasitoid wasp *Ophion luteus* were both strikingly abundant (I). Ophionine wasps (Hymenoptera, Ichneumonidae) are koinobiont solitary larval endoparasitoids (Askew and Shaw 1986, Gauld and Bolton 1988) of larger moths, and the *luteus* species group is known to attack exclusively noctuids (Brock 1982). *Ophion luteus* is one of the most abundant species of the genus throughout Europe, yet there are surprisingly few authentic rearing records in museum collections. Since none of the known hosts occur in Värriö, *O. luteus* has to parasitize a so far overlooked abundant host with a sufficiently large body size for the development of a relatively large endoparasitoid such as *O. luteus*. Given the nocturnal flight activity of the wasp (e.g. Brock 1982) and its clearly autumnal flight period in northern Europe, it seems inevitable that it parasitizes some noctuids that overwinter at the larval stage and the larvae of which are also nocturnal. A survey of the species-poor lepidopteran fauna of Värriö strongly suggests that *Xestia* are the hosts of *Ophion* in the area, though so far there are no direct observations of this biological link (I).

*Ophion luteus* is very abundant in the Värriö light-trap material in even years but scarce in odd years (I). Since *Xestia* moths in this region are abundant in odd years (see section 'Patterns of periodic occurrence'), this result suggests a host-parasitoid interaction between *Xestia* and *Ophion* that may regulate the minor *Xestia* cohorts. The necessary conditions for such an interaction are that the parasitoid has half as long a life cycle as its host and that the parasitoid is specialized to the host (see section 'Hypotheses to explain periodic occurrence in insects'). *Ophion luteus* has been shown to develop in one year in another host (I). The year-to-year sex ratio variation of *Ophion* in Värriö also provides evidence for a one-year development in the study area (I). That *O. luteus* fails to have abundant potential alternative hosts in the area is supported by the long-term intensive study of the local lepidopteran fauna. The frequency distribution of *Xestia* and *Ophion* among the permanent monitoring traps in Värriö also supports the host-parasitoid hypothesis. The pooled sample of *Xestia* and the sample of *Ophion* were largest in the same few traps, which indicates a shared habitat preference of the species.

Data from different parts of Finnish Lapland show that where adults of *Xestia* are abundant in odd years, *Ophion* is abundant in even years and vice versa (I, III). This pattern is parsimoniously explained by a host-parasitoid interaction between the species. Moreover, in the Värriö time series, the finite rate of change in *Xestia* over its two-year life
cycle was negatively related to the numbers of *Xestia* and *Ophion* two years earlier (I), indicating density dependence in the *Xestia* population and interaction with *Ophion*. The finite rate of change in the *Ophion* population over its one-year life span was negatively related to the numbers of *Ophion* one year earlier but positive related to the numbers of *Xestia* one year earlier (I), which result is also consistent with the natural enemy hypothesis. Regression models based on the alternative assumption of two-year life cycle in *Ophion* did not fit the empirical data well (I).

The third type of evidence supporting the *Xestia-Ophion* hypothesis comes from modelling (Rost et al. 2001, I). Our model is a traditional host-parasitoid model, with host dynamics based on the Ricker model (Ricker 1954) and with a specific assumption of a partial temporal refuge of the host from the parasitoid, resulting in unequal risk among hosts to become parasitized. The assumption of phenological asynchrony between the host and the parasitoid is realistic, and it has been widely used in modelling host-parasitoid interactions (Godfray et al. 1994, for a review see Hassell 2000). Our model (Rost et al. 2001, I) reads

\[
N_i = N_{i-2} \exp[r(1 - N_{i-2}) - \frac{1 - \exp(-aP_{i-2})}{aP_{i-2}}]
\]

\[
P_i = N_{i-1} \left[1 - \frac{1 - \exp(-aP_{i-1})}{aP_{i-1}}\right],
\]

where \(N\) and \(P\) denote the sizes of the *Xestia* cohorts and the *Ophion* population, respectively. Parameter \(a\) stands for the searching efficiency of the parasitoid, while \(r\) is the intrinsic rate of population increase of the host. This model, with \(a=20\) and \(r=1.5\) and with intermediate noise added, produces a strikingly similar time series as observed in the empirical data from Värriö in August 1995, intact egg batches laid by *X. tecta*, *X. alpicola* and *X. speciosa* in laboratory were exposed to parasitoid attack in the field, but not a single parasitoid was reared.

The early larval parasitoid guild (see II) seems to attack the small larvae before the first winter diapause (Fig. 2), since small larvae sampled simultaneously with snow melting after the winter already contained these species. The most common member of this guild is *Meloboris collector* (Hymenoptera, Ichneumonidae), a koinobiont solitary endoparasitoid, which had a substantially higher parasitism rate in 1997 than in 1996 (I). Since this species has never been reared from other moths in the area, it can be assumed to be a local specialist on *Xestia* (I). The yearly difference in parasitism rates suggests a similar host-parasitoid dynamics.

**Other parasitoids**

Although the direct evidence of *Ophion luteus* parasitizing *Xestia* is still lacking, several other parasitoids have been reared from *Xestia* during the past few years. Here I summarize the preliminary results from my own rearings and the literature.

Figure 2 depicts a scheme of the recognized interactions between *Xestia* moths and their parasitoids. There are no records of egg or egg-larval parasitoids of *Xestia*. In an experiment conducted in Värriö in August 1995, intact egg batches laid by *X. tecta*, *X. alpicola* and *X. speciosa* in laboratory were exposed to parasitoid attack in the field, but not a single parasitoid was reared.
as the hypothesized Xestia-Ophion interaction. The koinobiont solitary endoparasitoids Meteorus gyrator and Aleiodes borealis (Hymenoptera, Braconidae) are other common members of this guild. In turn, two unidentified species of Chalcidoidea (Hymenoptera) and Tachinidae (Diptera) are more accidental parasitoids of Xestia larvae in Värriö. The early larval parasitoid guild kills the host in 3rd or 4th instar, apparently due to some hormonal trigger within the host prior to molting.

The late larval parasitoid guild includes two unidentified species of Macrocentrus and Apanteles s.l. (Hymenoptera, Braconidae). Both species are koinobiont gregarious endoparasitoids, which emerge from final-instar Xestia larvae after the second winter diapause (Fig. 2). There is no evidence of the host stage these parasitoids attack. Species of Macrocentrus develop by polyembryony (Shaw and Huddleston 1991), that is, one or a few eggs are laid and zygotea split several times and produce genetically identical siblings. The Macrocentrus species attacking Xestia produces up to 50 offspring per host individual, including both males and females. This latter observation indicates that the female wasp lays more than one egg in the host larva. Since the brood size of Macrocentrus is rather large, it has the potential to contribute to the regulation of the minor Xestia cohorts. However, there is no knowledge of the host range of this species. The species of Apanteles...
s.l. seems to be much less common than *Macrocentrus*, and its clutch size is also smaller (up to 9 individuals). Cocoons of *Macrocentrus* are parasitized by an ichneumonid wasp, *Gelis* sp., which is a gregarious hyperparasitoid. Species of *Gelis* are idiobiont hyperparasitoids of cocoons and similar structures of insects, and they may facultatively attack the herbivore host or the primary parasitoid (Gauld and Bolton 1988). In this case, *Gelis* sp. attacks *Macrocentrus* clearly after the primary parasitoid has killed its host and formed its own cocoon. Hence, in this system *Gelis* is an obligate hyperparasitoid (Gauld 1988) or more precisely, a pseudohyperparasitoid (Shaw and Askew 1976).

There are no records of pupal parasitoids of *Xestia* from Finland, which is apparently due to the habit of most species pupating deep in the moss layer. All the known records come from the Scottish subspecies of *X. alpica*, the Northern Dart. The known pupal parasitoids are the gregarious pteromalid *Coelopisthia caledonica* (Hymenoptera, Chalcidoidea) and the solitary ichneumonid *Ichneumon megapodus* (Hymenoptera) (Yu and Horstmann 1997, M. R. Shaw and R. Leverton, personal communication). From a set of pupae of Scottish *X. alpica* sent over by R. Leverton, a single specimen of the generalist idiobiont pupal parasitoid *Pimpla melanacrias* (Hymenoptera, Ichneumonidae) and a brood of *C. caledonica* emerged.

At the moment it is impossible to conclusively assess the importance of different parasitoids attacking *Xestia* in terms of their contribution to the regulation of the minor *Xestia* cohort. The most likely candidates apart from *Ophion luteus* seem to be *Meloboris collector* and *Macrocentrus* sp.

**Predators and pathogens**

From 1983 onwards, a permanent set of 60 pitfall traps has been operated at the Väärriö Subarctic Research Station. These traps collected a unique time series of small mammals, including insectivorous shrews. Pooled densities of shrews in the genus *Sorex* show a correlated pattern with densities of *Xestia*, with high numbers in the odd years and low numbers in the even years (see fig. 2 in I). A likely explanation for this pattern is that larvae and pupae of *Xestia* represent such an important prey during the winter and early summer every second year that they improve both winter survival and reproduction in the shrew populations (I). Incorporating numbers of *Sorex* to the regression model of the finite rate of increase of *Xestia* over its two-year life cycle (see above) substantially improved model fit (I).

Other predators include abundant coleopterans (e.g. the ground beetle *Carabus glabratus*) and migratory birds (I), but these long-lived generalists may hardly contribute to the regulation of the rare *Xestia* cohort (I). Moreover, an unidentified pathogenic fungus caused high mortality in *Xestia* larvae in rainy summers. This fungus was not a specialist on *Xestia* but it killed a wide range of larvae dwelling in the ground vegetation (own observations).

**Movements of *Xestia* and *Ophion luteus***

Dispersal ability and movement behaviour of animal species connect local dynamics to spatial pattern formation. Knowledge of mobility and movement behaviour of *Xestia* moths and the parasitoid *Ophion luteus* is hence essential in terms of understanding their spatial dynamics.

**Movement behaviour of *Xestia fennica* and *X. speciosa***

In a mark-release-recapture (MRR) study conducted in 1999 in Kuhmo, eastern Finland, a total of 2577 individually marked adults of *Xestia speciosa*, *X. fennica* and *X. alpica* were released in a recently fragmented middle-boreal forest area (IV). The study area (Fig. 3, fig. 1 in IV) included spruce-dominated
Population biology of periodic *Xestia* moths

**Figure 3** Aerial photograph showing the study area of IV. Old-growth spruce forest corridors are dark grey, sapling stands light grey and openings light-coloured. The diagonal in the photograph is ca. 2 km. Permission for publication by Maanmittauslaitos, no. 7/MYY/03.

old-growth forest, sapling stands and clearcut openings. Retained old-growth forest strips (Fig. 3) were used to investigate whether corridors enhance functional connectivity (in sense of Baudry and Merriam 1988) of *Xestia* populations. The ultimate motivation for this study came from the debate about the role of corridors in conservation (Simberloff and Cox 1987, Noss 1987, Hobbs 1992, Simberloff et al. 1992, Hess 1994, Beier and Noss 1998, Haddad et al. 2000) and from the general lack of studies investigating movements of forest insects (IV). *Xestia* species were assumed to be appropriate targets for experiments in real-world situations with forested corridors of variable length, width and shape. Since the three *Xestia* species differ in their robustness, flight behaviour and habitat preferences, we also expected to observe various movement patterns and behavioural responses with respect to the forest edges.

Though recapture rates remained relatively low (IV), several patterns emerged in the analyses of recapture rates and the movements of recaptured moths. Since only a single *X. alpicola* individual was recaptured, we focused on the remaining two species in the analyses. Average flight distances of female and male moths ranged between 390–530 and 320–380 m in *X. speciosa* and *X. fennica*, respectively. The analysis of recapture rates revealed a clear difference between the two species. According to our results, *X. fennica* would behave like a capital breeder (see Drent and Daan 1980; Jönsson
1997), namely it stays in the habitat (flies shorter distances and is more likely to be recaptured than X. speciosa) and has low discrimination with respect to food source profitability. In contrast, X. speciosa would reproduce like an income breeder, with high vagility in searching for food and stronger discrimination with regard to food source profitability (IV). These behavioural patterns are consistent with the dissimilar habitat preferences of the two species: X. fennica is confined to old-growth and mature spruce forests, while X. speciosa occurs in various forest types from moist spruce forests to mesic pine-dominated forests with some spruce (IV).

We also demonstrated that the movement behaviour of female and male moths differed more markedly that that of the two species (IV). These results are consistent with the pheromone-mediated long-range mate-locating syndrome of male moths (e.g. Hardie et al. 2001). In order to find perching females, male moths track sex pheromone plumes by flying upwinds in a characteristic zigzag manner. Hence, males fly longer distances, use more energy per time unit and return earlier to food sources than female moths.

Both X. speciosa and X. fennica favoured corridors in their movements and tended to avoid crossing the edge of the breeding habitat. This pattern was more pronounced in females than in males, and in X. fennica females especially at the short range (0–250 m), while in X. speciosa females at the medium range (>250 m), apparently because of the shorter average flight distances of X. fennica than of X. speciosa.

In an analysis of the effect of the area of suitable habitat at different spatial scales on the abundances of Xestia in Lapland (III), a highly significant positive correlation was found between the total area of old-growth and mature forests within a range of 1.25 km around sampling plots and the pooled Xestia (mostly X. speciosa) abundance in the plots. There was no such correlation at larger or smaller spatial scales. The spatial scale at which tachinid fly parasitoids of the North American forest tent caterpillar perceive and respond to landscape structure has been shown to reflect their body sizes (Roland and Taylor 1997) and dispersal ranges (Roland 2000). Similarly, the scale at which the area of suitable habitat best explains Xestia abundances (1.25 km) may reflect the average dispersal distance of X. speciosa.

Mobility of Ophion luteus

Movements of Ophion luteus were studied in a MRR experiment in 1998 at the Värriö Subarctic Research Station (Fig. 1, fig. 1 in II). A total of 406 wasps were released during the peak flight period of the species. 43 wasps were recaptured using four effective light sources in the MRR study area (fig. 2 in II) and several permanent light traps located outside the study area (fig. 1 in II).

Recorded movements of O. luteus ranged from 40 to 430 m, with an average of 107 and 112 m for females and males (II). There was a clear lower temperature threshold for wasp flight at 4°C (II). After omitting the shortest movements (40 m), which were affected by the strong light attraction, flight directions correlated positively with wind direction in those nights when wind velocity was not close to zero (II). These results indicate that O. luteus is a rather passive flyer, being frequently driven by wind through its breeding habitat. The flight distances of O. luteus are on average shorter that those of Xestia (see previous section), and its mobility is limited by temperature. Nonetheless, O. luteus has been permanently abundant in Värriö in the even years (I), suggesting that female wasps have high searching efficiency (I).

Spatial dynamics of Xestia moths

The striking spatial synchrony of periodic Xestia populations over large areas (see section ‘Patterns of periodic occurrence’) calls for both
a theoretical explanation and for further empirical studies at different spatial scales. The important theoretical questions are how interaction with natural enemies may lead to spatial domain formation, what are the characteristics of such spatial dynamics, how the dynamics are affected by spatial and temporal heterogeneity, and what kind of dynamics evolve at the boundaries between domains with opposite-phase periodic oscillation of _Xestia_.

Rost et al. (2001) extended the host-parasitoid model (I, see section 'Interaction with _Ophion luteus_') to large spatial scales. In the spatially explicit model, we considered three types of variation in the carrying capacity (_k_) in space and time: spatially homogeneous environments, spatially heterogeneous environments and spatially homogeneous environment with temporal fluctuations. In a homogeneous environment where the carrying capacity is constant, domain walls become fixed only in the unrealistically case in which phase boundaries are straight. In homogeneous environments with curved domain walls, the dynamics prevailing behind any concave domain edge will invade the opposite space. Spatial heterogeneity in the environment tends to fix domain boundaries (Rost et al. 2001), which case corresponds to real-world situations with a range of habitats of dissimilar quality. As an example of this scenario is the situation where domains that are separated by areas with low carrying capacity, such as non-breeding areas for _Xestia_, wider than the average dispersal distance of adult moths (ca. 1 km, see above). Finally, temporal noise may switch domains to the opposite-phase dynamics (Rost et al. 2001).

The spatial domains of _Xestia_ in Finland have been mapped by Mikkola (1976) and Rost et al. (2001) using independent data sets. The results of these two studies are very similar. According to Rost et al. (2001), adults of _Xestia_ emerge predominantly in the even years in the western parts of Finnish Lapland, while all other locations in Finland where sufficient data were available exhibit the opposite odd year emergence pattern. Rost et al. (2001) postulated that the extensive wetlands and lakes in central Finnish Lapland, which possess low carrying capacity for forest moths like _Xestia_, would fix the domain boundary. There is no empirical evidence for any large-scale phase changes due to temporal fluctuations (such as exceptional weather conditions), though a short-term phase switch in _Xestia_ dynamics was discovered in the 1990’s in the province of Kainuu, eastern Finland (Rost et al. 2001).

Densities of the major and the minor _Xestia_ cohorts (both at the larval and the adult stage) and of adult _O. luteus_ have been studied in natural and natural-like forests along an east-west transect stretching across Finnish Forest Lapland (III and fig. 1 therein). The aim of the study was to refine the picture of spatial domain formation in _Xestia_ populations and to characterize the boundary between the eastern and western _Xestia_ domains. Results indicate that the inter-domain area is very distinct and relatively narrow, only of the order of 10 km. Densities of both _Xestia_ cohorts and of _O. luteus_ were very low in the transition zone in both the odd and even years, which result is consistent with the modelling results of Rost et al. (2001) about the _Xestia-Ophion_ interaction (I). In the southern Finnish parapatric populations of the pine bark bug _Aradus cinnamomeus_, population densities were not lower in the inter-domain transition zone (Heliövaara and Väisänen 1984), apparently because of the different mechanism maintaining periodicity in the bugs (inter-cohort competition; see section 'Hypotheses to explain periodic occurrence in insects').

Though most _Xestia_ individuals sampled in the transect belonged to _X. speciosa_ (83% of the total _Xestia_ sample), the dynamics of the coexisting species were highly synchronized in both domains (table 2 in III). This suggests that individual species share the same natural enemies. _Ophion_ samples were relatively small, but all sampling results
were consistent with the host-parasitoid hypothesis.

In an analysis of the landscape structure of central Finnish Lapland, I found that the proportions of suitable breeding habitat for *Xestia* are very low at and west of the boundary between the eastern and western *Xestia* domains (fig. 3 in III). This is due to two large water reservoirs, extensive wetlands and human impact (fig. 4 in III). These results are consistent with the predictions of the modelling results of Rost et al. (2001).

A new approach to the study of spatial dynamics of periodic *Xestia* populations is provided by an ongoing study, in which moths are sampled in both old-growth and managed forests in many areas in Kainuu and Russian Karelia. Preliminary results indicate that the density ratio between odd- and even-year cohorts in managed forests is smaller by as much as one order of magnitude than in natural forests. The abundance ratio of major *Xestia* cohorts in the old-growth and managed forests was only ca. 1.6, indicating that the difference in inter-cohort ratios cannot be solely attributed to lower population densities in managed forests. These results strongly suggest that modern forestry may have had a dramatic effect on the population dynamics of periodic *Xestia* moths. Further research is needed to uncover the mechanisms leading to such apparent reduced control of the minor *Xestia* cohorts in managed forests. The results so far suggest that decreasing the carrying capacity of the environment over extensive areas may not only facilitate domain boundaries, as expected from the modelling results of Rost et al. (2001), but may also change the basic characteristics of the dynamics. Roland and Taylor (1997) demonstrated that parasitism by four tachinid flies of the forest tent caterpillar in Canada is dissimilarly altered by anthropogenic forest fragmentation. Study of the composition and the rates of parasitism by the parasitoid guilds associated with *Xestia* in both managed and seminatural forests may reveal if reduced control of the minor *Xestia* cohorts may be attributed to altered parasitism in managed forests.

**Population genetics of *Xestia tecta***

Due to the fixed length of the life cycle in the subgenus *Pachnobia* s.l., coexisting cohorts are temporally isolated from each other. If a local *Xestia* population does not receive immigrants equally into both cohorts and if delayed development never occurs in the population, the major and minor cohort will become eventually genetically differentiated. The level of genetic differentiation among coexisting cohorts is hence an important source of information about hidden population dynamic processes. Differentiation among sympatric cohorts is expected also if the minor cohort has recently colonized the area (Leonard and Parker 1994). On the other hand, by assessing the degree of genetic differentiation between *Xestia* populations belonging to opposite-phase spatial domains one can test hypotheses about the origin of the populations. According to the postglacial recolonization history hypothesis (Mikkola and Kononenko 1989), current domain boundaries would reflect the colonisation history of moth populations after the last glaciation. If, as this hypothesis implies, these boundaries were formed at contact frontiers of expanding opposite-phase periodic moth populations originating from separate glacial refugia, one would expect a notable genetic differentiation between the populations.

We studied the extent of genetic differentiation among coexisting cohorts and between opposite-phase major cohorts of *X. tecta* in Finnish Lapland (V). We applied allozyme electrophoresis and mitochondrial genome sequencing to infer the extent of genetic differentiation among the major and minor *X. tecta* cohorts in Värriö and between major cohorts of Värriö (eastern Lapland) and Olostunturi (western Lapland). We
found no evidence for substantial genetic differentiation among the temporally isolated sympatric cohorts nor between the geographically and temporally isolated major cohorts (V). The most informative markers were the most polymorphic allozyme loci of phosphoglucoisomerase (PGM) and mannose phosphate isomerase (MPI) and the AT-rich region in the mitochondrial DNA. However, the general level of genetic variability was so low that it was impossible to establish conclusively the degree of genetic isolation between the different cohorts (V).

Our results are inconsistent with the postglacial recolonization history hypothesis (Mikkola and Kononenko 1989), the recent colonization hypothesis and the cryptic species hypothesis (see Leonard and Parker 1994). In contrast, the generally low level of genetic differentiation among all three studied cohorts is consistent with hypotheses of substantial gene flow between the cohorts and of recent common ancestor. Substantial between-cohort gene flow is not likely due to the fixed two-year life cycle of X. tecta (see section 'Length of life cycle, revisited') and because of the temporal mismatch between the eastern and western major cohorts. According to the recent common ancestor hypothesis (V), Xestia populations that survived the last glaciation in the Beringian refugium (Mikkola et al. 1991) would have lost much of their genetic variability due to repeated population bottlenecks during their expansion towards Fennoscandia. Hence, the present Finnish Xestia populations would be descendants of relatively small and genetically homogeneous founder populations. Xestia tecta populations in eastern and western Fennoscandia are not likely to have different post-glacial histories, and current spatial domain formation is probably due to population dynamic reasons rather than post-glacial history. This view is further supported by the post-glacial recolonization routes of Fennoscandia of Norway spruce (Picea abies). This is the most important forest tree with which periodic Xestia moths are associated (though X. tecta is not a true spruce forest species as demonstrated in II). Spruce recolonized Europe mainly—and Fennoscandia entirely—from the east (Lagercrantz and Ryman 1990, Taberlet et al. 1998), suggesting a subsequent westward expansion by Xestia from eastern refugia.

Conclusions and open questions

The main thread through my thesis is how interaction with natural enemies may lead to striking two-year periodic dynamics in Xestia moths and to alternate-year fluctuations in their parasitoids and predators (I, II, III). Multiple evidence strongly supports the hypothesis about a host-parasitoid interaction operating between Xestia moths and the ichneumonid wasp Ophion luteus in Finnish Lapland (I), though there are yet no direct observations of this biological link. Other parasitoids like the ichneumonid Meloboris collector and insectivorous shrews are likely to contribute to the regulation of the minor Xestia cohorts (I). Modelling results are rather robust with respect to the assumptions of the nature of the interaction, and the models predict well the observed dynamics (I). Further support for the Xestia-Ophion interaction comes from absolute population density estimates of Xestia and Ophion (II). Larvae and pupae of Xestia seem to play a crucial role in the food web of the natural forests of Finnish Lapland (I, II).

The boundary between the opposite-phase spatial domains of Xestia in central Lapland is found to be very distinct and relatively narrow, only of the order of 10 km (III). Extensive lakes and wetlands are likely to form a dispersal barrier for adult moths and to pin the boundary between the opposite-phase Xestia domains (III). Both the landscape structure in central Lapland and the densities
of *Xestia* and *Ophion* along an east-west transect stretching across the domain boundary are consistent with previous modelling results (Rost et al. 2001) (III).

Average dispersal ranges of *Xestia* and *Ophion* are estimated to be of the orders of $10^3$ and $10^2$ m, respectively (II, III). *Xestia* moths tend to avoid entering non-breeding habitat in a fragmented forest area and hence to favour old-growth forest corridors in their movements (IV). Movements of male and female moths were consistent with the pheromone-mediated mate-location syndrome (Hardie et al. 2001). Foraging strategies and movement patterns of the habitat generalist *X. speciosa* and the old-growth spruce forest specialist *X. fennica* suggested different reproductive strategies in the two species (IV).

The extent of genetic differentiation was very low among coexisting cohorts and between spatially and temporally isolated populations of *X. secta* in Finnish Lapland (V). The generally low levels of genetic variability are consistent with the recent common ancestor hypothesis (V), suggesting repeated population bottlenecks in *Xestia* during its post-glacial westward expansion from eastern refugia. The major boundary between opposite-phase *Xestia* domains in central Lapland is unlikely to reflect post-glacial recolonisation history but likely to be related to population dynamic processes.

Further challenges for research include a comprehensive examination of the parasitoid guilds associated with *Xestia*; especially further information of the biology of *Ophion luteus* is badly needed. Moreover, empirical studies are required to clarify how and to what extent host-parasitoid interactions involving *Xestia* are affected by the quality of the habitat and by the structure of the environment at different spatial scales. These questions relate to the dispersal ability in both the host and the parasitoid and to the searching efficiency of the parasitoid. A geographical approach to the study of host-parasitoid interactions in *Xestia* would include the description of the structure of the parasitoid assemblages at different latitudes to examine whether greater species richness of parasitoids and their alternative hosts in the south might affect periodic dynamics in *Xestia*.

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Population biology of periodic *Xestia* moths

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