

Sami Mikael Kivelä

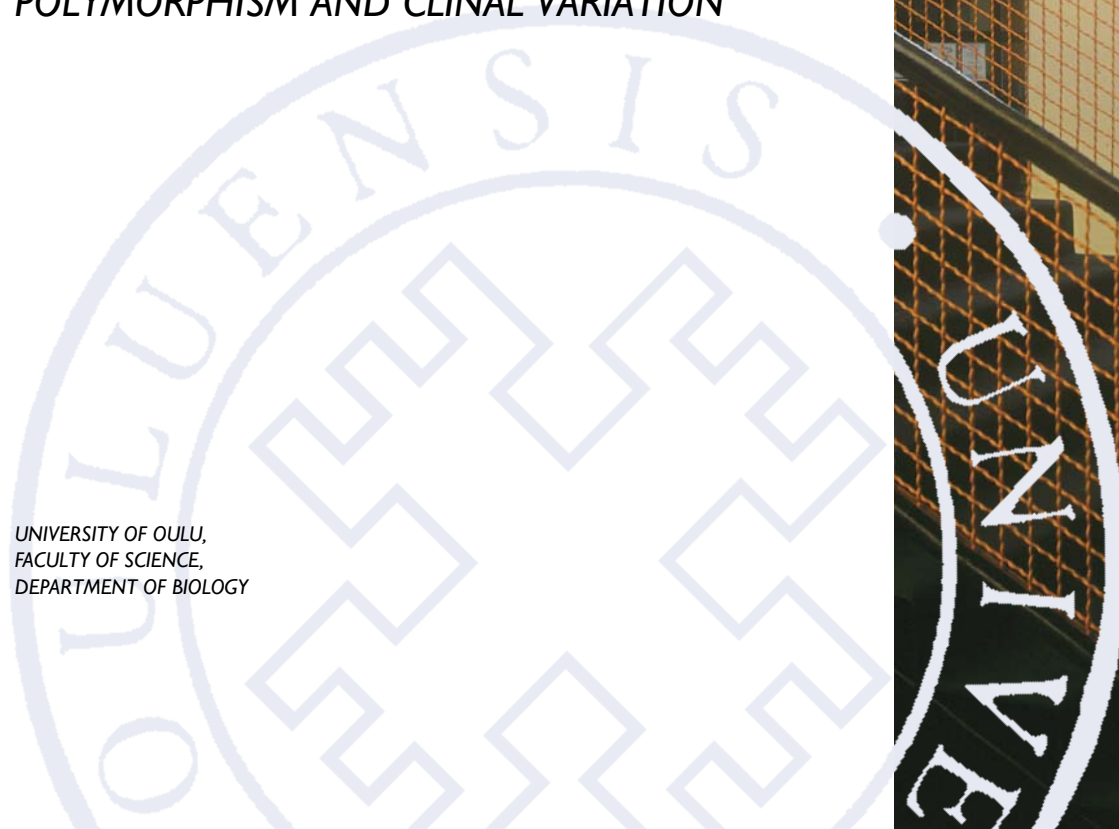
EVOLUTION OF INSECT LIFE
HISTORIES IN RELATION
TO TIME CONSTRAINTS IN
SEASONAL ENVIRONMENTS

POLYMORPHISM AND CLINAL VARIATION

UNIVERSITY OF OULU,
FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY

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SAMI MIKAEL KIVELÄ

**EVOLUTION OF INSECT LIFE
HISTORIES IN RELATION TO TIME
CONSTRAINTS IN SEASONAL
ENVIRONMENTS**

Polymorphism and clinal variation

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Abstract

Both the length of the season that is favourable for insect growth and reproduction and the number of generations emerging per season (voltinism) increase with decreasing latitude. Thus, time constraints on reproduction and juvenile development decrease with decreasing latitude, except where voltinism changes and time constraints suddenly increase as the season must be shared with one more generation.

I studied the evolution of insect life histories in relation to time constraints from two perspectives: polymorphism and clinal variation. Life history polymorphism in seasonal environments was studied with the butterfly *Pieris napi* that has discrete life history strategies, and polymorphic natural populations. Experimental studies showed that asymmetric intraspecific larval competition and divergent timing of reproduction between the strategies may promote the maintenance of polymorphism. A simulation model showed that the divergent timing of reproduction between the strategies is sufficient to maintain polymorphism even in the absence of intraspecific competition.

Clinal variation was studied empirically with four geometrid moths (*Cabera exanthemata*, *Cabera pusaria*, *Chiasmia clathrata* and *Lomaspilis marginata*) and generally in theory. Due to latitudinal saw-tooth variation in time constraints, traditional theory predicts a saw-tooth cline in body size and development time. A common garden experiment with the four geometrid moths did not support the traditional theory even when a saw-tooth cline in body size was found, suggesting that the theory is based on unrealistic assumptions. A theoretical analysis showed that reproductive effort should be high in populations under intense time constraints and low in populations experiencing no time constraints, resulting in a saw-tooth cline. In the four geometrid moths, support for these predictions was found, although the observed clinal variation deviated from the predicted pattern.

The results imply that clinal variation is expected in almost any continuous life history trait, whereas polymorphism of different strategies may emerge when life histories fall into discrete categories. When inferring the evolution of a single trait, complex interdependencies among several traits should be considered, as well as the possibility that the time constraints are not similar for each generation in multivoltine populations.

Keywords: genetic correlation, Geometridae, Lepidoptera, monandry, Pieridae, polyandry, reproductive effort, voltinism

Kivelä, Sami, Mikael, Hyönteisten elinkierto-ominaisuuksien evoluutio suhteessa vuodenaikaisympäristöjen aikarajoitteisiin. Diskreetti ja jatkuva muuntelu

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Tiivistelmä

Hyönteisten kasvu ja kehitys ovat pääsääntöisesti mahdollisia vain kesän aikana. Etelään päin mentäessä kesä pitenee, ja saman kesän aikana kehittyvien hyönteissukupolvien määrä kasvaa. Kesän pituus aiheuttaa lisääntymiseen ja toukkien kasvuun kohdistuvan aikarajoitteen, joka heikkenee etelään päin siirryttäessä. Aikarajoite kuitenkin tiukkenee siellä, missä yksi uusi sukupolvi ehtii juuri kehittymään saman kesän aikana, sillä kesä on nyt jaettava useamman sukupolven kesken.

Väitöstyössä tarkastelin hyönteisten elinkierto-ominaisuuksien evoluutiota suhteessa aikarajoitteisiin sekä diskreetin että jatkuvan muuntelun näkökulmista. Diskreettiä muuntelua tutkin lantuperhosella (*Pieris napi*), jolla esiintyy diskreettejä elinkiertostrategioita. Kokeellisesti osoitin, että toukkien välinen kilpailu on epäsymmetristä, mikä yhdessä eri elinkiertostrategioiden erilaisen lisääntymisen ajoittumisen kanssa voi ylläpitää diskreettiä muuntelua. Simulaatiomalli osoitti, että erilaiset elinkiertostrategiat voivat säilyä populaatiossa pelkästään niiden erilaisen lisääntymisen ajoittumisen ansiosta.

Elinkierto-ominaisuuksien jatkuvaa muuntelua tutkin neljän mittariperhosen (*Cabera exantemata*, *Cabera pusaria*, *Chiasmia clathrata* ja *Lomaspilis marginata*) avulla ja teoreettisesti yleisellä tasolla. Aikaisempi teoria ennustaa ruumiinkoon ja kehitysajan muuntelevan sahalaitakuvion mukaisesti siirryttäessä pohjoisesta etelään, koska aikarajoitteet muuntelevat samalla tavalla. Tämä teoria perustuu epärealistisiin oletuksiin, koska kokeelliset tulokset eivät tue teorian silloinkaan, kun mittariperhosten ruumiinkoko muunteli ennustetulla tavalla. Teoreettinen tutkimus osoitti, että myös lisääntymispanostuksen tulisi muunnella sahalaitakuvion mukaisesti suhteessa kesän pituuteen siten, että se on korkeimmillaan siellä, missä aikarajoitteet ovat tiukat. Mittariperhosten tutkiminen antoi jossain määrin tukea tälle ennusteelle.

Tulosten perusteella jatkuvaa maantieteellistä muuntelua ennustetaan elinkierto-ominaisuuksille, jotka muuntelevat jatkuvalla asteikolla. Erilaiset elinkiertostrategiat voivat sen sijaan säilyä populaatiossa, jos elinkierto-ominaisuuksien muuntelu on diskreettiä. Eri ominaisuuksien monimutkaiset vuorovaikutukset sekä eri sukupolvien mahdollisesti kokemat erilaiset aikarajoitteet olisi syytä tuntea, kun tarkastelun kohteena on yksittäisen ominaisuuden evoluutio.

Asiasanat: elinkierto, Geometridae, Lepidoptera, lisääntymiskäyttäytyminen, lisääntymispanostus, Pieridae

To my parents

Acknowledgements

The chain of events that led to this thesis began around the time I was in the upper level of the comprehensive school. Around that time I read a book about the origin of life and subsequent evolution introduced by my teacher in biology. Well, I have had an intrinsic interest in nature, in animals in particular, ever since I can remember, but reading that book probably led me to the path that eventually made me an evolutionary biologist. Anyway, even though I was interested in evolution, I did not know that I would eventually become an evolutionary biologist at the time when I began my studies in biology at the university, but it soon became quite clear to me that evolutionary biology is the discipline I want to concentrate on. Around the same time, my increasing interest in the theoretical aspects arose, probably because of some intrinsic bias for that.

I was lucky that I was able to continue with evolutionary biology after my master's degree. This was mainly because Arja Kaitala (who had already supervised my master's thesis) was willing to take me as a Ph.D. student in her research group. I am grateful for that. Moreover, I am especially grateful to her because of her encouragement and support during my Ph.D. project as well as the possibility to study the questions I wanted within the framework of insect life histories in seasonal environments. I was privileged to get two additional supervisors: Jari Oksanen and Veijo Kaitala. Their help and incredible expertise was invaluable when I was implementing my interest in theoretical issues, and I am deeply indebted for that. Furthermore, I acknowledge all my supervisors for their valuable comments concerning my manuscripts and thesis, and for their indispensable help in finding funding for my work.

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The former Biological Research facility of the University of Oulu provided facilities for studying water striders in the beginning of my thesis work. Although the water strider studies were eventually not included in the thesis due to difficulties in completing the life cycle of the study species in laboratory conditions, I am grateful to Jari Ylönen and the personnel of the Biological Research facility for their invaluable help in this project.

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List of original articles

- I Kivelä SM & Välimäki P (2008) Competition between larvae in a butterfly *Pieris napi* and maintenance of different life history strategies. *Journal of Animal Ecology* 77: 529–539.
- II Välimäki P, Kivelä SM, Jääskeläinen L, Kaitala A, Kaitala V & Oksanen J (2008) Divergent timing of egg-laying may maintain life-history polymorphism in potentially multivoltine insects in seasonal environments. *Journal of Evolutionary Biology* 21: 1711–1723.
- III Kivelä SM, Välimäki P, Carrasco D & Mäenpää MI Latitudinal insect body size clines revisited: a critical evaluation of the saw-tooth model. Manuscript.
- IV Kivelä SM, Välimäki P, Oksanen J, Kaitala A & Kaitala V (2009) Seasonal clines of evolutionarily stable reproductive effort in insects. *American Naturalist* 174: 526–536.
- V Kivelä SM, Välimäki P, Carrasco D, Mäenpää MI & Mänttari S Latitudinal variation in resource allocation to reproduction in geometrid moths. Manuscript.

Contents

Abstract

Tiivistelmä

Acknowledgements 9

List of original articles 13

Contents 15

1 Introduction 17

1.1 Insect life cycles and phenologies in seasonal environments..... 17

1.2 Time constraints due to seasonality and voltinism..... 20

1.3 Time constraints due to intraspecific competition..... 20

1.4 Time constraints and life history evolution..... 21

1.5 Aims of the study 24

2 Materials and methods 27

2.1 Maintenance of life history polymorphism in seasonal environments..... 27

2.1.1 The study species..... 27

2.1.2 The effect of asynchronous hatching on survival probability (I) 27

2.1.3 The incidence of monandry in different generations (II)..... 29

2.1.4 A stochastic simulation model on the maintenance of polymorphism (II) 30

2.2 Clinal variation in life history traits 32

2.2.1 The study species..... 32

2.2.2 Latitudinal variation in body size, development time and growth rate (III)..... 33

2.2.3 Genetic correlations among body size, development time and growth rate (III) 35

2.2.4 Modelling clinal variation in reproductive effort (IV)..... 36

2.2.5 Measuring clinal variation in reproductive resource allocation (V)..... 39

2.3 Statistical analyses 40

3 Results and discussion 43

3.1 Life history polymorphism in seasonal environments 43

3.2 Latitudinal clines in life history traits 48

3.2.1 Clinal variation in body size and associated life history traits..... 49

3.2.2 Clinal variation in reproductive effort and resource allocation	52
4 Conclusions	57
References	61
Original papers	69

1 Introduction

Temperate seasonal environments are characterised by the annual cycle between summer and winter. The lengths of these seasons, as well as their mean temperatures, covary with latitude and altitude, summer becoming shorter and cooler and winter becoming longer and colder with increasing latitude or altitude (see Angilletta 2009). These patterns of latitudinal and altitudinal variation in seasonality are predictable despite stochastic inter-year variation in both the lengths and the temperatures of the seasons, which means that populations along a latitudinal or altitudinal gradient experience different selection regimes due to seasonality. Hence, large-scale geographical variation is expected in life histories in species whose life cycles are constrained by seasonality. Most ectotherms, and especially insects, fall into this category.

1.1 Insect life cycles and phenologies in seasonal environments

The ultimate limits for insect activity, growth and reproduction are set by the species-specific minimum and maximum temperature thresholds for these activities (see Angilletta 2009). Temperature falls within the range defined by these thresholds during only a part of the year in temperate seasonal environments. Yet, the actual season when growth and reproduction are possible may be shorter than the one defined by the temperature thresholds alone. This is because food or other resources necessary for juvenile growth or adult reproduction may be available only during a part of the season when the temperature is favourable. I will refer to the part of the year that is favourable for growth and reproduction as season hereafter. It is worth noting that – despite being favourable – the thermal conditions change predictably during the course of the season (see Angilletta 2009, Gotthard & Berger 2010), and the same may hold true for herbivorous insects' food quality (*e.g.* Schroeder 1986, Ayres & MacLean 1987, van Asch & Visser 2007). This together with seasonal variation in predation risk (Rommel *et al.* 2009) means that insect performance and mortality risk may vary throughout the course of the season (Schroeder 1986, Ayres & MacLean 1987, Gotthard *et al.* 2007, van Asch & Visser 2007, Rommel *et al.* 2009, Gotthard & Berger 2010). Most insects survive the adverse winter conditions only in a dormant or quiescent stage called diapause, which is typically restricted to a particular species-specific developmental stage (Tauber *et al.* 1986, Danks 1987). This sets an important

constraint for insect life cycles and phenologies, because the developmental stage able to diapause must be reached before the onset of adverse conditions (Fig. 1).

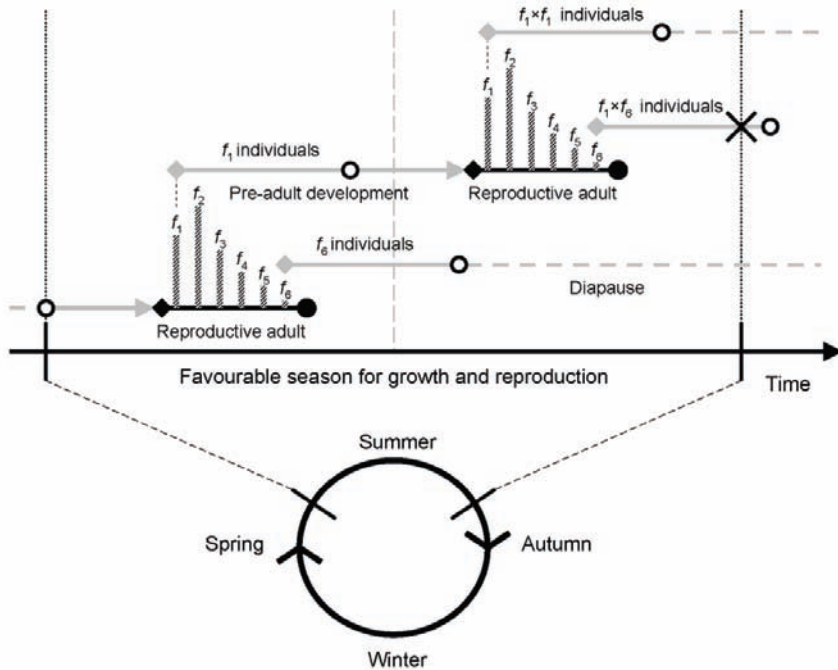


Fig. 1. Graphical summary of the constraints and factors affecting insect life cycles in seasonal environments. The seasonal cycle is shown at the bottom. The season that is favourable for insect growth and reproduction is shown at the top (delimited by the vertical bars on the time axis and by the vertical dashed lines above the time axis). The (partially bivoltine) phenology of a hypothetical insect is shown. The grey arrows denote the pre-adult development (the developmental stage able to diapause is indicated by an open circle) and the black lines the reproductive adult stage (the closed circle denotes the death of the adult). Adult age-specific fecundities are illustrated with vertical hatched bars along the adult lifespan, and marked with f_i ($i = 1, \dots, 6$). The fates of the first and the last offspring cohorts are shown. A single female is assumed at the beginning of the season, and the number of her descendants belonging to a particular cohort in a particular generation is indicated above the grey arrows (mortality is ignored). A photoperiodic switch determines the developmental pathway induced during pre-adult development. If the sensitive stage for diapause induction (assumed to be the same as the diapause stage, for simplicity) is reached before the critical day length (indicated by a grey hatched vertical line), direct development is induced. Otherwise diapause (indicated by hatching of the grey arrows) will be induced. Individuals not reaching the diapause stage before the end of the season die (marked with black cross on the grey arrow).

Depending on the season length, many insects may complete several generations within a season. The number of generations emerging per season (voltinism) is positively correlated with season length in many species (e.g. Masaki 1972, Tauber *et al.* 1986, Mousseau & Roff 1989, Nylin & Svård 1991, Blanckenhorn & Fairbairn 1995, Gomi & Takeda 1996, Burke *et al.* 2005), because fitness is positively correlated with the number of generations emerging, provided that a sufficient number of individuals successfully enter diapause at the end of the season. The emergence of more than one generation per season is associated with a possibility for two alternative developmental pathways (Fig. 1). In univoltine phenology, where a single generation is completed within a season, all individuals follow the developmental pathway leading to diapause, which means that diapause is included in the life cycle of all individuals in a population. The emergence of additional generations within a season is associated with the alternative developmental pathway; individuals do not enter diapause in the developmental stage able to do so, but develop directly into reproductive adults within the same season (Fig. 1). In multivoltine phenology, where several generations emerge within a season, diapause is included within the life cycle only in the diapause generation that overwinters, not in the life cycle of the remaining nondiapause generations.

In potentially multivoltine species, the alternative developmental pathways are a consequence of phenotypic plasticity in relation to environmental cues that are predictably associated with the seasonal cycle (Tauber *et al.* 1986, Danks 1987, see Fig. 1). Photoperiod is the most common environmental cue affecting diapause induction, because it reliably indicates the stage of the seasonal cycle (Tauber *et al.* 1986, Danks 1987). However, the stage of the seasonal cycle indicated by a particular photoperiod depends on latitude. This is because day length on any particular date during the summer months increases with increasing latitude. Local adaptations are therefore needed to facilitate the induction of diapause during a locally appropriate time in relation to the seasonal cycle. That is why potentially multivoltine insects usually have intraspecific variation in the critical day length that induces the switch from direct development to diapause, the critical day length increasing with increasing latitude (Tauber *et al.* 1986, Danks 1987, Mousseau & Roff 1989, Blanckenhorn & Fairbairn 1995, Gomi & Takeda 1996).

1.2 Time constraints due to seasonality and voltinism

Season length sets an obvious constraint as a life cycle must be completed within that time. The time available per generation to complete the life cycle decreases with decreasing season length and with increasing number of generations, all else being equal. This means that time constraints become more intense (*i.e.*, the time available per generation decreases) with increasing latitude or altitude and with increasing voltinism. There are no time constraints when the time available per generation is much longer than is generation length of an insect, and there is not enough time for an additional nondiapauses generation to emerge. Time constraints arise when the time available per generation is close to generation length, and generation length must be adjusted so that the diapausing developmental stage will be reached before conditions turn adverse. A change in voltinism has a pronounced effect on the time available per generation. A change from univoltine to bivoltine (two generations per season) phenology within a particular season length would halve the time available per generation, while the reduction in time available per generation is 1/3 at a change from bivoltine to trivoltine (three generations per season) phenology.

Because both season length and voltinism decrease with increasing latitude or altitude (see above), there is predictable geographic variation in the time constraints affecting insect life cycles. Unlike season length, voltinism shows discontinuous variation across latitudes or altitudes. As a consequence, there will be discontinuous variation in the time constraints in species with latitudinal or altitudinal variation in voltinism.

1.3 Time constraints due to intraspecific competition

In addition to seasonality and voltinism, time constraints may also arise due to intraspecific interactions among individuals. This is the case, if intraspecific competition strongly reduces individual performance or survival, and consequently fitness. Juvenile survival and performance are sensitive to intraspecific competition (Sullivan & Sokal 1963, Peters & Barbosa 1977, Livdahl 1982, Wall & Begon 1986, Averill & Prokopy 1987, Simmons 1987, Hard *et al.* 1989, Broadie & Bradshaw 1991, Messina 1991, Reeve *et al.* 1998, Dukas *et al.* 2001, Agnew *et al.* 2002, Gibbs *et al.* 2004), competition being usually asymmetric so that larger individuals outcompete smaller ones (Livdahl 1982, Begon 1984, Wall & Begon 1986, Averill & Prokopy 1987, Broadie &

Bradshaw 1991, Messina 1991, Edgerly & Livdahl 1992, Koenraadt *et al.* 2004, Cameron *et al.* 2007). Asynchronous hatching of eggs may generate size variation among juveniles, the first to hatch being the largest at any moment of time during development. Hence, the larvae in the earliest cohorts are expected to gain a competitive advantage over those belonging to later cohorts. This will generate a time constraint for adult reproduction, because delayed reproduction would result in low survival and performance of offspring.

1.4 Time constraints and life history evolution

When time constraints due to seasonality and voltinism become more intense, generation length must decrease to ascertain survival. The length of juvenile development is the major determinant of generation length in insects, so development time is expected to decrease with decreasing season length, that is, with increasing latitude or altitude (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994). Development time is expected to decrease also when an additional nondiapause generation is added to the phenology, so that when moving towards increasing season length (*i.e.*, towards decreasing latitude or altitude), there would be a sudden decrease in development time at the season length where phenology changes (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994). Insects are assumed to use all available time for growth to maximise body size (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994), because body size is positively correlated with fecundity (Honěk 1993), and large body size may be attainable only by prolonging growth (Roff 1992, Stearns 1992). Consequently, both development time and body size would be positively correlated with season length when the number of generations is constant, a phenomenon called cogradient variation (Conover & Schultz 1995). This kind of clinal variation, where trait value (especially body size) decreases with increasing latitude or altitude, is often referred to as a converse Bergmann cline (*e.g.* Masaki 1967, Mousseau 1997, Blanckenhorn & Demont 2004), because it is converse to the one predicted by Bergmann's rule (Blackburn *et al.* 1999). However, the key characteristic of this life history model is that a saw-tooth cline is predicted to arise in both age and size at maturity across latitudes (or altitudes) in species with latitudinal (or altitudinal) variation in voltinism, the saw-teeth arising due to discontinuity in voltinism (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994) (Fig. 2 a). I will refer to this model as the traditional saw-tooth model hereafter.

The traditional saw-tooth model assumes that time constraints for development time and fecundity selection for large body size drive life history evolution, and that the resulting cline would be based on genetic adaptation to local conditions (Masaki 1967, 1972, Roff 1980, 1983, but see Iwasa *et al.* 1994 for the effect of resource availability on this). The effect of time constraints on life history evolution should be strong in species that have long development times in relation to season length, so the traditional saw-tooth model should be best applicable to this kind of species (Chown & Gaston 1999). This idea is supported also by the finding that species with long development times in relation to season length tend to express converse Bergmann clines in body size (Blanckenhorn & Demont 2004), which is an effect of time constraints. In accordance with this, empirical support for the traditional saw-tooth model, and its genetic basis, comes from species with relatively long development times (Masaki 1972, Mousseau & Roff 1989, Burke *et al.* 2005). However, not all observations fit to the model. In species where the model should be applicable, the saw-tooth pattern is not always found despite a shift in voltinism (Blanckenhorn & Fairbairn 1995, Blanckenhorn & Demont 2004 [data from Nylin & Svärd 1991]), and even Bergmann clines (*i.e.*, body size increases with increasing latitude or altitude) in body size have been reported (Blanckenhorn & Demont 2004 [data from Nylin & Svärd 1991]).

Variation in growth rate in relation to season length may provide an explanation for some of the contradictory observations. The traditional saw-tooth model implicitly assumed that growth rate does not vary (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994), but there is evidence for latitudinal growth rate variation in insects, indicating that growth rate increases with increasing latitude (Telfer & Hassall 1999, Blanckenhorn & Demont 2004, De Block *et al.* 2008, Pöykkö & Tammaru 2010). As (genetically determined) growth rate increases with decreasing season length, growth rate shows countergradient variation (Conover & Schultz 1995). The effect of countergradient variation in growth rate on the clinal variation in body size has been analysed (Blanckenhorn & Demont 2004), but not in relation to variation in voltinism. If countergradient variation in growth rate is added to the traditional saw-tooth model, the resulting body size cline may change. In the case that increasing growth rate perfectly compensates for the decrease in development time, body size remains constant across the gradient of season length (Fig. 2 b). If growth rate increases more than is needed to maintain constant body size (*i.e.*, overcompensation), body size would increase with decreasing season length within a particular phenology, and

reverse the traditional saw-tooth cline (Fig. 2 c). It is also possible that the traditional saw-tooth cline in body size remains despite countergradient variation in growth rate. This happens if the countergradient variation in growth rate is so slight that it cannot prevent body size from decreasing with decreasing season length (*i.e.*, undercompensation).

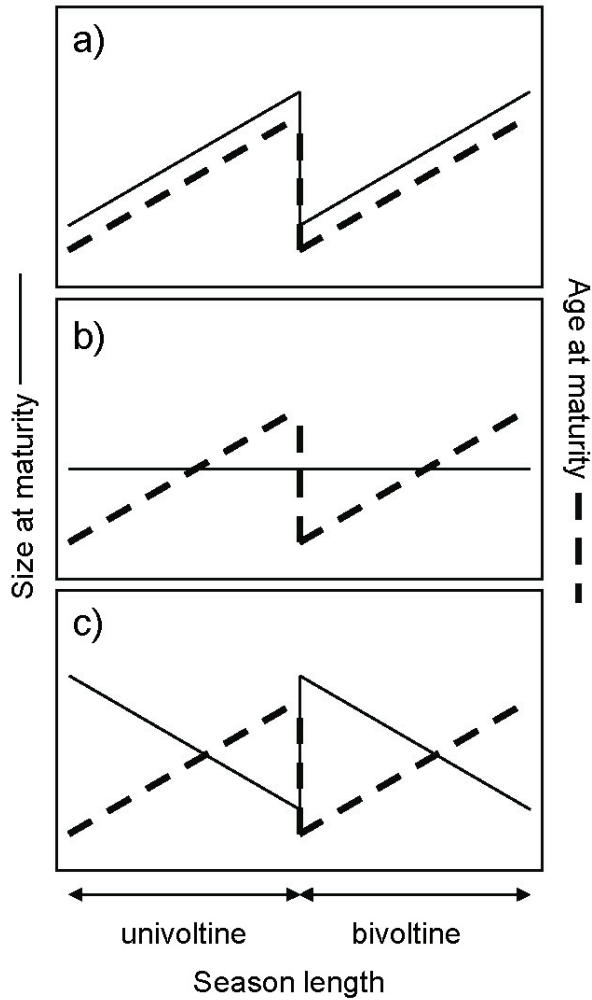


Fig. 2. Expected clines in age and size at maturity under the traditional saw-tooth model (a), and when growth rate shows perfectly compensating (b) or overcompensating (c) countergradient variation. The cline in age at maturity is the same in each case, because it is assumed that insects use all available time for growth.

The above life history models assumed a deterministic environment, but in reality, there is stochastic variation in season length. The intensity of time constraints a particular population experiences will vary among years, though it is predictable to some extent. As a consequence, the optimal life history may be different in different years. If there are genotype by environment interactions, different genotypes produce the optimal life histories in different years, which may, in principle, maintain additive genetic variation within a population (see Roff 1992). In the case that intraspecific variation in life histories is discontinuous (*i.e.*, discrete life history strategies), temporal variation in time constraints due to seasonality, voltinism or intraspecific competition may promote maintenance of polymorphism in life history strategies. When there is discontinuous variation in life histories, polymorphism might, in principle, be maintained also in a deterministic environment, but the conditions favouring it would be more restrictive than under environmental stochasticity.

Discontinuous variation in life history traits, like age-specific fecundities, has been observed in many insects, mainly in relation to wing length polymorphism (*e.g.* Solbreck 1986, Spence 1989, Denno *et al.* 1989, Zera & Rankin 1989, Roff & Bradford 1996, Välimäki *et al.* 2006). Natural populations are commonly polymorphic in these traits (*e.g.* Andersen 1973, Vepsäläinen 1974, Harrison 1980, Zera & Denno 1997, Bergström *et al.* 2002, Välimäki & Kaitala 2006), so the maintenance of polymorphism in life history traits is not a trivial issue. The maintenance of polymorphism has been studied extensively from the habitat persistence point of view (*e.g.* Harrison 1980, Roff 1986, 1994, Kaitala *et al.* 1989, Zera & Denno 1997), but the role of various time constraints in it has not been assessed. For example, the fitness value of early reproduction would be high whenever time constraints due to seasonality, voltinism or intraspecific juvenile competition are intense, so a strategy for early reproduction might be maintained in a population under these conditions, given the expected trade-off between early fecundity and lifetime fecundity (Charlesworth 1980, Roff 1992, Stearns 1992).

1.5 Aims of the study

The aims of the study fall into two categories: (1) to study which factors promote the maintenance of polymorphism in life history strategies in seasonal environments and (2) to study the evolution of clinal variation in several life history traits. In the first part of the thesis, I study whether the time constraints due to seasonality, voltinism or intraspecific competition might promote the

maintenance of life history polymorphism when there is discontinuous variation in life history traits. I utilise both experimental and modelling methods, the experiments being conducted with a butterfly (Lepidoptera: Pieridae) that is polymorphic in female mating frequency and associated life history traits in natural populations (see 2.1.1). Without loss of generality, the different life history strategies are dichotomised as monandry and polyandry, monandry being a strategy for early reproduction and polyandry for high offspring production (see 2.1.1 for details). I investigate experimentally whether larval competition is asymmetric (Table 1 [A], I), and whether the divergence in age-specific fecundities between monandry and polyandry would give monandry a time-advantage over polyandry, resulting in higher propensity to enter into direct development in monandry than in polyandry (Table 1 [B], II). In study II, the empirical approach is supplemented with modelling. Although the model is parameterised for the study species, the predictions are general.

In the second part of the thesis, I study empirically the evolution of clinal variation in body size, development time and growth rate in four geometrid moths (Lepidoptera: Geometridae) to evaluate whether the traditional saw-tooth model (Fig. 2 a, Table 1 [C]) or the alternative models including countergradient variation in growth rate (Fig. 2 b, c, Table 1 [D, E]) could explain the data (III). Given a hypothesised mechanism underlying expected age-specific fecundities (Table 1 [F]), I analyse the evolution of reproductive effort theoretically in relation to season length and voltinism in insects in general (IV). Finally, I empirically test the predictions derived in study IV (Table 1 [F1, F2]) with the four geometrid moths (V).

Table 1. The hypotheses and predictions tested in empirical studies.

Study	Hypothesis	Predictions
I	A. Intraspecific competition among juveniles is asymmetric	A1. Larger (= older) larvae have higher survival probability than smaller (younger) ones A2. When age difference between competing cohorts increases, survival probability increases in the older cohort and decreases in the younger cohort
II	B. High early fecundity of monandry compared to polyandry provides offspring of monandry line a time-advantage over polyandry	B1. Monandry has a higher propensity to produce a nondiapause generation when the nondiapause generation is partial B2. Individuals of monandry line are the first to emerge in the nondiapause generation when the nondiapause generation is complete
III	C. Time constraints due to seasonality and voltinism generate cogradient variation in development time and body size; growth rate is constant	C1. Saw-tooth clines in development time and body size C2. Genetic correlations ¹ : +, 0, 0
	D. Time constraints due to seasonality and voltinism generate cogradient variation in development time and perfectly compensating countergradient variation in growth rate	D1. Saw-tooth cline in development time, no cline in body size D2. Genetic correlations ¹ : 0, 0, -
	E. Time constraints due to seasonality and voltinism generate cogradient variation in development time and overcompensating countergradient variation in growth rate	E1. Saw-tooth cline in development time, reversed saw-tooth cline in body size E2. Genetic correlations ¹ : -, +, -
V	F. Insect age-specific fecundity and survival are increasing and decreasing concave functions of reproductive effort, respectively	F1. Reproductive effort is high in partially bivoltine populations and in northernmost univoltine populations F2. Saw-tooth cline in reproductive effort

¹ Expected genetic correlations (- = negative correlation, 0 = no correlation, + = positive correlation) between body size and development time, between body size and growth rate, and between development time and growth rate, respectively.

2 Materials and methods

2.1 Maintenance of life history polymorphism in seasonal environments

2.1.1 *The study species*

Pieris napi (L. 1758) (Lepidoptera: Pieridae) is an abundant butterfly that occurs throughout Finland (Marttila *et al.* 1990, Huldén *et al.* 2000). Its phenology is bivoltine in southern Finland, partially bivoltine in central Finland and univoltine in northern Finland (Marttila *et al.* 1990). It is a suitable species for studying life history polymorphism, because all studied populations are known to be polymorphic for female mating frequency (Bergström *et al.* 2002, Välimäki & Kaitala 2006, II), which is a trait under genetic control (Wedell *et al.* 2002). Mating frequency is associated with life history traits so that, relative to monandry (*i.e.*, a single mating), polyandry (*i.e.*, multiple mating) is associated with long lifespan and high lifetime fecundity due to male nutrient provisioning, but low early fecundity due to time cost of mating (Wiklund *et al.* 1993, Kaitala & Wiklund 1994, Bergström & Wiklund 2002, Wedell *et al.* 2002, Välimäki *et al.* 2006).

2.1.2 *The effect of asynchronous hatching on survival probability (I)*

A laboratory experiment was conducted to investigate juvenile survival probability in relation to asynchrony in hatching of eggs. Both *P. napi* females collected from the field (southern and central Finland) and derived from a laboratory stock (northern Finland) were used in this experiment. Females were maintained solitarily in flight cages (0.32 m × 0.65 m × 0.65 m [height]) next to large windows in a laboratory, and allowed to oviposit on natural host plants (*Thlaspi arvense* and *Rorippa palustris*).

The eggs were monitored daily to determine the date of hatching. The female parent of the larvae was used as a block factor to increase genetic homogeneity within a replicate, because offspring performance may vary among females (see Välimäki & Kaitala 2007). Offspring of 24 females were divided into four treatments. Firstly, 10 neonate larvae (cohort 1) were placed into four 0.75 l plastic containers provided with moist soil at the bottom and fresh leaves of *R.*

palustris. Into first of the four containers extra larvae were not placed during the experiment. Into the second, 10 extra neonate larvae (cohort 2) were placed on the same day as the 10 original larvae (no age difference between the cohorts). Finally, 10 neonate larvae (cohort 2) were introduced after four and eight days into the remaining two containers (4 and 8 days age difference between the cohorts, respectively).

The age-differences of four and eight days between the cohorts closely approximate natural intervals in the timing of offspring hatching between monandrous and polyandrous females in different generations. Time cost of remating delays egg-laying of highly polyandrous females so that, on average, their offspring are produced ca. four days later than those of monandrous ones (Välimäki *et al.* 2006), if the beginning of the reproductive period is synchronous for both strategies like in the beginning of the summer. There seems to be no variation in growth rate between offspring of monandrous and polyandrous females under natural conditions (see Välimäki & Kaitala 2007, II). In addition, the time cost of remating may be a general implication of polyandry (Daly 1978, Thornhill & Alcock 1983). Thus, the asynchrony in reproduction between monandrous and highly polyandrous females is expected to be doubled to eight days in the additional nondiapauses generation.

The larvae were reared in the laboratory under a 7 h day length (light : dark = 7 h : 17 h [temperature 30 : 20 °C]) to prevent larvae from developing directly into adults (see Masaki 1972, Tauber *et al.* 1986, Danks 1987, Gomi & Takeda 1996, Musolin & Numata 2003, Burke *et al.* 2005). This was important because direct development would generate unwanted variation in growth rate, and consequently in body size and development time (Wiklund *et al.* 1991, Välimäki & Kaitala 2007). On the other hand, short day length reliably indicates that the growing season is about to end, and thus prevents large prolongation of development time. Only minor variation in development time was allowed by the experimental design (see below), which further supported the choice of short day length. The leaves of the host plant were replaced with fresh ones daily in each container. The number of larvae that survived until pupal stage was recorded from each container as well as the date of pupation for the survived individuals.

The division of the survived individuals into the cohorts was done retrospectively, because the larvae could not be monitored individually through all instars. In the treatment with no age difference between the cohorts, the individuals were divided into the cohorts randomly with the restriction of at most ten individuals per cohort. For treatments with age difference between the cohorts,

individuals were placed into the cohort whose expected distribution of pupation dates would more likely include the observed date. The expected distribution of pupation dates for the older cohort was the observed distribution in the treatment with a single cohort and, for the younger cohort, this distribution was moved either four or eight days forwards in the time axis. For full details of cohort determination and the discussion of the reliability of the method, see study I.

2.1.3 The incidence of monandry in different generations (II)

The frequencies of monandrous and polyandrous *P. napi* females in the diapause and nondiapause generations were investigated with wild-caught females, whose mating frequencies were determined in the laboratory. Eight populations were sampled. Four of them (southern Finland; 59°–60° N: 23°–25° E) were located in the region where environmental conditions allow a completely bivoltine phenology. Four populations (central Finland; 64°–65° N: 25°–26° E) were located in the region where the species' phenology is partially bivoltine.

Samples of 25–35 females were taken on three and two occasions in the bivoltine and partially bivoltine populations, respectively. Due to variation in fecundity schedules among females (Välimäki *et al.* 2006), females with different mating tactics may emerge asynchronously in the nondiapause generation (see also 2.1.2). To make comparison between completely and partially bivoltine populations relevant, age distributions of females need to be identical in the samples to be compared. Therefore, sampling dates were standardised across populations on the grounds of the beginning of the flight season of a particular generation. The diapause generation was sampled in the middle of the flight season (cohort 1) in both bivoltine and partially bivoltine populations (see II for details). The nondiapause generation was sampled in the beginning (cohort 2) and in the middle (cohort 3) of the flight season in completely bivoltine populations (see II for details). The only nondiapause generation sample from partially bivoltine populations was taken in the middle of the flight season (cohort 3). Cohorts 1 and 3 were comparable samples from the diapause and nondiapause generations, respectively.

Captured females were transported to laboratory and released into flight cages (0.65 × 0.65 × 0.65 m) that were next to large windows. The butterflies were exposed to natural light intensity during daytime. Day length was 7 h (light : dark = 7 h : 17 h [temperature 30 : 20 °C]). The number of males released into the cages was 1.5 times the number of females (at most 50 individuals per cage), and

this sex ratio was maintained through the experiment. Males were of the same origin as the females. The male-biased sex ratio ensured that females had access to potential mates all the time (see Bissoondath & Wiklund, 1996, Wiklund *et al.* 1998). Fresh shoots of natural host plants (*Thlaspi arvense*, *Rorippa palustris*, *Erysimum cheiranthoides*) were provided for egg-laying. For adult feeding, the cages were provided with both natural nectar sources and artificial flowers. The females were allowed to mate and lay eggs until they died. After death, the females were dissected, and the number of spermatophore (one is delivered at each mating) residues in each female's *bursa copulatrix* was counted (see Drummond 1984). Determination of female mating frequency is reliable with this procedure, because residues of depleted spermatophores remain in the female throughout her life (Wiklund *et al.* 1993).

2.1.4 A stochastic simulation model on the maintenance of polymorphism (II)

The data on the incidence of monandry in different generations (see 2.1.3) are based on wild-caught females and may therefore be confounded by uncontrolled factors, such as stochastic variation in weather or phenotypic plasticity in male and female traits affecting female mating frequency. Hence, a stochastic model was developed to analyse whether the differences in age-specific fecundities between monandrous and highly polyandrous *P. napi* females are sufficient to produce the observed patterns alone.

Female lifetime fecundity increases with mating frequency in *P. napi*, but so do the time costs of reproduction, resulting in low early fecundity of polyandrous females (Välimäki *et al.* 2006). The observed distributions of egg-laying times of the different strategies (degree of polyandry), dichotomised here as “monandry” and “polyandry”, for simplicity, closely resemble Gamma distributions (data from Välimäki *et al.* 2006). This enabled me to model age-specific fecundities with Gamma distributions with appropriate parameters (see II for parameter values) that were estimated with the maximum-likelihood method by the function `fitdistr` (Venables & Ripley 2002) in R (R Development Core Team 2006).

In the discrete time individual-based model, lifetime fecundities (female offspring) of both monandrous and polyandrous females are derived from appropriate Poisson distributions (see II for parameter values). The time of oviposition is derived for each egg in the population from the appropriate Gamma distribution. For each individual, larval development time (t_i) from egg-laying to

pupation, and pupal development time (t_p) from the beginning of pupal development to adult eclosion are derived randomly from the known distributions of these parameters (data from Välimäki & Kaitala [2007] and from larvae reared outdoors; see II for parameter values). Possible variation in t_l between strategies (Wedell *et al.* 2002) was ignored because polyandrous individuals seem able to realise their potential for higher growth rate only in optimal conditions (Välimäki & Kaitala 2007), which may not occur in the wild like suggested by late emergence of polyandrous females in the nondiapause generation (see II).

Asymmetric competition among larvae may affect the relative successes of monandry and polyandry. In *P. napi*, larval competition is asymmetric at high densities so that older larvae have a competitive advantage over younger ones (I). Accordingly, I assumed that survival of larvae hatching on a given day depends on the number of older larvae alive in the population on that particular day. Hence, the number of larvae alive in each of the i days older cohorts (*i.e.*, larvae hatched i days earlier than the present cohort) was weighted according to

$$W(i) = 1 + w \Phi_w(i), \quad i = 1, \dots, 30 \quad (1)$$

where w is a parameter determining the strength and type of competition, and Φ_w is the cumulative normal distribution function (mean = 8, SD = 4). Values $-1 \leq w < 0$ refer to scrambles among larvae of similar age, the effect becoming weaker with increasing values of w . Values $w > 0$ refer to contests where older larvae have increasingly negative effects on the survival of younger ones, whereas $w = 0$ refers to interactions where all older larvae alive have an equal effect on the survival of larvae in a particular cohort. Assuming that mortality is independent of reproductive strategy, the proportion of monandrous and polyandrous larvae surviving within a cohort j is

$$s(j) = \frac{K}{K + N(j) + \sum_{i=1}^{30} W(i)n(j-i)}, \quad (2)$$

where $N(j)$ is the total number of hatching larvae on day j , $n(j)$ is the total number of survived larvae that hatched on day j ($n(j-i) = 0$, when $j-i < 1$), and K defines the maximum number of surviving individuals within the cohort.

The season is divided into two parts. T_l defines the number of days from the beginning of pupal development in spring until the critical day length that determines the developmental pathway induced. An individual that reaches the pupal stage, starting from the beginning of the season within time T_l , develops

directly into an adult and reproduces immediately. An individual that reaches the pupal stage later enters diapause and reproduces in the following spring. T_2 is the number of days from the critical day length until the end of the favourable season. Only individuals that manage to pupate before the end of the season survive and contribute to the overwintering population. I set T_1 to be 0.46 times the season length, which maximises the number of surviving descendants produced by monandrous individuals when season length allows only the first few cohorts of offspring to develop directly into adults. The optimal switching point for polyandry tends to be earlier than that for monandry as the season length increases. As long as the critical day length is the same for both monandry and polyandry, the location of the switching point from one developmental pathway to another on the time axis does not affect the qualitative results, but only the season length where a particular pattern emerges.

At first, I used this model to investigate the resulting population dynamics in relation to season length and type of competition, w . Secondly, I investigated the invasion ability of the strategies in relation to season length because a stable polymorphism prevails only if a polyandrous population can be invaded by monandry, and vice versa. Finally, I did a sensitivity analysis to investigate how small changes in either the distribution parameters defining the egg-laying times or the relative lifetime fecundity disadvantage of monandry affect the invasion probability of the strategy.

2.2 Clinal variation in life history traits

2.2.1 The study species

Four widespread and abundant geometrid moths (Lepidoptera: Geometridae) – *Cabera exanthemata* (Scop. 1763), *Cabera pusaria* (L. 1758), *Chiasmia clathrata* (L. 1758) and *Lomaspilis marginata* (L. 1758) – were selected as the study species. These species are bivoltine in southern Finland and univoltine in central and northern Finland (Mikkola *et al.* 1989), strongly suggesting that the species have long development times in relation to season length under natural conditions. The diapause generation of each species emerges in early summer (June – early July) and the species' nondiapause generations emerge in late summer (late July – August). The larvae of *C. exanthemata* and *L. marginata* feed mainly on *Salix* spp., while *Alnus* and *Betula* species are the main hosts of *C. pusaria* (Mikkola *et*

al. 1989). The host plants of *C. clathrata* are several leguminous plants (Fabaceae) and *Galium* (Mikkola *et al.* 1989). Overwintering takes place obligatorily in the pupal stage (Mikkola *et al.* 1989).

The study species can be classified as capital breeders that use only larval-derived resources for reproduction (see Tammaru & Javoš 2000 for *C. pusaria* and *C. clathrata*). This is because adult feeding on nectar is rare (Mikkola *et al.* 1989, P. Välimäki, personal communication), and females have a large number of eggs ready to be laid at adult eclosion (personal observations).

2.2.2 Latitudinal variation in body size, development time and growth rate (III)

2.2.2.1 Sampling

To study latitudinal clines in body size, development time and growth rate, these traits need to be measured in several latitudinally distinct populations. Thus, each study species was sampled from six geographical regions along a latitudinal gradient (60° 5' N – 67° 56' N) from southern to northern Finland (see III for details). When moving northwards along the gradient, the average length of the growing season decreases, and the study species' phenology changes from bivoltine in the southernmost region to partially bivoltine in the next two regions and to univoltine in the remaining northern regions (Hyönteistietokanta 2009, see III for details).

At least two populations of each species were sampled within each region, given that the species occurs in that particular region. As an exception, only one *C. exanthemata* and *C. pusaria* population was sampled in one of the northern regions (see III). Altitudinal variation was slight among the study populations (all within 60–250 m above sea level). Only diapause generation individuals were sampled, because life histories may differ between individuals representing the different developmental pathways (Spence 1989, Wiklund *et al.* 1991, Blanckenhorn 1994, Fischer & Fiedler 2001, Karlsson & Johansson 2008, Karlsson *et al.* 2008, Larsdotter Mellström *et al.* 2010, Teder *et al.* 2010). Sampling was conducted in June and July, and the generation individuals belonged to was determined subjectively based on the date of capture.

2.2.2.2 Common garden experiment

Alive captured females were placed into 0.1 l plastic containers with leaves of appropriate host plants as an oviposition substrates. *Salix phylicifolia* was used as a host for *C. exanthemata* and *L. marginata*, *Alnus incana* for *C. pusaria* and *Lathyrus pratensis* for *C. clathrata*. The females were allowed to oviposit until they died. Eggs were monitored daily for hatching. Five offspring of each female ($N_{\text{female}} = 125, 103, 114$ and 99 for *C. exanthemata*, *C. pusaria*, *C. clathrata* and *L. marginata*, respectively) were taken for rearing, and individually placed into 0.2 l plastic containers provided with moist garden peat at the bottom and a fresh host plant. Each container was monitored daily, and the host plant was changed to a fresh one and some water added to maintain humidity when necessary. The larvae were reared until pupation in a laboratory in a constant temperature of 20 ± 1 °C. Day length was set to 8 h (light : dark = 8 h : 16 h) to induce diapause (see Masaki 1972, Tauber *et al.* 1986, Danks 1987, Gomi & Takeda 1996, Musolin & Numata 2003, Burke *et al.* 2005). The larval period was considered to end the day when a larva burrowed into the peat to pupate. Five days later, the pupa was unearthed and weighed. Larval growth trajectory was assumed to follow a power function (Tammaru & Esperk 2007), so larval growth rate (c) was calculated as

$$c = \frac{m_{\text{pupa}}}{t_{\text{larva}}^B}, \quad (3)$$

where m_{pupa} is pupal mass, t_{larva} is larval development time and $B = 1/(1-b)$, b being an allometric exponent relating anabolism to body mass. According to results of Tammaru and Esperk (2007), $b = 0.8$ seems realistic for the study species, and was thus used in calculation of growth rate.

2.2.2.3 Assessment of maternal effects

Because offspring of wild-caught females were used in the common garden experiment, potential nongenetic effects of maternal condition on the offspring phenotype may influence the results. Nongenetic maternal effects are known to affect life history traits in arthropods (Mousseau & Dingle 1991, Mousseau & Fox 1998, Beckerman *et al.* 2006, Zehnder *et al.* 2007). Thus, to make sure that the data presents the genetic component of phenotypic variation, an evaluation of the potential maternal influence on the data was needed.

An experiment was conducted with *C. exanthemata* to assess the potential maternal effects on pupal mass, larval development time and larval growth rate. Starting with rearing extra larvae (1st laboratory generation) from 14 females from the northernmost region (7 females from both populations), *C. exanthemata* was reared in constant laboratory conditions for two generations (see III for details). After two generations in constant laboratory conditions, potential maternal effects on offspring phenotype due to variation in maternal growing conditions in the parental generation should be removed (see Conover & Schultz 1995, Bernardo 1996). The third laboratory generation should therefore be free of any such maternal effects, so larvae belonging to the third laboratory generation were reared in the same conditions as those in the main experiment (see 2.2.2.2). I then compared the measured life history traits between the first and the third laboratory generations. Any difference in life history traits between the first and the third laboratory generations indicates that maternal effects affected the data in the first laboratory generation. I included only those maternal lineages that were represented in both datasets in the comparison. There were six such lineages in both populations.

2.2.3 Genetic correlations among body size, development time and growth rate (III)

The genetic correlation structure among body size, development time and growth rate is predicted to be different under the three models of clinal variation under study (see Table 1). To assess the models, it is therefore necessary to estimate the genetic correlation structure. Thus, to estimate genetic correlations among pupal mass, larval development time and larval growth rate in each of the four study species, I fitted a trivariate animal model (Kruuk 2004, Wilson *et al.* 2010) to the data by using Markov chain Monte Carlo methods in the Bayesian framework as implemented in R (R Development Core Team 2009) function MCMCglmm (Hadfield 2010). A model where pupal mass, larval development time and larval growth rate were set as response variables was fitted to the data in each species. Sex-specific trait means were set as fixed effects and individual breeding value and population as random effects. See study III for full details.

The pedigree required in the analysis was created for each species by assuming that the data consisted of full-sib families. Thus, a single male parent was assumed for each family in addition to the known female parent of each individual. This assumption is unlikely to bias the results, because a few wild-

caught females were dissected and all of them were singly mated (P. Välimäki, personal communication), and under polyandry, strong last male fertilization success is common in Lepidoptera (Simmons 2001). In addition, a small amount of misassigned paternity does not change the results (Charmantier & Réale 2005).

2.2.4 Modelling clinal variation in reproductive effort (IV)

To analyse the evolution of reproductive effort along a gradient of season length, I developed a simulation model. For simplicity, I assumed daily fecundity, f , of a female insect to be independent of age and to increase asymptotically with reproductive effort, E , measured as a proportion of daily energy budget allocated to reproduction. Hence, fecundity on day i can be described by the function

$$f(i) = f_{\max} (1 - e^{-c_1 E(i)}), \quad (4)$$

where f_{\max} is maximal number of female eggs that can be laid during a day, c_1 is a constant defining the increase rate of fecundity as a function of $E(i)$, and $E(i)$ is reproductive effort on day i .

I assumed survival from day i to day $i + 1$, s , to be a decreasing function of reproductive effort on day i . Survival function is assumed to be concave, so survival from day i to day $i + 1$ can be described by the function

$$s(i+1) = 1 - E(i)^{c_2}, \quad (5)$$

where c_2 ($c_2 > 1$) is a constant defining the shape of the function. Concavity of both fecundity and survival functions is a realistic assumption in life history with age-structured adult population (Schaffer 1974).

The life cycle was modelled so that a photoperiodic switch determines the developmental pathway induced, which is a realistic assumption as photoperiod is the main determinant of the developmental pathway in many insects (*e.g.* Tauber *et al.* 1986, Danks 1987). An individual reaching the diapause stage before critical photoperiod matures directly, whereas an individual that reaches the diapause stage later on enters diapause, and matures in the next year. The time required for development from the oviposition of an egg to the diapause stage is t_1 days, and from diapause stage to reproductive adult, t_2 days. It is assumed that populations are adapted to local conditions so that they can react adaptively to gradual change in day length (Masaki 1972, Tauber *et al.* 1986, Danks 1987, Mousseau & Roff 1989, Blanckenhorn & Fairbairn 1995, Burke *et al.* 2005). Accordingly, in a deterministic environment, the location of the critical photoperiod on a time axis

is at the halfway point of the season, so that an additional generation can be produced immediately when the length of the season allows it. When the season length is T , only individuals that reach the diapause stage within time T from the beginning of the season survive and form the diapausing population. I restricted the analysis to a situation where a maximum of two generations can be produced within a season.

The model is continuous in population size but discrete in time. Deriving from equations 4 and 5, the expected number of eggs laid by a single female with reproductive effort E on i^{th} ($i = 1, \dots, \omega$) day since adult emergence, $F(i, E)$, is

$$F(i, E) = f_{\max} (1 - e^{-c_1 E})(1 - E^{c_2})^{i-1}. \quad (6)$$

Given that emergence of adults is synchronous in the diapause generation in the beginning of the season, the total number of eggs produced by all females with reproductive effort E , on day i ($i = 1, \dots, \omega$) since emergence, is $F(i, E)$ multiplied by the number of females with reproductive effort E in that particular generation. The offspring that reach the diapause stage before the critical photoperiod give rise to the additional nondiapause generation. In the nondiapause generation, the adult emergence is asynchronous, if at least two cohorts of offspring of the diapause generation develop directly. Therefore, the total number of eggs laid by all females with reproductive effort E on day j ($j = 1, \dots, \omega - 1 + n_{\text{coh}}$; n_{coh} is the number of cohorts that develop directly into adults) since emergence of the first females in the non-diapause generation is

$$\sum_{x=1}^{n_{\text{coh}}} N_x F(j - x + 1, E), \quad (7)$$

where N_x is the number of adults with reproductive effort E in cohort x , and $F(j - x + 1, E) = 0$, if $j - x + 1 < 1$, or if $j - x + 1 > \omega$.

I modelled density dependence in two ways. Firstly, I included density dependent mortality in the juvenile stage. Density dependence was calculated independently for each cohort and no density dependence was assumed to occur between generations. I selected parameter values used in simulations so that they produced non-overlapping adult generations. Under this within-cohort mortality model, the number of survived juvenile females within a cohort i (in the diapause generation $i = 1, \dots, \omega$; in the nondiapause generation $i = 1, \dots, \omega - 1 + n_{\text{coh}}$) is given by

$$\frac{KN_i}{K + N_i}, \quad (8)$$

where N_i is the number of hatching juveniles in the cohort i , and K is a parameter defining the maximum size of a cohort.

Secondly, I relaxed the assumption that density dependence occurs in the juvenile stage and included density dependent mortality in the diapausing population. This was because of interspecific variation in the magnitude of density dependence in juvenile populations. Mortality was assumed to be independent of reproductive effort and developmental pathway. According to this winter mortality model, the number of surviving females from year t to year $t + 1$ is then

$$\frac{K_w N_t}{K_w + N_t}, \quad (9)$$

where N_t is the number of diapausing females in the overwintering population in the beginning of the adverse season in year t , and K_w is a parameter defining the maximum size of the overwintering population.

I investigated the evolutionary stability of different strategies determined by the level of reproductive effort with invasion analysis. I tested the whole possible range of reproductive effort (*i.e.*, from 0 to 1) of invading strategy against the whole possible range of reproductive effort of the resident strategy. I set the initial number of individuals utilizing the invading strategy to one, and the initial number of resident individuals to the maximum population size that can be reached with the given parameter values minus one. The mutant strategy was able to invade the population if its frequency increased in a simulation over one season, when only the resident density contributed to density dependence. It was not possible to analyse the change in mutant frequency over one season under the winter mortality model, so I analysed the mutant's invasion ability by simulating the change in frequencies of mutant and resident strategies until equilibrium was found. Initial frequencies of the strategies were chosen as above, but both resident and mutant densities affected density dependence in this case. Finally, I solved the evolutionarily stable reproductive effort as a function of season length and number of generations emerging.

2.2.5 Measuring clinal variation in reproductive resource allocation (V)

2.2.5.1 Study material

Reproductive resource allocation needs to be measured in several latitudinally distinct populations to assess clinal variation in this trait. The individuals reared in study III (see 2.2.2.2) provided suitable material for that. The pupae from study III were placed individually into 0.2 l plastic containers with moist moss (*Sphagnum* spp.). Then the pupae overwintered in a dark refrigerator (5 °C) either 6–7.5 (*C. exanthemata*, *C. pusaria*) or 8.5–9.5 (*C. clathrata*, *L. marginata*) months. After hibernation, the pupae were exposed to a constant temperature of 20 °C and continuous light. The pupae were monitored daily for eclosion, and eclosed moths were frozen once they had ejected meconium. The reproductive resource allocation of these individuals was then measured.

2.2.5.2 Measurement of reproductive resource allocation

I dissected the bodies of the frozen females into two parts: abdomen and the rest of the body (*i.e.*, head and thorax, including wings, legs and antennae). The body parts were dried for 48 hours in 38 °C and weighed with a precision balance. Then, lipid and protein contents of the body parts were analysed from one female from each family (modified sulfophosphovanillin method [Frings *et al.* 1972, see V for details] for lipids; method by Bradford [1976] for proteins). The remaining females were further dried in 67 °C for a minimum of 16 h and analysed for total carbon and total nitrogen content (controlled combustion and gas chromatography; EA1110 automatic elemental analyser, Fisons Instruments S.p.A., Italy).

I used resource allocation to the abdomen as a surrogate of resource allocation to reproduction (see Boggs 1981, Karlsson & Wickman 1989a, b, 1990). This is reasonable especially for capital breeders where the female abdomen is almost completely filled by ovaries at adult eclosion. I calculated the proportion of total body “resources” that were allocated to abdomen for each “resource” measured; dry mass, total carbon, total nitrogen, total proteins and total lipids.

I also calculated abdomen lipid:protein ratio, because the fat allocation trade-off between reproduction and survival cannot be measured solely by comparing lipid contents of the abdomen and the rest of the body. Fat is stored in the fat body, which is mostly located in the abdomen, and the reserves can be used for both

reproduction and survival (Ellers 1996, Ellers & van Alphen 1997, Jervis *et al.* 2008, Arrese & Soulages 2010). A high lipid:protein ratio in the abdomen would indicate that part of the fat reserves are available for somatic maintenance, but this requires that the ratio is constant in eggs. Empirical evidence suggests that egg composition is rather constant in capital breeders (Diss *et al.* 1996).

2.3 Statistical analyses

All data analyses (summarised in Table 2, see also 2.2.3) were conducted with R versions 2.3.1-2.10.1 (R Development Core Team 2006, 2009). Linear mixed effects models (function `lme` [Pinheiro *et al.* 2008]) were fitted to the data with maximum likelihood method when the data contained random effects and the assumption of normal distribution was appropriate. The need to include a particular random effect was evaluated with the likelihood ratio test and Akaike's information criterion when the estimated variance corresponding to this effect was very low. In some cases, random effects were removed altogether (Pinheiro & Bates 2000), and then a corresponding linear model (function `lm`) or generalised least squares linear model (function `gls` [Pinheiro *et al.* 2008]; fitted with maximum likelihood method) was fitted to the data. If visual evaluation of residual plots indicated heteroscedasticity, a variance function was included to weigh the observations appropriately (see III and V for details). When the type of clinal variation was analysed, orthogonal polynomial contrasts were calculated for the region (see III and V for details).

For survival data, a generalised linear model (function `glm`) with binomial error distribution and logistic link function was fitted to the data. As there were some fitted survival probabilities numerically either 0 or 1, and consequent problems in Wald approximation (Venables & Ripley 2002), a permutation test was conducted to assess the significances of parameter estimates of the model. Frequency data (incidence of different reproductive strategies, see II) were analysed with log-linear models (function `glm`, Poisson error distribution, logarithmic link function). In these cases, model goodness of fit was assessed by visual evaluation of residual plots and the residual deviance of the model.

When at least two fixed explanatory variables were included in the analysis, a model with all the main effects and interactions among them was fitted to the data at fist. Then the model was reduced according to the principle of hierarchy to get the definitive model.

Table 2. Summary of statistical analyses.

Study	Aim	Method (R function)	Response variable(s)	Explanatory variable(s)	Random effects	Error distribution (link function)
I	To find out how age difference between cohorts affects survival probabilities in different cohorts	generalised linear model (glm)	survival (0/1)	age difference between cohorts, cohort, family	-	binomial (logistic)
II	To find out how the proportion of monandrous females in a population changes within a season	log-linear model (glm)	frequency of monandry	population, cohort (time of sampling)	-	Poisson (logarithmic)
III	To find out the clinal variation in the analysed traits	linear mixed effects model (lme)	pupal mass, development time, growth rate	region, sex	family nested within a population	normal (identity)
	To determine the genetic correlation structure among body size, development time and growth rate	animal model (MCMCglmm)	pupal mass, development time, growth rate ¹	sex-specific trait means	individual breeding value, population	Gaussian (identity) ²
V	To find out the clinal variation in the analysed traits	linear mixed effects model (lme)	mass allocation, PC1 ³ , protein allocation, lipid allocation, abdomen lipid:protein ratio	region, diapause time	family nested within a population ⁴ , population ⁵	normal (identity)

¹ Multivariate analysis.

² Distribution of the response variables (Bayesian analysis).

³ 1st principal component of mass-, carbon- and nitrogen allocation.

⁴ For the former two response variables.

⁵ For the latter three response variables.

3 Results and discussion

Seasonality may be a factor promoting the maintenance of polymorphism in discrete life history strategies in certain conditions (II), the effect of seasonality being possibly enhanced by asymmetric intraspecific competition (I, II). When intraspecific variation in life histories is continuous, clinal variation in key life history traits is predicted (IV) and observed (III, V) along a latitudinal gradient of changing season length.

3.1 Life history polymorphism in seasonal environments

When intraspecific competition between cohorts of differently aged larvae was induced in *P. napi*, the larvae belonging to the older cohort had higher survival probability than the larvae belonging to the younger cohort (I) as predicted (Table 1 [A1]). This effect was dependent on the age difference between the competing cohorts. When age difference between the cohorts increased, individual survival probability increased in the older cohort but decreased in the younger one (I), which supports the prediction (Table 1 [A2]). According to these results, intraspecific competition among larvae is asymmetric in *P. napi*, so that older, and thus larger, individuals have a competitive advantage over younger and smaller ones. Asymmetry in intraspecific competition favouring large individuals is an expected (Begon 1984) and commonly observed (Livdahl 1982, Wall & Begon 1986, Averill & Prokopy 1987, Broadie & Bradshaw 1991, Messina 1991, Edgerly & Livdahl 1992, Koenraad *et al.* 2004, Cameron *et al.* 2007) phenomenon. Despite the general competitive advantage of large individuals, the presence of small individuals had a negative effect on the survival probability of large individuals, especially when the age (*i.e.*, size) difference between them was relatively small. This was emphasised by the increasing survival probability of the older larvae with increasing age difference between the competing cohorts (I).

The asymmetry in larval competition in *P. napi* favours early reproduction whenever there is a risk of intraspecific competition among larvae. As monandrous *P. napi* females have higher early fecundity than polyandrous ones (Välimäki *et al.* 2006), there is an inherent asynchrony in the hatching of offspring between these life history strategies. Owing to this, larval mortality may be biased towards offspring of polyandrous females, if larval density is high enough to induce intraspecific competition. This may well be the case in bivoltine populations, where the offspring of the nondiapause generation females may face

high population densities, because bivoltine phenology provides exponential increase in population size within a season. The effect of increasing population density is reinforced by increasing asynchrony in hatching of offspring of monandrous and polyandrous females, because the asynchrony is expected to be doubled from four to eight days in the nondiapause generation. Asymmetric larval competition has, thus, potential to maintain life history polymorphism in *P. napi*. However, it is unlikely to be the main mechanism maintaining polymorphism as it is strongly dependent on population density.

Although the different age-specific fecundities of monandrous and polyandrous females (Välimäki *et al.* 2006) may generate asymmetric competition among larvae, the difference in the fecundity schedules as such may be involved in the maintenance of polymorphism. This is because the time constraints set by seasonality and voltinism affect the fitness benefit of high early fecundity, and associated short generation time. Compared to polyandry, monandry is associated with relatively high early fecundity (Välimäki *et al.* 2006) and relatively short adult lifespan (Wiklund *et al.* 1993, Bergström & Wiklund 2002, Wedell *et al.* 2002). Therefore, monandry has a shorter generation time than polyandry as development times seem not to differ between the strategies in natural conditions (see Välimäki & Kaitala 2007). Hence, monandry should be more prone to direct development, and consequently to bivoltine phenology, than polyandry in conditions where a partial nondiapause generation may emerge (see Table 1 [B1]). This prediction was supported as the frequency of monandry was higher in the nondiapause generation than in the diapause generation in partially bivoltine *P. napi* populations (II). The predicted (Table 1 [B2]) time advantage of monandry was also evident in completely bivoltine populations, because the frequency of monandry was high in the beginning of the flight season of the nondiapause generation (II). When measured in the middle of the flight seasons of diapause and nondiapause generations, the frequency of monandry was rather constant in completely bivoltine populations (II). Interestingly, the frequency of monandry was higher than expected by its reproductive potential relative to polyandry in the nondiapause generations of all studied populations (II). This suggests that even in populations where *P. napi* was presumed to follow completely bivoltine phenology, not all offspring of the diapause generation developed directly, and that diapause propensity was higher in polyandry than in monandry.

The stochastic model confirmed that the differences in age-specific fecundities between monandry and polyandry are alone sufficient to maintain the

polymorphism in certain conditions. The investigation of population dynamics revealed that monandry was maintained in the population with polyandry, if univoltine phenology was time limited or phenology was either partially or completely bivoltine (II). If univoltine phenology was not time limited, monandry was invariably excluded by polyandry (II). In bivoltine phenology, the frequency of monandry decreased with increasing season length both in diapause and nondiapause generations, the response being strong in the nondiapause generation (II). In partially bivoltine phenology, the frequency of monandry increased from the diapause to nondiapause generation, like in the empirical data (see above), whereas the opposite was true in completely bivoltine phenology (II). Increasing asymmetry in larval competition increased the frequency of monandry in both generations, but did not change the qualitative results (II). Invasion analysis showed that the invasion probability of monandry was relatively high in those regions where monandry was maintained in a population in the population dynamics simulations (Fig. 3). Invasion probability of monandry was insensitive to the type of competition and relatively insensitive to small changes in some other key parameters of the model, whereas invasion probability of polyandry strongly decreased as the asymmetry in the competition increased (II).

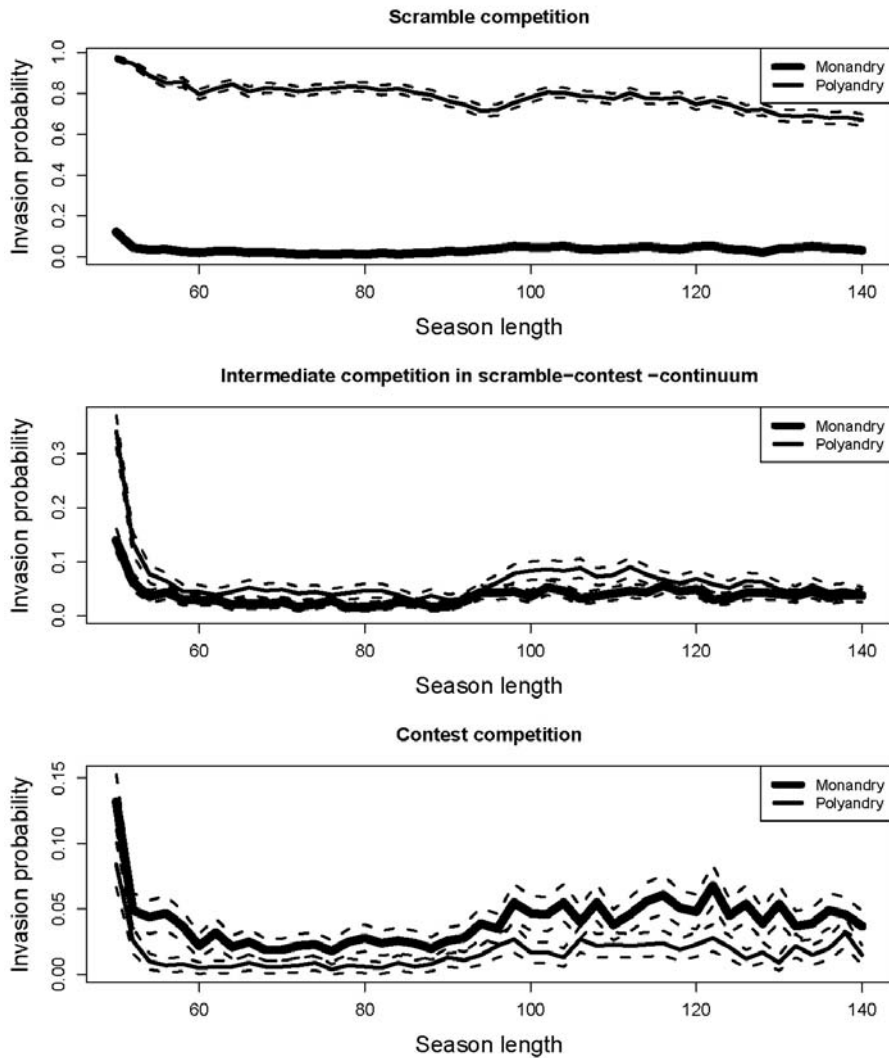


Fig. 3. Invasion probabilities of monandry and polyandry in relation to season length. Dashed lines indicate the 95% confidence intervals of the invasion probabilities. In the top panel, competition among larvae is of the scramble type ($w = -1$; see equation 1). In the bottom panel, competition among larvae is of the contest type ($w = 1$). The type of competition is intermediate between these extremes in the middle panel ($w = 0$). Phenology is univoltine, when the season length is less than ca. 100 days, and bivoltine when the season length is longer than this (II, published by permission of John Wiley and Sons).

According to the results, the divergence in fecundity schedules of monandry and polyandry is sufficient to maintain polymorphism in all bivoltine and in time-constrained univoltine *P. napi* populations. Interestingly, all *P. napi* populations studied for mating frequency are polymorphic (Bergström *et al.* 2002, Välimäki & Kaitala 2006, II), and all of them fall into the categories where the model predicts polymorphism, so the empirical data fits the predictions well. Whenever time constraints are intense, the relatively high early fecundity of monandry gives it an advantage over polyandry. In time-constrained univoltine populations this is obvious as only the earliest offspring produced have enough time to reach the overwintering pupal stage before conditions become adverse. Only early fecundity contributes to fitness in this case. In time-constrained bivoltine populations the summer is so long that even late-life offspring production contributes to fitness of the diapause generation individuals. In this case, the early-life offspring production contributes to fitness the most, because these offspring will develop directly into adults within the same season and form the nondiapause generation. Provided that a large enough number of offspring of the nondiapause generation individuals survive, completing two generations within a season provides higher fitness than is attainable with one generation per season. Thus, monandry is able to compensate its relatively low lifetime offspring production by producing two generations per season more likely than polyandry. This is enough to prevent monandry from being excluded by polyandry in partially bivoltine populations.

When the phenology is approximately completely bivoltine, monandrous females are still the first to emerge and lay eggs in the nondiapause generation. The reproductive period of monandry is much shorter than that of polyandry in the nondiapause generation, because monandrous nondiapause generation females emerge within a shorter period than the polyandrous nondiapause generation females do, and because monandrous females have a shorter lifespan than polyandrous ones. This, together with the early emergence of monandrous females in the nondiapause generation, means that all offspring of monandrous nondiapause generation females have a relatively high probability of reaching the overwintering pupal stage before autumn frosts. Polyandry, on the contrary, results in extended reproductive period in the nondiapause generation, which, together with the relatively late emergence of polyandrous nondiapause generation females, may result in low survival of the late-life offspring of polyandrous females. This risk may be severe especially for females emerging late in the flight season of the nondiapause generation, which should select for a

higher diapause propensity in polyandry than in monandry. Consequently, monandry escapes competition with polyandry in the arising second juvenile generation, and has a higher probability than polyandry that all lifetime offspring production contributes to fitness. Thus, monandry cannot be excluded from a bivoltine population. Although monandry would get a strong competitive advantage over polyandry in the larval population, asymmetric larval competition is not needed for the maintenance of polymorphism in completely bivoltine populations either. However, asymmetry in larval competition may increase the frequency of monandry.

The expected and observed frequency of monandry is lower than that of polyandry in bivoltine populations (Bergström *et al.* 2002, Välimäki & Kaitala 2006, II). This does not necessarily mean that monandry is more vulnerable to extinction due to stochastic variation in season length than polyandry. Monandry can be seen as a bet-hedging strategy that sacrifices some potential offspring production to decrease variance in the number of surviving offspring produced, resulting in high geometric mean fitness in the long term (Dempster 1955, Gillespie 1977, Seger & Brockmann 1987). Stochastic variation in the season length is, thus, an additional factor probably involved in the maintenance of life history polymorphism in *P. napi*. In years of an exceptionally short summer, polyandry may lose a large proportion of its fitness, whereas the fitness of monandry is affected less. Even though the divergence in fecundity schedules of monandry and polyandry can alone maintain polymorphism in a deterministic environment, stochastic environmental variation may further promote the maintenance of monandry, and so increase the stability of the polymorphism in natural populations.

3.2 Latitudinal clines in life history traits

Latitudinal variation was found in almost every life history trait studied (III, V). The latitudinal clines found are based on genetic differentiation among populations, because the common garden design reveals the genetic component of variation, and the data were not confounded by nongenetic maternal effects in the species explicitly analysed in this respect (III). The main results concerning observed clinal variation in the four study species are summarised in Table 3. Two main points emerge. Firstly, the observed clines in body size and associated traits as well as the genetic correlations among them do not support the traditional saw-tooth model, yet the consistency of development time and growth rate clines

across species suggest a common mechanism underlying the observations. Secondly, resource allocation to reproduction tended to be relatively high in time-constrained populations, although the expected saw-tooth cline was not found.

3.2.1 Clinal variation in body size and associated life history traits

The observed body size clines fitted the predictions in two out of the four study species. Pupal mass followed the traditional saw-tooth cline (Table 1 [C1], Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994) in *C. exanthemata*, except that female pupal mass increased towards the north at the northernmost end of the cline (III). In *C. clathrata*, pupal mass was rather constant across the studied gradient (III), which fits the prediction under perfectly compensating countergradient variation in growth rate (Table 1 [D1]). Body size variation in *C. pusaria* and *L. marginata* contradicted all the predictions presented in Table 1 as their pupal masses decreased rather uniformly northwards, except that sexual size dimorphism was reversed in one region in *L. marginata* (III). A shift in voltinism was clearly reflected toward pupal mass only in *C. exanthemata*.

Table 3. Summary of the empirical results concerning clinal variation in life history traits in the four geometrid moths studied.

Study	Prediction	Observations			
		<i>C. exanthemata</i>	<i>C. pusaria</i>	<i>C. clathrata</i>	<i>L. marginata</i>
III	Saw-tooth cline in development time	no	no	no	no
	Saw-tooth cline in body size	yes	no	no	no
	Countergradient variation in growth rate	yes	yes (a slight saw-tooth pattern)	yes	yes
	Genetic correlations ¹	+, 0, -	0, 0, -	0, 0, -	0, +, -
V	Reproductive effort high in partially bivoltine populations	yes (protein allocation)	yes	yes	yes
	Reproductive effort high in northernmost univoltine populations	yes (mass allocation)	no	yes	no
	Saw-tooth cline in reproductive effort	no	no	no	no (only univoltine regions violate the prediction)

¹ Genetic correlations (- = negative correlation, 0 = no correlation, + = positive correlation) between body size and development time, between body size and growth rate, and between development time and growth rate, respectively.

In insects with latitudinal variation in voltinism, a saw-tooth cline in development time is predicted (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994), especially in species with long development times in relation to season length (Chown & Gaston 1999). Contrary to this prediction, none of the species showed a saw-tooth cline in development time (III, Table 3). The expected cogradients variation in development time (Table 1) was, however, apparent in each species as development time uniformly decreased towards the north, resulting in a converse Bergmann cline (III). The contradiction arose because the shift in voltinism was not reflected in development time. In addition, each study species expressed countergradient variation in growth rate as growth rate increased northwards (III). When countergradient variation in growth rate exists, the clinal variation in growth rate is expected to be approximately opposite to the clinal variation in development time. A slight saw-tooth pattern was found in the growth rate cline in *C. pusaria*, but in all the other study species the cline was uniform (III), which is not surprising as the shift in voltinism was not reflected in the development time clines. A strong negative genetic correlation was observed between development time and growth rate in each species (III, Table 3), which is expected under countergradient variation in growth rate (Table 1 [D2, E2]).

Countergradient variation in growth rate contradicts the traditional saw-tooth model that assumes constant growth rate (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994). In addition, the observed combination of genetic correlations among body size, development time and growth rate did not fit to the expectation under the traditional saw-tooth model (Table 1 [C2]) in any of the study species (Table 3). The observed genetic correlations fitted those predicted under perfectly compensating countergradient variation in growth rate in *C. pusaria* and *C. clathrata* (Table 1 [D2], Table 3). In *C. exanthemata* and *L. marginata*, the observed genetic correlations did not fit to any of the predictions presented in Table 1 (Table 3). Thus, even though the observed body size cline fitted the traditional saw-tooth model fairly well in *C. exanthemata*, the underlying mechanisms seem different from those assumed under the traditional model.

The contradiction between the traditional saw-tooth model (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994) and the observations may arise because of the overly simplistic assumptions of the model; that age-structure in the adult population is unimportant, and that voltinism changes suddenly without any transition region between the two phenologies. Many insects have such long reproductive periods in the adult stage that it is unrealistic to assume reproduction to be a point event in time. This holds true for the study species as well. Because

of age-structure in the adult population, and phenotypic plasticity in diapause induction (Masaki 1972, Tauber *et al.* 1986, Danks 1987, Gomi & Takeda 1996, Musolin & Numata 2003, Burke *et al.* 2005), a partial nondiapause generation will emerge when the season length allows only the earliest offspring cohorts of the diapause generation to develop directly into adults. Consequently, phenology will change gradually with a partial nondiapause generation, which has been observed in several species (Masaki 1972, Andersen 1973, Vepsäläinen 1974, Mousseau & Roff 1989, Spence 1989, Blanckenhorn & Fairbairn 1995, Pöykkö & Tammaru 2010, II). Owing to the gradual transition between phenologies, there need not to be any abrupt changes in the time constraints experienced by the individuals entering diapause, but they can prolong their development as the season length increases. This may explain why the change in phenology was not reflected in development time in study III, where the developmental pathway leading to diapause was investigated. Instead, those individuals that enter direct development face intense time constraints in the transition region between the phenologies. Thus, individual life histories may be different between the two developmental pathways, which has commonly been observed (Spence 1989, Wiklund *et al.* 1991, Blanckenhorn 1994, Fischer & Fiedler 2001, Karlsson & Johansson 2008, Karlsson *et al.* 2008, Larsdotter Mellström *et al.* 2010, Teder *et al.* 2010). This further contradicts the traditional saw-tooth model that implicitly assumed life history to be independent of the developmental pathway (Masaki 1967, 1972, Roff 1980, 1983, but see Iwasa *et al.* 1994 for plasticity in relation to resource availability).

Body size is the consequence of development time and growth rate, so the interdependencies of these three traits need to be taken into account when studying the evolution of body size. The developmental mechanism connecting body size, development time and growth rate is complex in the only lepidopteran species studied in respect to this (Nijhout *et al.* 2010). Because of the complex interdependencies of the traits, the evolutionary trajectories of body size and development time are almost orthogonal within the space determined by the factors underlying both body size and development time, resulting in a conflict when both traits are simultaneously under directional selection (Nijhout *et al.* 2010). If development time is the trait under the most intense selection due to time constraints of seasonality, the consistent cogradient variation of development time with season length across species is understandable. The strong negative genetic correlation between development time and growth rate would then explain the consistent countergradient variation of growth rate with season length.

Simultaneous selection for short development time due to time constraints and fecundity selection for large body size would conflict, and, assuming the selection on development time to be stronger, interspecific variation in body size clines would be expected. In addition to the diversity of body size clines observed in study III, a diversity of body size clines has been found in other species of Lepidoptera as well (Blanckenhorn & Demont 2004 [data from Nylin & Svård 1991], Burke *et al.* 2005), which fits well with the expectation from the above mechanism.

3.2.2 Clinal variation in reproductive effort and resource allocation

According to the modelling results, a saw-tooth cline in reproductive effort (resource allocation to reproduction) should evolve across latitudes in insects with changing voltinism (IV, Fig. 4). Reproductive effort was predicted to be high in the northernmost populations in a species' distribution, and decrease southwards until the season becomes so long that time constraints for univoltine phenology are relaxed. Once the season becomes long enough for a partial nondiapausing generation to emerge, reproductive effort should suddenly increase, and thereafter decrease again southwards until the time constraints for bivoltine phenology are relaxed. The magnitude of the saw-tooth variation was dependent on the stage of density dependence (IV). Reproductive effort increased only slightly at the transition from univoltine to partially bivoltine phenology, if density dependence was included in the juvenile stage (Fig. 4 a), whereas it increased substantially, if juvenile stage was density independent (Fig. 4 b). When juvenile population is density dependent, the fitness value of the nondiapausing generation is reduced, because the number of survivors in the earliest offspring cohorts is relatively low, resulting in a relatively small nondiapausing generation. On the other hand, exponential increase in the number of descendants results in high mortality among offspring of the nondiapausing generation adults, which further reduces the fitness benefit of the nondiapausing generation. Although density dependence in the juvenile stage decreases the fitness value of early fecundity, it increases the fitness value of late-life offspring production as the offspring survival probability is relatively high in the latest cohorts, because they are the smallest ones. If there is no density dependence in the juvenile stage, timing of reproduction is the most important factor contributing to fitness. Thus, the fitness value of the nondiapausing generation is high, and high early fecundity is strongly selected for.

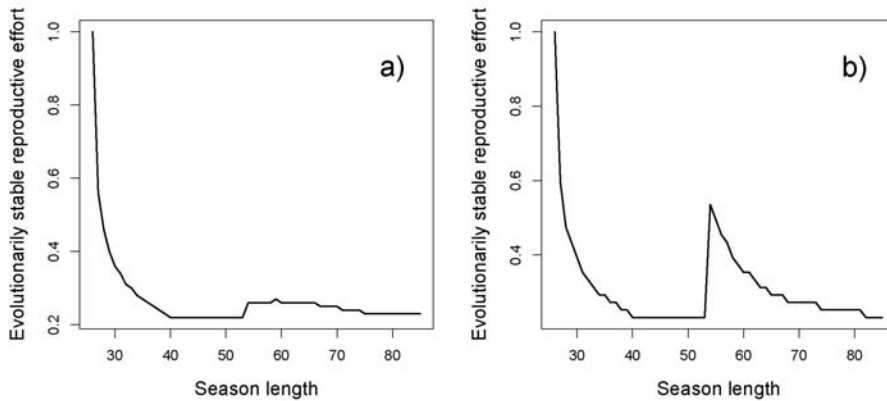


Fig. 4. Evolutionarily stable reproductive effort as a function of season length when juvenile mortality is density dependent (a), and when winter mortality is density dependent (b). Parameter values were $c_1 = 2.5$, $c_2 = 2$, $\omega = 15$, $f_{max} = 50$, $K = K_w = 30$, $t_1 = 15$, $t_2 = 10$ (see 2.2.4 for definition of the parameters). Phenology is univoltine when season length is less than 54 days, and bivoltine when season length is at least 54 days (IV, published by permission of University of Chicago Press).

The above predictions are based on the hypothesis that daily fecundity of an insect female is an increasing and concave function of the proportion of resources allocated to reproduction, whereas the probability of surviving until the next day is a decreasing and concave function of the proportion of resources allocated to reproduction. Accordingly, there is a trade-off between reproduction and survival, so increasing investment in current reproduction decreases the probability of future reproduction, which decreases the expected future fecundity. Life history theory predicts these trade-offs (Charlesworth 1980, Roff 1992, Stearns 1992), and there is firm empirical support for the genetic basis of these (Rose & Charlesworth 1981a, b, Zwaan *et al.* 1995, Tucić *et al.* 1996, 1997, Miyatake 1997, Gasser *et al.* 2000, reviews by Reznick 1985, Roff 1992), although a few studies have failed to demonstrate this (Mueller 1987; Partridge and Fowler 1992). In addition, the choice of concave functions to describe fecundity and survival in relation to reproductive effort seems realistic (Schaffer 1974). Thus, the hypothesis is realistic, and the predictions generally applicable.

Reproductive effort is expected to be genetically determined. Even though it was assumed to remain constant through the adult stage in the theoretical analysis (IV), it may vary with age, especially in income breeders that use resources

gathered at the adult stage for reproduction. However, reproductive effort in the beginning of the adult stage is positively correlated with early fecundity that is an important fitness component when time constraints are intense. Therefore, it is suffice to measure reproductive resource allocation at the time of adult eclosion to study whether the fecundity schedule shows adaptive variation in relation to time constraints. In holometabolous insects, reproductive resource allocation at adult eclosion is determined by the allocation of the larval-derived resources during metamorphosis. As the resources accumulated by the larva are allocated to several structures and functions, trade-offs are inevitable (van Noordwijk & de Jong 1986, de Jong & van Noordwijk 1992). There are two such trade-offs involved in the determination of reproductive effort at adult eclosion. First, resources are allocated between soma (exoskeleton and musculature) and nonsoma (energy reserves and reproductive organs) (Jervis *et al.* 2005, 2008). Secondly, the nonsomatic resources are allocated between initial eggs and initial energy reserves (Jervis *et al.* 2005, 2008).

Resource allocation to nonsoma, measured as the proportion of total body dry mass, total body carbon and total body nitrogen allocated to the abdomen (all of these corrected for body size; see V for details), was relatively high in partially bivoltine populations in *C. pusaria*, *C. clathrata* and *L. marginata* (Table 3, V). It was also relatively high in the northernmost univoltine populations in *C. exanthemata* and *C. clathrata* (Table 3, V). These observations fit well the theoretical predictions (Table 1 [F1], IV), but the predicted (Table 1 [F2], Fig. 4, IV) saw-tooth cline in resource allocation was not found (Table 3, V). Nevertheless, clinal variation in dry mass allocation to nonsoma in *L. marginata* is close to the predicted saw-tooth cline, with only the lack of latitudinal variation across the univoltine regions violating the prediction (Table 3, V). These results show that dry matter allocation to nonsoma versus soma showed clinal variation in each study species. Because insect eggs contain significant amounts of proteins and lipids (Briegel 1990, Diss *et al.* 1996, Karl *et al.* 2007, Geister *et al.* 2008, Arrese & Soulages 2010), analysis of these substances may better indicate how substances that can readily be used for reproduction are divided between nonsoma and soma. Analysis of protein and lipid allocation was successful only in *C. exanthemata* (see V). In this species, the proportion of total body proteins allocated to nonsoma was relatively high in partially bivoltine populations, supporting the predictions (V). There was no unambiguous evidence for clinal variation in the proportion of total body lipids allocated to nonsoma in this species (V). Despite statistical significance, the estimated clinal variation may be

only due to inaccuracy in the estimated allocation pattern in one of the studied regions.

There was positive allometry between body size and the proportions of dry mass, total body carbon and total body nitrogen allocated to nonsoma (V), which is in accordance with earlier observations (Karlsson & Wickman 1989a, b, 1990). Despite allometry, relative allocation to early reproduction does not need to increase with body size. Although absolute investment in early reproduction increases with body size, relative investment in early reproduction is predicted to decrease with body size in parasitoid wasps (Ellers & Jervis 2003), and there is empirical support for this prediction (Thorne *et al.* 2006, Jervis *et al.* 2003). If this is a general phenomenon in insects, or at least in holometabolous insects, it fits the predictions well (IV), as the individuals, especially in the *Cabera* species, tended to be the largest in regions where the fitness value of early fecundity was presumed to be the smallest (III).

No latitudinal variation was found in the division of nonsomatic resources between initial eggs and initial energy reserves as abdomen lipid:protein ratio was constant across latitudes in *C. exanthemata* (V). This analysis may, however, be confounded by possible variation in egg lipid:protein ratio. Although the available data on capital breeders suggests that egg composition is rather constant (Diss *et al.* 1996), it is known that egg composition varies in income breeders in relation to female body size and egg size (Briegel 1990, Karl *et al.* 2007). It is therefore possible that abdomen lipid:protein ratio does not measure resource allocation between initial eggs and initial energy reserves accurately enough to assess the resolution of the allocation trade-off. Abdomen lipid:protein ratio was independent of body size (V), but the trade-off between initial eggs and initial energy reserves may be confounded by variation in body size. Large females have more capital to be invested in both traits than small ones, which may obscure the trade-off (van Noordwijk & de Jong 1986, de Jong & van Noordwijk 1992). In accordance with this, both initial egg load and initial fat reserves are positively correlated with body size (Ellers 1996, Pexton & Mayhew 2002, Thorne *et al.* 2006, see also V). It is intriguing that the females from the time-constrained populations had more nonsomatic resources than would be predicted by their body size (V), which may slightly reduce the significance of the allocation trade-off of the nonsomatic resources.

4 Conclusions

Time constraints due to both seasonality (*i.e.*, season length) and voltinism (*i.e.*, the number of generations per season) affect the evolution of insect life histories. Season length sets the ultimate constraint, because the whole life cycle, or the whole life cycle of each generation emerging in multivoltine species, must be completed within the favourable time for growth and reproduction. The remaining part of the year must be spent in the species-specific developmental stage that is able to diapause (Tauber *et al.* 1986, Danks 1987). Time constraints have the strongest effect on life history evolution in species with long development times in relation to season length, that is, in species that can complete at most two or three generations per season (Chown & Gaston 1999). This is because the seasonal time constraints experienced by a particular generation decrease as the number of generations increases (Chown & Gaston 1999) and, consequently, the selection regime approaches the aseasonal one (Nylin & Gotthard 1998, Chown & Gaston 2010).

Because of the ultimate constraint set by season length, generation length should show cogradient variation with season length when the number of generations emerging is constant. However, at the season length where the number of generations emerging changes, an abrupt change in the time available per generation takes place, which is expected to give rise to the predicted saw-teeth in the clines of life history traits (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994, IV). Theoretical and empirical studies have concentrated on cases where at least one generation arises per season, but it is worth noting that the change in time constraints between univoltine and semivoltine (two-year development, *i.e.*, half a generation per season) phenologies is of the same magnitude as in the transition between univoltine and bivoltine phenologies. Earlier models of the evolution of saw-tooth clines assumed that, in multivoltine phenology, the generations share the season equally (Masaki 1967, 1972, Roff 1980, 1983, but see Iwasa *et al.* 1994 for plasticity in generation length in relation to resource availability), but as the results of this thesis suggest, it need not be the case (III). Individuals of different generations frequently have different life histories (Spence 1989, Wiklund *et al.* 1991, Blanckenhorn 1994, Fischer & Fiedler 2001, Karlsson & Johansson 2008, Karlsson *et al.* 2008, Larsdotter Mellström *et al.* 2010, Teder *et al.* 2010), most likely as an adaptive plasticity in relation to the developmental pathway induced (*i.e.*, diapause or direct development), and the consequent selection regime associated with the

developmental pathway (Gotthard & Berger 2010). Therefore, there may not be any saw-tooth pattern in the cline, when only individuals following a particular developmental pathway are studied, but the abrupt change in time available manifests itself only in the life history of individuals following the alternative developmental pathway.

The time constraints affect not only generation length or juvenile development time, but also other key life history traits either by a correlated response of selection acting on juvenile development time or direct selection on the traits. The former alternative emphasises the need to understand the genetic correlations among life history traits and the underlying physiological and developmental mechanisms. The latter alternative emphasises the fact that time constraints as such may generate selection on life history traits like age-specific fecundities independently of juvenile development time (see II, IV). On the other hand, selection due to time constraints is not the only selection pressure affecting life history traits, but there may be fecundity selection for large body size, for example. The evolution of traits like body size or adult lifespan may be constrained, if selection on them conflicts with selection on juvenile development time due to genetic and developmental correlations among the traits.

Theoretical studies on life history evolution in seasonal environments have traditionally focused on single traits (Roff 1980, 1983, Iwasa *et al.* 1994), although the actual “trait” under selection is the whole life history. The most important characteristics of a life history are the age at maturity and the expected age-specific fecundities thereafter. A comprehensive analysis should take these factors into account. In this thesis, the analyses in studies II and IV were close to this as the actual trait under selection was the adult fecundity schedule, but for simplicity, age at maturity was assumed constant (only random variation in II). These studies showed that the fitness value of a particular fecundity schedule depends on season length and voltinism. Consequently, clinal variation in the fecundity schedule is expected, if the fecundity schedule is allowed to vary continuously (IV). If the fecundity schedule shows discrete variation, the number of possible classes being small, polymorphism of different strategies defined by their fecundity schedules may emerge in particular conditions, and the frequencies of different strategies may show clinal variation (II). In study II, only two strategies were analysed, because of simplicity, and because of a lack of data for reliably estimating the fecundity schedule for each possible strategy defined by female mating frequency. In reality, the polymorphism in *P. napi* involves more than two strategies (Bergström *et al.* 2002, Välimäki & Kaitala 2006, II),

and even when monomorphism for polyandry was predicted, a polymorphism of polyandrous strategies may be possible.

Owing to clinal variation in fecundity schedule, clinal variation is also expected in traits like early fecundity, lifetime fecundity, adult lifespan and reproductive effort that are associated with fecundity schedule. Thus, in addition to the previously predicted clinal variation in age and size at maturity (Masaki 1967, 1972, Roff 1980, 1983, Iwasa *et al.* 1994), clinal variation is predicted to occur in several other life history traits. In fact, clinal variation would be expected in any trait that is associated with either age at maturity or fecundity schedule. The cline would show a saw-tooth pattern, if a change in voltinism reflects in the time constraints to the extent that it generates selection pressure on the trait itself or on a trait genetically correlated with that trait in the developmental pathway studied.

Early fecundity has a key role in relation to time constraints. It is selected for, if only early-life offspring production contributes to the nondiapause generation, resulting in a sudden increase in it at the transition from univoltine to bivoltine phenology (IV). This is congruent with earlier analyses showing that early reproduction is beneficial in growing populations (Roff 1992, Stearns 1992). Given that an insect population may be constant across years, the above statement seems contradictory. Nevertheless, there is no contradiction as early reproduction is associated with growth in population size within a season by facilitating an additional nondiapause generation. Only in the time-constrained univoltine populations, the fitness value of early reproduction is decoupled from population growth.

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