

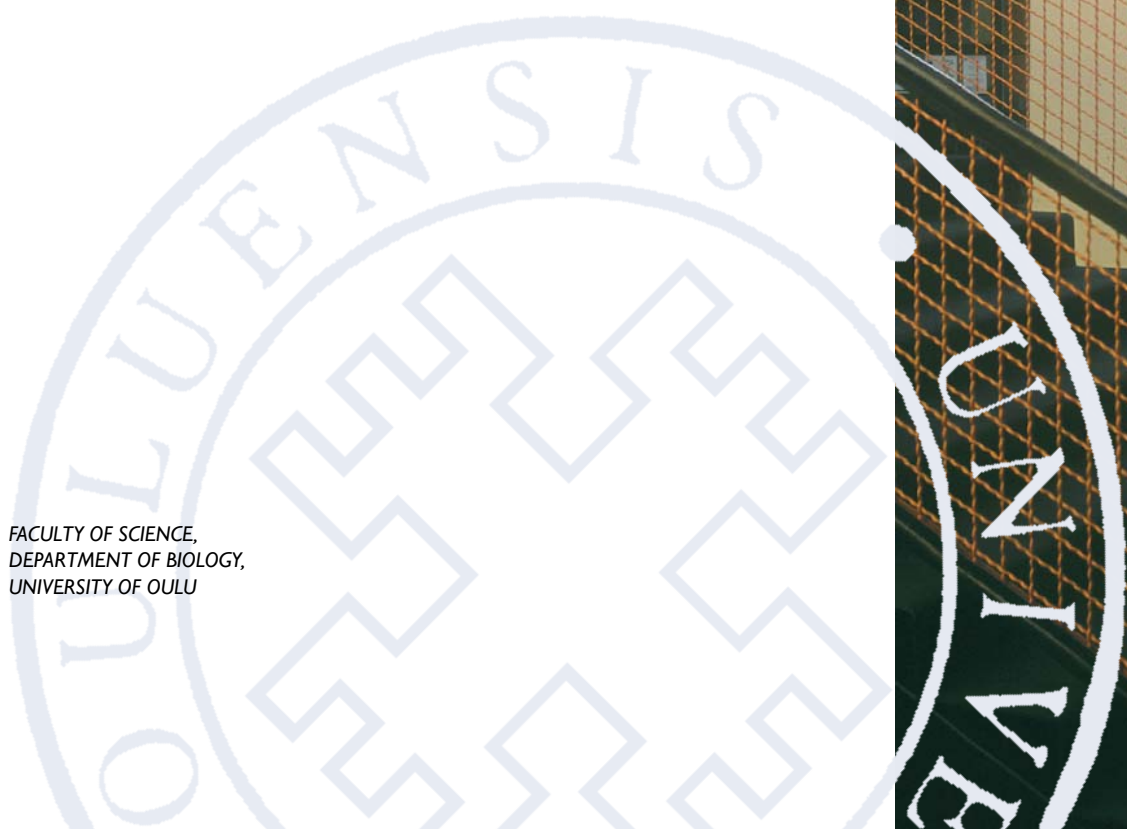
Panu Välimäki

REPRODUCTIVE TACTICS
IN BUTTERFLIES –
THE ADAPTIVE SIGNIFICANCE
OF MONANDRY VERSUS
POLYANDRY IN *PIERIS NAPI*

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

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PANU VÄLIMÄKI

**REPRODUCTIVE TACTICS IN
BUTTERFLIES – THE ADAPTIVE
SIGNIFICANCE OF MONANDRY
VERSUS POLYANDRY IN *PIERIS NAPI***

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Abstract

Females may either mate with one (monandry) or several (polyandry) males during a single breeding season. The polyandrous mating system has prompted numerous studies since the recognition of a widespread occurrence of mixed paternity among animals. Consequently, the benefits of polyandry have become well-established, and the female role in sexual selection upgraded. Females may gain both material and genetic benefits from multiple mating. Hence, the occurrence of polyandry is understandable, whereas monandry remains an evolutionary puzzle especially among species with male nutrient provisioning.

I studied both the life history variation among female mating tactics and the adaptive significance of monandry in varying environmental conditions in the green-veined white butterfly [*Pieris napi*, (L. 1758)], which is a predominantly polyandrous species with nuptial feeding. I used a combination of explicit laboratory experiments and field studies.

My results show that monandry and degrees of polyandry are distinct strategies with life history differences reaching beyond mating frequencies. Polyandry corresponded with a higher lifetime fecundity than monandry in *P. napi*. Polyandry was, however, associated with relatively low fecundity during the early days of reproduction. Thus, monandry is beneficial if time for reproduction is limited severely enough or other female traits or behaviours associated with polyandry are traded off against longevity. Due to temporal variation in reproductive rate among mating tactics, offspring of polyandrous females have less time to complete development. Accordingly, polyandrous females developed at a faster rate as larvae than monandrous ones under optimal conditions. Despite growth rate variation, monandrous females were more likely to contribute to additional summer generation in conditions that allow production of only a partial second generation, and thus monandry is favoured under these conditions. Genetic variation in female mating tactics will not only prevail if environmental conditions do not allow all individuals to contribute evenly to the directly breeding generation in bivoltine populations, but also if even the production of a single generation per year is time-limited.

A general conclusion would be that seasonality and unpredictability of fitness in the wild drives the evolution of optimal female mating tactics and promotes the maintenance genetic variation in mating frequencies, regardless of the direct benefits of nuptial feeding. Even if a high degree of polyandry would be the most profitable mating tactic in an average year, strong annual variation in weather conditions and the duration of summer may create possibilities for a temporally fluctuating selection that promotes a co-existence of different mating tactics because variance of fitness is likely increase with an increasing mating frequency.

Keywords: life history theory, seasonality, sexual selection, The green-veined white, voltinism

To my family,

Acknowledgements

I still remember a seven-year-old boy whose dream was to become professional lepidopterist, and, above all, to catch a death's head hawkmoth. The first part has become true, although probably not in the exact form that I imagined way back when. Unfortunately, the second dream still waits for its fulfilment. Anyway, I realise that even this achievement would not have been possible without help from numerous friends and colleagues.

First of all, I represent genuine gratitude for unconditional support to my parents, Sirkka and Olli. Actually, my father is to “blame” for turning my intrinsic bias into gradually evolving addiction towards entomology. The most amazing thing is, however, that you allowed me to spend not only days, but also nights in the wild since I was about eight years old. This is something that I would never allow my own children to do, but you didn't hesitate. I respected that trust, although, I admit, all things done during the nights spent in the wild were not exclusively aimed at entomology.

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Oulu April 2007

Panu Välimäki

List of original papers

The thesis is based on the following papers, which are referred to by their Roman numerals.

- I Välimäki P & Kaitala A (2006) Does a lack of mating opportunities explain monandry in the green-veined white butterfly (*Pieris napi*)? – *Oikos* 115: 110–116.
- II Välimäki P & Kaitala A (2007) Male properties do not effect spatial variation in female mating frequency in a nuptial gift-giving butterfly *Pieris napi* (Manuscript).
- III Välimäki P, Kaitala A & Kokko H (2006) Temporal patterns in reproduction may explain variation in mating frequencies in the green-veined white butterfly *Pieris napi*. – *Behavioral Ecology and Sociobiology* 61: 99–107.
- IV Välimäki P & Kaitala A (2007) Life history trade-offs in relation to the degree of polyandry and developmental pathway in *Pieris napi* (Lepidoptera, Pieridae). – *Oikos* (In print).
- V Välimäki P, Jääskeläinen L, Kivelä S & Kaitala A (2007) Seasonality may promote polymorphism in female mating tactics in a bivoltine butterfly *Pieris napi* (Pieridae) (Manuscript).

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1 Introduction

Females may either mate with one (monandry) or several (polyandry) males during a single breeding season, which affects the level of sexual selection and reflects on animal behaviour and life histories (Parker 1970, Thornhill & Alcock 1983, Eberhard 1996, Birkhead & Møller 1998). Mixed paternity among offspring, and thus polyandry, is a common phenomenon in the animal kingdom, and it has been reported in such taxa as molluscs, arthropods, fish, reptiles including birds, and mammals (Birkhead & Møller 1998, Arnqvist & Rowe 2005). Females may gain indirect (i.e., offspring of higher quality) and/or direct (i.e., increased offspring production) benefits from multiple mating (e.g., Vahed 1998, Zeh & Zeh 1996, Arnqvist & Nilsson 2000, Jennions & Petrie 2000). However, there is considerable variation in female mating frequency both across and within species (Drummond 1984, Andersson 1994, Birkhead & Møller 1998). It is becoming increasingly clear that optimal female mating frequency is determined by multiple costs and benefits of mating that interact with often conflicting interests of sexes (Andersson 1994, Arnqvist & Rowe 2005). Due to the positive net effects of multiple mating, a widespread occurrence of polyandry is understandable, whereas monandry remains an evolutionary puzzle especially among species with male nutrient provisioning (Arnqvist & Nilsson 2000).

1.1 Determinants of female mating frequencies

The indirect benefits for a female from polyandry are often connected with an acquisition of good genes, or an increased genetic diversity among her offspring (Yasui 1988, Zeh & Zeh 2001). Both the direct and indirect benefits may be mediated by an increased genetic compatibility, and they may arise from the mere presence of diverse sperm in the female reproductive tract (Zeh & Zeh 1996, 1997, Brown 1997, Tregenza & Wedell 1998, 2000, Jennions & Petrie 2000, Fedorka & Mousseau 2002, Dunn *et al.* 2005). Direct benefits may also arise from a replenishment of sperm storages (Gromko *et al.* 1984, Wedell *et al.* 2002a, Wang & Davis 2006) and other aspects of mating, besides a sperm transfer that enhance a female's egg production (Opp & Prokopy 1986, Simmons 2001). Most importantly, however, the evolution of a polyandrous mating system is not surprising in species where males provide females with nutrition in the form of items of nutritional value and/or accessory gland substances transferred at mating, which increase female fitness (Eberhard & Cordero 1995, Vahed 1998,

Arnqvist & Nilsson 2000). In the case of direct benefits, indirect benefits are not needed to explain the evolution of polyandry (Yasui 1988). On the other hand, possibilities for indirect genetic benefits are inherently present every time females engage themselves in matings with multiple partners (Jennions & Petrie 2000).

Although multiple mating may be beneficial, it may incur costs for a female as well. Mating and associated behaviour (including both pre- and post-mating processes) are both time-consuming and energetically demanding, and these costs are no doubt the most general ones (Daly 1978, Thornhill & Alcock 1983, Martens & Rehfeldt 1989, Watson *et al.* 1998). There is also a growing body of evidence that females may be more vulnerable to predators during reproductive activities, due to increased conspicuousness or decreased mobility and attentiveness of mating pairs (Ward 1986, Wing 1988, Arnqvist 1989, Magnhagen 1991, Fairbairn 1993, Rowe 1994). Moreover, mating is the source of sexually transmitted diseases (Hurst *et al.* 1995, Thrall *et al.* 2000).

Reproduction in species with internal fertilisation necessarily involves some co-operation between the sexes, but still, the evolutionary interests of males and females concerning matings do not need to coincide. Even though females gain fitness benefits from polyandry, the benefits acquired through additional matings will generally accumulate at a faster rate for males (Bateman 1948, Parker 1970, Trivers 1972). This basic asymmetry promotes both male and female adaptations that tend to change average mating frequencies towards their own optima (Arnqvist & Rowe 2005). In pond skaters, surplus matings are costly for females, but males are able to coerce females to mate, and as a consequence, females may mate repeatedly for reasons of convenience, if avoiding matings is more costly than accepting courting males to mate (Arnqvist 1989, Fairbairn 1993, Rowe 1994). On the other hand, whenever there is a risk that females might mate with more than one male during a single breeding season, male characteristics that prevent or delay the remating of their mates are favoured due to the males' need to assure paternity (Birkhead & Møller 1998). These male properties include behavioural, morphological and physiological adaptations that may ultimately reduce female fitness (Fowler & Partridge 1989, Rice 1996, Arnqvist & Rowe 2005). In the fruit fly, *Drosophila melanogaster*, male ejaculates contain compounds that appear to be toxic to the opposite sex, decreasing female longevity (Chapman *et al.* 1995). Similarly, females of the bean weevil may suffer from a reduced lifespan due to genital damage induced by the spiny male genitalia (Crudgington & Siva-Jothy 2000). In social bumble bees,

males provide females with a mating plug during mating, and thus most females remain monandrous (Baer *et al.* 2001, Sauter *et al.* 2001). This contradicts female interests of any fitness benefits achievable by multiple mating (Baer & Schmid-Hempel 1999).

1.2 Polyandry and monandry in butterflies

In most butterflies and moths, females are regarded as capital breeders (Boggs 1992, Stearns 1992), which means that female reproductive output is largely dependent on the resources they gain during the larval period. In support of this, many studies show that female fecundity is generally correlated with body mass both within and among species (Haukioja & Neuvonen 1985, Wickman & Karlsson 1989, Karlsson & Wickman 1990). In quite many species, however, females may be partly characterised as income breeders, because their reproductive output is determined not only by larval-derived resources but also by resources acquired during the adult stage. The latter include resources gained from feeding (Gilbert 1972, Pivnick & McNeil 1987, Braby & Jones 1995, O'Brien *et al.* 2000), and those ones that females receive from males within a spermatophore at mating (Boggs & Gilbert 1979, Kaitala & Wiklund 1994).

Female mating strategies vary from strict monandry to a high degree of polyandry both among and within butterfly species (Drummond 1984, Wiklund & Forsberg 1991, Gage 1994, Kaitala & Wiklund 1994, Simmons 2001). The ultimate reason for female multiple mating in butterflies seems to be the acquisition of nutrients from the male spermatophore (Boggs 1990). In accordance, the degree of polyandry correlates positively with relative spermatophore size across species (Svärd & Wiklund 1989 and references therein). Females in at least the *Colias* (Boggs & Gilbert 1979), *Papilio* (Watanabe 1988), *Danaus* (Oberhauser 1989) and *Pieris* (Wiklund *et al.* 1993) genera utilise male-derived nutritious accessory gland substances. These male-derived substances, often referred to as nuptial gifts, increase female fitness by affecting directly upon female egg production, lifespan or offspring quality (Boggs & Gilbert 1979, Boggs & Watt 1981, Watanabe 1988, Oberhauser 1989, Kaitala & Wiklund 1994, Wiklund *et al.* 2001). Increased offspring production may also be partly mediated by male-induced changes in female resource allocation, so that females mating several times allocate more resources to reproduction at the expense of somatic maintenance (Karlsson 1998, Stjernholm & Karlsson 2000). Females' needs to replenish their sperm storages and male

coercion do not offer adequate explanations for the polyandrous mating system in butterflies since, as a rule, one spermatophore contains enough sperm to fertilise all of a female butterfly's eggs (Sims 1979, Lederhouse 1981, Svård & Wiklund 1988, Wiklund *et al.* 1993) and, with a one exception, the monarch butterfly (*Danaus plexippus*), females are able to resist male mating attempts (Svård & Wiklund 1988, Bergström & Wiklund 2005).

1.3 Variation in female mating tactics in nuptial gift-giving butterflies

In nuptial gift-giving species, polyandrous and monandrous females follow different life histories, polyandrous ones being dependent on male-derived nutrients to realise their reproductive output, while monandrous ones rely on their own resources for offspring production (Wedell *et al.* 2002b). There is a widespread variation in the degree of polyandry among females, even if nuptial feeding is involved (Svård & Wiklund 1988, Wiklund & Forsberg 1991). In the pierid butterfly, *Pieris napi*, female mating frequency varies from one up to five, the proportion of females that mate only once and twice being approximately 12% and 35%, respectively (Bergström *et al.* 2002). Although males' ability for nutrient provisioning offers a plausible explanation for variation in mating strategies across species, it cannot explain variation in mating tactics among individual females within a species. Energetic costs of mating (Watson *et al.* 1998), toxic properties of male ejaculates (Chapman *et al.* 1995, but see Kemp & Rutowski 2004) and the risk of physical injury (Crudgington & Siva-Jothy 2000) probably play a minor role in the evolution of mating frequencies in nuptial gift-giving species, since the net effect of multiple mating on female fitness is generally positive (Vahed 1998, Arnqvist & Nilsson 2000).

The maintenance of low mating frequencies requires that the direct benefits of polyandry are not as pronounced over the long-term, as laboratory experiments within a generation suggest (see Arnqvist & Nilsson 2000 for review). The geometric-mean is the natural measure of long-term fitness under temporal variation on a scale of generations (Dempster 1955, Seger & Brockmann 1987). The geometric-mean principle states that, of competing morphs, the morph with the highest geometric-mean fitness will prevail (Seger & Brockmann 1987). A determination of the geometric-mean values of reproductive success of each mating tactic would require long-term data on the realised fecundity of females in the wild, which is practically impossible. Anyway, the geometric-mean is very

sensitive to occasional small values, and thus, if there is any variation, it will be less than an arithmetic mean. This implies that the variance of success is important in addition to average success (Gillespie 1977, Seger & Brockmann 1987). Therefore, variation in female mating tactics may prevail if there is an evolutionary trade-off between expected fitness and the variance of fitness. Put in other words, given that monandry yields relative constant reproductive output, any factor that increases variation in realised fecundity among polyandrous females between generations would tend to promote a co-existence of different mating tactics, regardless of the high reproductive potential associated with polyandry.

Because the potential benefits of polyandry are realised only if remating is possible, a variation in female mating tactics could be maintained if some females face a lack of mating opportunities, or if males prevent females from remating in the wild (Sauter *et al.* 2001, Wedell *et al.* 2002b, Kokko & Mappes 2005). A lack of mating opportunities may be promoted by harsh weather conditions that render butterfly activity impossible. The immediate consequence would be that female mating frequency decreases and the prevalence of monandry increases towards the north. This is because the northern environment is characterised by a range of features that appear to be disadvantageous to insects in comparison with those of more southern latitudes, the most important ones being a short summer and the year-round low temperature, which limits development and reproduction (Strathdee & Bale 1998). At least in northern Scandinavia, the sunny weather obligatory to butterfly reproduction is irregular, and frequently interrupted by cold and rainy periods. A lack of mating opportunities may also be caused by an unfavourable operational sex ratio. This seems not to be a generally applicable explanation, however, since males are able to mate more often than females even in species with large nuptial gifts that are costly to produce (Svärd & Wiklund 1989, Wiklund *et al.* 1998).

Variation in female mating tactics will also follow if males are able to suppress female mating frequency below their optimum. The simultaneous presence of two or more ejaculates in the female reproductive organs will result in sperm competition among males and create chances for post-copulatory (i.e., cryptic) female choice (Parker 1970, Eberhard & Cordero 1995). Both processes may drive a wide variety of evolutionary changes in males and their reproductive investment, including also ones that are likely to have sexually antagonistic implications (Eberhard 1996, Birkhead & Møller 1998, Arnqvist & Rowe 2005). In some pierids, female remating behaviour is dependent on the remaining size of

the spermatophore, so that they become more active when the last ejaculate is absorbed to a certain degree (Sugawara 1979, Rutowski *et al.* 1981). Accordingly, a larger ejaculate induces a longer female refractory period than a smaller one in butterflies (Sugawara 1979, Boggs 1981, Rutowski 1981, Oberhauser 1989, Kaitala & Wiklund 1994). Besides sperm, male ejaculates contain also chemical compounds, or anti-aphrodisiacs, that render females unattractive to other males, and hence decrease female receptivity temporarily (Gilbert 1976, Andersson *et al.* 2000). Male-induced prolonged remating interval will gradually turn into a sexual conflict because females will eventually want to remate to achieve the benefits of polyandry.

The reproductive output of females is generally a combination of fertility, reproductive rate and life span. Life spans of butterflies are relatively short and unpredictable, for example, due to predation (Chew 1981, Scott 1986, Dennis 1993), and there is always a risk of weather conditions inappropriate for reproduction. Thus, the actual reproductive output of a female may be more dependent on her egg-laying rate than on her fertility as such. Polyandry may be coupled with a low egg-laying rate for two reasons. Firstly, a low early fecundity of polyandrous females compared to monandrous ones may arise from the time cost of remating (e.g., Daly 1978) because egg-laying and mating are mutually exclusive. Alternatively, it may arise from polyandrous females' physiological need to mate according to their "intrinsic" mating frequency to realise their potential fecundity (Stjernholm & Karlsson 2000, Wedell *et al.* 2002b, see also Wiklund *et al.* 2001). Either way, low female mating frequencies could be regarded as adaptive in areas with weather conditions that reduce the time for reproduction so that polyandrous females can either never or only on the most favourable years take full advantage of their higher lifetime fecundity. Again, the prevalence of monandry may increase with an increasing latitude. Despite a shared prediction with the hypothesis based on a lack of mating opportunities, these two hypotheses are separable based on distinct processes that underlie the pattern. Moreover, it should be noted that these two processes are not mutually exclusive, and thus they may occur at the same time.

A low early egg-laying rate of polyandrous females (III) may have implications on female life histories that explain the maintenance of varying mating tactics in seasonal environments, where favourable and unfavourable times for insect reproduction recur in regular annual rhythm. Firstly, female growth rate is expected to be positively correlated with the degree of polyandry, which in turn may result in biased juvenile mortality. In this scenario, a variation

in the egg-laying rate and consequent negative correlation between female mating frequency and time available for development would be the ultimate reasons for variation in juvenile development among mating tactics. Given that larvae of at least such butterflies that produce more than one generation per year are time-constrained in seasonal environments (Wiklund *et al.* 1991, Wiklund *et al.* 1992), polyandry should be associated with a short larval period. Generally, there is a trade-off between development time and achievable body size, which means that a short juvenile period results in small size while a larger size can be achieved only by a prolonged juvenile period (Roff 1992, Stearns 1992). Although female fecundity is often correlated with body size (Haukioja & Neuvonen 1985, Wickman & Karlsson 1989, Karlsson & Wickman 1990, Honěk 1993), maturing at suboptimal size may not be a problem for polyandrous females in nuptial gift-giving species due to nutrient compensation provided by males (Leimar *et al.* 1994). The assumption of an age/size trade-off is, however, not even always met (Nylín *et al.* 1989, Reavey & Lawton 1991, Wiklund & Forsberg 1991, Wiklund *et al.* 1991, Nylín *et al.* 1993, Nylín 1994, Abrams *et al.* 1996, Nylín & Gotthard 1998). Hence, there is a possibility that polyandrous females mature within a shorter period than monandrous ones, but pay no cost of maturing at a suboptimal size. Either way, offspring of polyandrous females may suffer from increased mortality due to the physiological costs of fast development at least during suboptimal weather conditions or under food shortage (Clutton-Brock *et al.* 1985, Conover & Present 1990, Stockhoff 1991, Wiklund *et al.* 1991, Gotthard *et al.* 1994).

Secondly, variation in the reproductive rate among females and the relatively long egg-laying period of polyandrous females (III) may create variation in voltinism, i.e. the number of generations produced within a season. In seasonal environments, development and reproduction have to be synchronised with favourable times of year and diapause with unfavourable periods, and thus, production of more than one generation a year involves a choice between alternative developmental pathways (diapause or direct development). Due to severe time constraints in seasonal environments (Wiklund *et al.* 1991, Wiklund *et al.* 1992), individuals that start to reproduce the earliest in spring may also be the ones that contribute proportionally more to the second generation than individuals whose offspring are produced later on (see also Vepsäläinen 1974, Seger & Brockmann 1987). This may serve as a counter-selection against polyandry in potentially multivoltine insects, because individuals, or more precisely genotypes, that are able to complete additional generations successfully

within a given time have a higher intrinsic rate of increase than the ones giving rise to a lower number of generations.

Table 1. Hypotheses explaining co-existence of varying female mating tactics, and experiments conducted with their specific predictions (mf = mating frequency, F = female, M = male, s = south, n = north).

Study	Hypothesis	Experiment	Prediction
I	Mating tactics are maintained by a lack of mates	<ol style="list-style-type: none"> mf distribution between wild and laboratory females mf distribution between populations 	<ol style="list-style-type: none"> average mf: laboratory (lab) > wild prevalence of monandry: lab < wild average mf: south > north prevalence of monandry: south < north
II	Spatial variation in mating tactics is maintained by male properties	<ol style="list-style-type: none"> the effect of male size on female remating interval spatial variation in the level of sexual dimorphism spatial variation in ejaculate contents 	<ol style="list-style-type: none"> remating interval: large male > small male ratio of male and female size: north > south average mf: $(F_s \times M_s) > (F_s \times M_n)$, $(F_n \times M_n) < (F_n \times M_s)$
III	Mating tactics are maintained by temporal variation in reproductive rate	<ol style="list-style-type: none"> temporal variation in egg-laying rate among females with different mating tactics either due to time or life history costs 	<ol style="list-style-type: none"> early egg-laying rate: polyandry < monandry daily fecundity: monandry = non-mating polyandry > mating polyandry (time cost of mating) daily fecundity: monandry > non-mating polyandry = mating polyandry (life history cost) daily fecundity: monandry > non-mating polyandry > mating polyandry (time cost + life history cost)
IV	Mating tactics are maintained by physiological costs of high juvenile growth rate	<ol style="list-style-type: none"> variation in juvenile growth rate among females with different mating tactics offspring performance and mortality under high density or low diet quality 	<ol style="list-style-type: none"> juvenile growth rate: polyandry > monandry final size: polyandry < monandry development time: polyandry > monandry survival: polyandry < monandry
V	Mating tactics are maintained by seasonality	<ol style="list-style-type: none"> variation in relative contribution to the 2nd generation among females with different mating tactics 	<ol style="list-style-type: none"> average mf: 1st gen. > 2nd gen. prevalence of monandry: 1st gen. < 2nd gen.

1.4 The aims of the study

The polyandrous mating system has prompted numerous studies since the recognition of a widespread occurrence of mixed paternity among animals (Keller & Reeve 1995, Zeh & Zeh 1996, 2001, Sherman *et al.* 1998, Yasui 1998, Vahed 1998, Arnqvist & Nilsson 2000, Jennions & Petrie 2000, Hosken & Stockley 2003, Simmons 2005). As a consequence, the benefits of polyandry have become well-established, and the female role in sexual selection upgraded. Meanwhile, monandry has achieved much less attention, at least outside the context of sexual conflict. Hence, the factors affecting the maintenance of monandry are still poorly known especially in species with nuptial feeding.

This thesis concentrates on both the life history variation among female mating tactics and the adaptive significance of monandry in varying environmental conditions in the green-veined white butterfly [*Pieris napi*, (L. 1758)]. I use a combination of laboratory experiments and field studies. Specifically, I study if variation in female mating tactics and spatial variation in the degree of polyandry is due to a lack of mating opportunities promoted by climatic factors (I) or whether conjectures of sexually antagonistic co-evolution apply (II). I also explore variation in reproductive rate among females with varying mating tactics (III), and its implications on individual development and survival under various selection pressures (IV). Finally, I study if the adaptive significance of monandry and polyandry depends on voltinism in seasonal environments (V). The questions studied are briefly summarised in table 1, and predictions further explained in 2.3 (see below).

2 Material and methods

2.1 The study species

P. napi is among the most abundant butterflies in Finland, and its geographical distribution extends up to northern Lapland (Huldén *et al.* 2000). The species has two alternative life cycles, which are largely determined by the length of the day so that larvae that face longer than the critical day length at hatching will develop directly into adults, while those facing a shorter day will develop into over-wintering pupae (Wiklund *et al.* 1991). The critical day length, like generally in insects, varies spatially so that individuals enter a developmental pathway that results in the over-wintering stage of development at a locally appropriate time (Tauber *et al.* 1986, Nylin *et al.* 1989). In southern Finland, *P. napi* is predominantly bivoltine with two complete generations per year. The first generation flies from mid-May to mid-June and gives rise to the second generation that flies from mid-July to the end of August. Offspring of the second generation develop into pupae that do not hatch until the next spring after diapause. In the north, the species is strictly univoltine with only one generation flying in late June and early July in spite of the light conditions that promote direct development in more southern latitudes. In central Finland, there is a transition region where there is only a partial second generation, which means that the additional summer generation is irregular and scarcer than the first one in spring.

P. napi is a predominantly polyandrous species with male nutrient provisioning. Nutritious male accessory gland products transferred within a spermatophore are incorporated in both female soma and eggs (Wiklund *et al.* 1993). Highly polyandrous females have about 1.6 times higher lifetime fecundity and they live longer than monandrous ones (Wiklund *et al.* 1993, 1998, Kaitala & Wiklund 1994, Karlsson 1998, Bergström & Wiklund 2002). Interestingly, female mating tactics in *P. napi* vary from strict monandry to a high degree of polyandry in the wild (Bergström *et al.* 2002). The degree of polyandry has a genetic component, and it is a highly heritable trait (Wedell *et al.* 2002b), although traits that have direct effects on fecundity do not usually show additive genetic variation (Mousseau & Roff 1987, Falconer 1989).

For a male, an enlarged spermatophore averaging 15% of male body weight represents a costly investment, and its volume is strongly correlated with male

size (Forsberg & Wiklund 1989, Svård & Wiklund 1989, Bissoondath & Wiklund 1996). Females that receive a large spermatophore delay remating longer than ones receiving a smaller spermatophore (Kaitala & Wiklund 1994), and a male who has delivered the largest spermatophore will enjoy the highest fertilisation success (Bissoondath & Wiklund 1997). Besides sperm and nutritious accessory gland substances, male ejaculates contain also anti-aphrodisiacs that render females unattractive to other males (Andersson *et al.* 2000, Andersson *et al.* 2004).

2.2 Preparation for the experiments

2.2.1 Origin of butterflies

To study reasons for variation in female mating tactics, I used butterflies that were offspring of wild females captured either from northern (67°–69°N:20°–26°E) or southern (59°–60°N:23°–25°E) Finland (I–IV) with three exceptions, in which I used either wild-caught females from northern (I) or southern and central Finland (V) or artificially selected butterflies that derived from some Swedish populations (III). Artificial selection lines consisted of females with either a high (HMR) or a low (LMR) intrinsic mating rate, which allowed the categorisation of females into polyandrous and monandrous ones beforehand when comparing the life history characteristics of mating tactics (see Bergström 2004, III for selection procedure). The southern populations were predominantly bivoltine, while the northern ones were strictly univoltine. Populations from central Finland (64°–65°N: 25°–26°E) originated from the region where environmental conditions allow the production of only a partial second generation.

2.2.2 Rearing procedure and measured variables

Females used in the experiments were reared individually in plastic cups (0.2 l) to obtain a sufficient number of butterflies whose mating pattern could not be affected by poor larval conditions, except in IV where some larvae were exposed to high density or low food quality treatments. Additional larvae were reared in groups of 10–20 in larger buckets (10 l) to produce a surplus of males that were used to determine the intrinsic mating frequencies of individually reared females. Larvae deriving from different populations were kept separately all the times and

reared on the fresh leaves of a natural host, *Thlaspi arvense*, in a ca. 20°C and 10h:14h light:dark cycle to prevent direct development (I–III). Females that derived from artificially selected HMR and LMR lines were reared on *Alliaria petiolata* (Bergström 2004, III). Larvae used to explore life history variation among mating tactics were reared in a ca. 20°C and they faced a light rhythm of 16h:8h (light:dark) (IV). Day length was set at 16 hours to simulate conditions that allow direct development in the southern, but not in the northern populations. Over-wintering lasted for nine months and took place in a cold room at 4–6°C (I–IV).

From the individually reared butterflies, I recorded durations of larval and pupal periods, pupal mass, growth rate (GR) and sex (II, IV). Basically, I was interested in the relative differences between mating tactics only, and thus all variables were transformed into relative values by dividing the value of individual i by a population mean of the same variable (relative growth rate $RGR_{ij} = RG_i / \text{mean RG of population } j$) (IV). By this transformation, I deducted possible confounding variation due to experimental effects and body size variation in absolute values, especially among the northern and southern populations. Durations of larval and pupal periods were defined as the days from the hatching of an egg to pupation of a larva and from the pupation to adult emergence, respectively. For over-wintering individuals, the length of the pupal period was defined as the days since the termination of diapause to adult emergence. Pupal mass was measured with a precision balance (Mettler Toledo MT 5) with an accuracy of 0.01 mg. Growth rate was obtained by dividing the pupal mass by the duration of the larval period. The sex of each pupa was determined based on genital scars. In *P. napi*, as in other Ditrysia, males have a genital scar only on the 9th abdominal segment, while in females, both the 8th and the 9th segments have a scar (Scoble 1992).

2.2.3 Determination of female mating tactics

The mating tactic of each female was determined by exposing females to an abundance of males in flight cages (0.65×0.65×0.65 m³) that were placed in a laboratory with large windows so that butterflies could enjoy natural sunlight during the day time. Females that were either marked individually (I–IV) or based on their origin (V) were released into the flight cages provided with fresh shoots of natural hosts for egg-laying and sources for adults to feed on. I used *Arabis alpina* (III), *Erysimum cheiranthoides* (V), *E. strictum* (III), *Rorippa*

palustris (III, V) and *T. arvensis* (I–V) as egg-laying substrates. For adult feeding, I used natural nectar sources and 20 % liquid honey solution that was either added on inflorescence or soaked in cotton wool tips of artificial flowers. Butterflies faced slightly varying light rhythm depending on the experiment [8h:16h (I–IV); 7h:17h (II, V); 10h:14h (III)] and a temperature regime of 30:20°C (light:dark). Females were constantly accompanied by at least 1.5 (range 1.5–3) times more males of either the same (I–V) or different origin (II). The maximum number of butterflies per cage was either 3 (III), 30 (I, II, IV) or 50 (II, V). Under these circumstances, I let the females to mate, feed and lay eggs until they died. When expedient for the study, the cages were inspected every 20 minutes for matings. Finally, I confirmed the intrinsic mating frequency of each female by spermatophore counts (see below).

Given that males can mate at a higher rate than females (Wiklund *et al.* 1998), offered sex ratio ensured that females had an opportunity to mate as many times as they wanted. Since female mating frequency is also affected by the mating history of the previous mate (Kaitala & Wiklund 1994), I substituted each male immediately after copulation or alternatively every third day if mating had not been detected by then. I used either virgin males or males that had not mated during the three preceding days, which is justifiable because males can produce full-sized spermatophore within the given time (Svärd & Wiklund 1989).

2.2.4 Spermatophore counts

Butterflies, in general, are well-suited for studying female mating frequencies because spermatophore (one is delivered at each mating) residues remain within females *bursa copulatrix* throughout her life, and those can be routinely counted under microscope by dissecting female abdomen (Drummond 1984). Mating frequencies of both wild females (I) and females that mated in the laboratory (I–V) were determined by spermatophore counts. This way I could diminish any bias due to undetected matings.

2.3 Description of the experiments

2.3.1 Males as a limited resource for females in the wild

To study whether variation in female mating tactics is maintained due to a lack of mating opportunities and if this refers to spatial variation in mating frequency distribution among populations, I first exposed reared females with varying origin to the abundance of males in the laboratory (I). Experimental butterflies were derived from four southern (N = 99) and four northern (N = 100) populations. If the maintenance of low mating frequencies is simply due to the detrimental effects of forced monandry, the observed proportion of singly mated females should be higher and average mating frequency lower within a population in the wild than in laboratory conditions (Table 1). For testing this, I collected old females (N = 84) from one of the northern populations during 2001–2004 and compared their mating frequency with that of the ones of the same origin (N = 46) in laboratory conditions with an unlimited mate supply. The age of wild-caught females was determined based on their wing wear on a scale of 1–6 (intact–very worn). This classification correlates with butterfly age with reasonable accuracy since wing scales are not being renewed as a butterfly ages (Bergström *et al.* 2002). To ensure that wild-caught females had had enough time to mate in the field, only females that were classified into classes 4–6 were included in the analyses.

2.3.2 Female mating tactics and conflicting interests of sexes

From a sexual conflict point of view, a low average female mating frequency and high prevalence of monandry in the northern populations (I) may be due to spatial variation in male manipulative ability, which results in suboptimal mating frequency of some polyandrous females. Males may control remating behaviour of females either by ejaculate size or contents. I studied these possibilities by exploring spatial variation in the level of sexual dimorphism and the effect of male origin on female mating frequency (II). I used butterflies that derived from four southern and four northern populations that show latitudinal variation in the average degree of polyandry (I). From each population, I produced two consecutive hibernating generations. F₁ butterflies (N = 512, males: N = 250, females: N = 262) were used to test spatial variation in the level of sexual

dimorphism, which is informative due to the correlation between male size and ejaculate volume (Forsberg & Wiklund 1989, Svård & Wiklund 1989, Bissoondath & Wiklund 1996). To explore the effects of male size on female remating interval between the first and the second mating, I allowed some northern F_1 females ($N = 68$) to mate freely with virgin males of varying size in the laboratory. F_2 females ($N = 160$, south: $N = 80$, north: $N = 80$) were used to study possible variation in ejaculate contents between southern and northern males. This was done with a cross-breeding experiment in the laboratory. I used only middle-sized males to diminish variation in the amount of spermatophore material received per mating among females (see Wiklund & Kaitala 1995). Females from the same area (south/north) were divided evenly between two treatments (male of the same origin vs. male of different origin). Thus, I ended up with four experimental groups: southern females accompanied by southern males ($F_s \times M_s$), southern females accompanied by northern males ($F_s \times M_n$), northern females accompanied by northern males ($F_n \times M_n$) and northern females accompanied by southern males ($F_n \times M_s$).

I predicted that if low mating frequencies of northern females are due to spatial variation in ejaculate size, northern males should be bigger in relation to co-existing females than southern ones. If male manipulative ability manifests itself via ejaculate contents, southern females accompanied by northern males should have a lower mating frequency than while mating with males of the same origin. In contrast, mating frequency of northern females should increase if they mate with southern males, compared to their realised mating frequency with northern males. Female influence would be indicated if females maintain a similar average mating frequency irrespective of male origin (Table 1).

2.3.3 Temporal variation in egg-laying rate among females

To study if the maintenance of variation in female mating tactics is due to a low reproductive rate associated with polyandry, I explored temporal variation in the egg-laying rate between females with varying mating tactics in the laboratory (III). I used both wild-type females ($N = 21$) with a varying mating rate and females that derived from artificially selected LMR and HMR lines. The average mating frequency of artificially selected HMR females ($N = 12$) was 3.00 ± 0.17 (S.E.), whereas LMR females ($N = 12$) mated 1.17 ± 0.11 times. Wild-type females were derived from 47 females that were captured from northern Finland. Northern females were used simply because monandrous and

polyandrous females are inseparable by external appearance and the probability of obtaining monandrous females into a random sample appears to increase with latitude (I). To obtain mating frequency variation of similar magnitude between wild-type LMR and HMR females as between the artificially selected lines, the 6 slowest females to remate and 9 females that mated 3 or 4 times were included in wild-type LMR and HMR groups, respectively. Wild-type HMR females mated 3.44 ± 0.18 times on average, whereas the average mating frequency of LMR females was 1.16 ± 0.17 . Each female had a flight cage of her own, and the number of eggs laid by each female was calculated daily. Secondly, I related the reproductive success of females from the selection lines to a model that predicts realised female fecundity in relation to mating tactic by taking the unpredictability of effective lifespan into account (see 3.5.1).

I predicted that if the maintenance of monandry is due to a temporal variation in the egg-laying rate among females with different mating tactics, monandry should yield a higher early fecundity than polyandry (Table 1). If this difference arises from the time costs of mating, the daily fecundity of both non-mating polyandrous and monandrous females should be higher than that of polyandrous females that mate on those particular days. If there are additional physiological costs of polyandry involved, monandrous females should have a higher daily fecundity during the early days of reproduction than non-mating polyandrous ones.

2.3.4 Variation in individual development and offspring survival among females

Polyandry is coupled with a lower early fecundity than monandry (III). I studied the implications of this variation on female life histories by rearing larvae under similar conditions in the laboratory (IV). Specifically, I examined variation in larval growth rate, development time and final size across female mating tactics in relation to developmental pathway (i.e., whether females developed directly into adults or into over-wintering pupae). Both southern ($N = 96$) and northern ($N = 100$) individuals were utilised due to their life cycle variation, which allowed me to produce both directly developing and over-wintering cohorts without manipulating larval conditions. The mating tactics of females with a known juvenile history was explored in the flight cages.

There was a positive correlation between larval growth rate and female mating frequency (IV, see also Wedell *et al.* 2002b). Hence, I predicted that if the

maintenance of monandry is due to the physiological cost of a high growth rate, offspring of polyandrous females should perform worse than offspring of monandrous ones resulting either in higher mortality or smaller size and/or longer development times in suboptimal conditions (Table 1). To explore the effects of environmental factors on juvenile performance, I divided the offspring of females ($N = 66$) with a varying degree of polyandry (1–4) into three treatments. Four eggs were exposed to similar conditions like their individually reared parents (high food quality, low larval density). The next four offspring faced conditions that were otherwise similar, but larval density at hatching was fourfold (high food quality, high larval density). Thirdly, four offspring were reared singly, but food items were replaced every third day (low food quality, low larval density). In the first treatment, I had 264 eggs (of which 243 hatched) from 66 females. In the second and third treatments, I had 248 (235) and 228 (217) eggs from 62 and 57 females, respectively. Because all the larvae of a certain female were full-sibs, and consequently more closely related with each other than with offspring of other females, I used the mean values of all female offspring within a brood as an indicator of offspring performance. In mortality analyses, larvae were treated as independent sample units regardless of sex and the family they derived from.

2.3.5 Adaptive significance of monandry in seasonal environments

In study V, I examined if seasonality may promote the maintenance of variation in female mating tactics. The fact that *P. napi* is more numerous in the first than in the second generation implies that only a fraction of the eggs laid in spring will develop into adults without diapause within the same season in central Finland. This gives rise to the possibility that monandrous females that have the highest early fecundity and the shortest egg-laying period (III), and may also be the ones that contribute proportionally more to the second generation than individuals whose offspring are produced later on (see also Vepsäläinen 1974, Seger & Brockmann 1987, Wiklund *et al.* 1991). Basically, the proportion of polyandrous females should increase, while the proportion of monandrous females should decrease within a population from the first to the second generation, because female fecundity increases monotonically with an increasing mating frequency. A possible variation in the number of generations produced within a season between mating tactics would be indicated if the average female mating frequency decreases and the proportion of monandrous females increases from the first to the second generation (Table 1). This was studied by exploring the

frequencies of female mating tactics in different generations. I used wild-caught females whose intrinsic mating tactic was determined in flight cages in laboratory conditions. Butterflies were captured from four bivoltine populations and four partially bivoltine populations on three and two occasions, respectively. The samples from the first generation were taken in the middle of the flight season 10–12 days after the first butterflies were seen on their wings (bivoltine: $N = 117$, partially bivoltine: $N = 107$). Bivoltine populations were sampled for the second time 4–6 days after the first individuals of the second generation were observed ($N = 132$), and for the third time 9–10 days later on ($N = 125$). Partially bivoltine populations were re-sampled 12–17 days after the first butterflies of the second generation were seen ($N = 124$). The sampling dates were standardised across populations based on the beginning of the flight season because comparison between regions with either a bivoltine or partially bivoltine life cycle is reasonable only if age the distribution of females within cohorts does not vary among populations.

3 Results and discussion

There is no doubt that polyandry corresponds with a higher lifetime fecundity than monandry in *P. napi* under optimal conditions (III). Still, female mating frequencies vary both within (I, V) and among (I, II) populations. The remating propensity of females decreases towards the north (I, II). Variation in mating tactics is, however, unlikely driven by a lack of mating opportunities resulting in suboptimal female mating frequency in the wild (I). I did not find evidence that a variation in female mating tactics could be maintained by a variation in male manipulative ability due to sexual conflict over mating rates either (I, II), but rather by selection acting upon female life history traits associated with their degree of polyandry (II–V).

Seasonality and unpredictability of fitness in the wild drives the evolution of optimal female mating tactics in *P. napi*. My results show that polyandry, although coupled with a high reproductive potential, is associated with low fecundity during the early days of reproduction (III). Thus, the benefits of polyandry would not materialise if a reproductively effective lifespan is short. Moreover, it suggests that offspring of polyandrous females would have less time to complete development, which, in turn, selects for fast development coupled with polyandry in seasonal environments. Accordingly, polyandrous females can develop at a faster rate than monandrous ones (IV). Despite growth rate variation, monandrous females are more likely to contribute to additional summer generation in conditions that allow production of only a partial second generation (V). These together suggest that the benefits of polyandry diminish and therefore low female mating frequencies are favoured if periods of suitable weather for reproduction are fairly short or juvenile development is time-limited (III, V). Even if a high degree of polyandry would be the most profitable mating tactic in an average year, strong annual variation in weather conditions may promote a co-existence of different mating tactics because variance of fitness is likely increase with an increasing mating frequency (III, IV).

3.1 Development time and size at maturity

Polyandrous females developed at a faster rate than monandrous ones, and this difference was observed both among females that developed directly into adults within the same season and among females that entered diapause (Fig. 1, IV). Growth rate variation between mating tactics persisted in the next univoltine

cohort as well, which suggests that not only the degree of polyandry (Wedell *et al.* 2002b), but also variation in individual development with respect to mating tactic pass to the next generation (IV). This underpins polyandry and monandry as distinct strategies in *P. napi* with life history differences reaching beyond mating frequency.

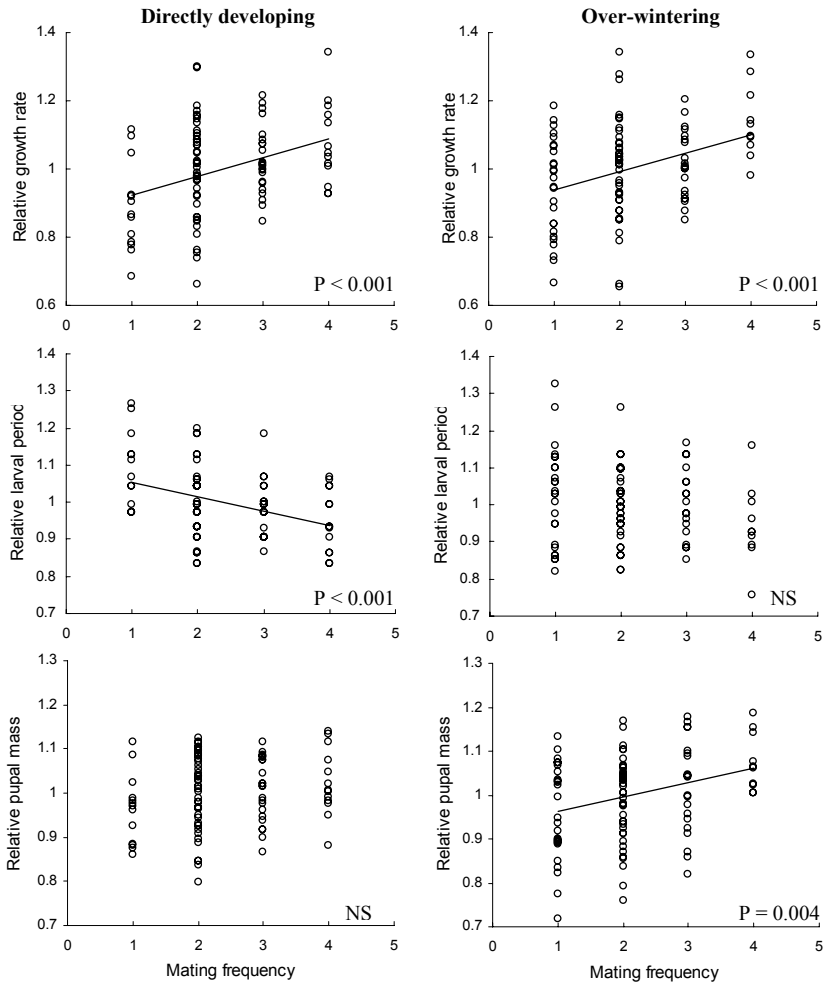


Fig. 1. Relative growth rate, relative duration of larval period and relative pupal mass in relation to the mating tactic for directly developing and over-wintering *Pieris napi* females. P-values for significance (NS = non-significant) according to linear regression analysis (IV).

Temporal variation in reproductive rate among females results in a negative correlation between the time available for development and the degree of polyandry (III). Thus, the notion that the duration of the larval period was negatively correlated with the degree of polyandry among directly developing females (IV) is consistent with the assumption that high growth rates result in short larval and/or pupal periods in butterflies with only limited time to complete development (Wiklund *et al.* 1991, Gotthard *et al.* 1994, Leimar 1996, Nylin *et al.* 1996). On the other hand, polyandry was coupled with a large size within the over-wintering cohort (IV) suggesting that, unlike the case of directly developing females, a short larval period is of relatively lower value than large body size for individuals that develop into over-wintering pupae.

A short juvenile period and a large adult size are generally beneficial due to their positive effects on individual fitness (Bell 1980, Haukioja & Neuvonen 1985, Sibly & Calow 1986, Wickman & Karlsson 1989, Karlsson & Wickman 1990, Honěk 1993, Iyengar & Eisner 1999, Bergström & Wiklund 2002), but both cannot be achieved simultaneously if juvenile growth rate is invariable (Stearns & Koella 1986, Roff 1992, Stearns 1992). On that basis, highly polyandrous females should trade large size for short larval period, because directly developing butterfly larvae are time-constrained in seasonal environments (Wiklund *et al.* 1991, Wiklund *et al.* 1992) and the relative significance of body size is likely to be negatively correlated with the degree of polyandry in species with male nutrient provisioning (Leimar *et al.* 1994, Wiklund & Kaitala 1995). Polyandrous females that developed into adults without diapause achieved, however, the same pupal mass as females with a lower degree of polyandry, regardless of their relatively shorter larval period (IV). Alternatively, highly polyandrous females grew larger than less polyandrous ones within the same time, as in the case of the over-wintering cohort. This indicates that, depending on the exact selection regime, the high growth rate of polyandrous females is directed at a life history variable with the highest relative value to an extent that it just offsets the effects of an age/size trade-off in relation to other individuals (Fig. 1, IV). This is in good agreement with recent life history considerations, suggesting that growth rate is an independent life history variable that may vary in an adaptive way (Reavey & Lawton 1991, Wiklund *et al.* 1991, Nylin *et al.* 1993, Nylin 1994, Abrams *et al.* 1996, Nylin & Gotthard 1998).

Both generations of *P. napi* are protandrous (i.e., males emerge before females) (Wiklund *et al.* 1991) and males do not survive as long as females (Wedell *et al.* 2002b, own observations), which is understandable due to the

exceptionally high mating effort of *P. napi* males among butterflies (Wiklund & Forsberg 1991). The benefits of polyandry depends on females' opportunities to mate repeatedly (Sauter *et al.* 2001, Wedell *et al.* 2002b, Kokko & Mappes 2005) with recently unmated males (Kaitala & Wiklund 1994), which partly depends on the co-occurrence of males and females. Therefore, the observed short larval period of polyandrous females could be interpreted as a way to avoid reproductive depression due to unobtainable male donations. This point of view should be applied only to the directly developing cohort, because highly polyandrous females need not enter diapause early to emerge in synchrony with males in the following spring. In the over-wintering cohort, synchrony at emergence will depend on development time after diapause, and it is assured by the pupal period, which I showed to be independent of mating tactic (IV). Thus, in both univoltine populations and the over-wintering cohort within bivoltine populations, highly polyandrous females probably have a double advantage over females with a lower degree of polyandry, because, as a consequence of a high growth rate, polyandry is coupled with a large adult size (see also Bergström & Wiklund 2002).

3.2 Spatial variation in female mating tactics

P. napi females follow different heritable reproductive tactics, with monandrous females relying on larval-derived resources to realize their fecundity, and polyandrous females being more dependent on male donations (Wedell *et al.* 2002b). I studied spatial variation in mating frequency distribution among populations along with the increasing latitude. The proportion of monandrous females in the south averaged over all populations was 0.113, but in the northern populations their proportion was evidently higher (0.266) (Fig. 2, I). There was almost no variation in the proportion of females mating twice, and they were always the most numerous ones with the proportion ranging from 0.435 up to 0.538. Females with a mating frequency higher than two were consistently more abundant in the southern than in the northern populations. Bergström *et al.* (2002) have reported an almost exactly similar mating frequency distribution as with the southern study sites of this work for *P. napi* females that originated ca. 300 km SW from my southern populations. For reasons explained in the following sections, monandry may be a more profitable mating tactic in the north than high degrees of polyandry, which explains simultaneous decrease in average female mating frequency. When offered an unlimited mate supply, females from northern

Scandinavia mated 2.11 (95 % CI: 1.94–2.28) times on the average, while the lifetime number of matings for southern females was approximately 2.43 (95 % CI: 2.25–2.61) (I, see also II, V). In central Finland, which lies geographically between the two extremes, mating frequency distributions in the first generation were more or less the same as those observed in more southern latitudes (V)

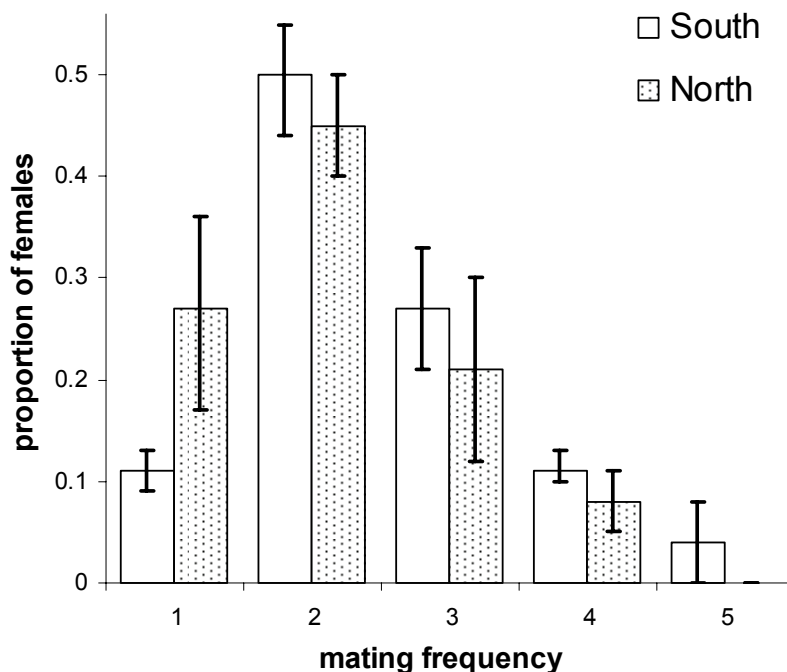


Fig. 2. Proportion of *P. napi* females following each mating tactic in the southern and northern populations with 95% confidence intervals (I).

3.3 Males as a limited resource for polyandrous females

The benefits of polyandry are lost if mating opportunities are scarce (Sauter *et al.* 2001, Wedell *et al.* 2002b, Kokko & Mappes 2005), which may be promoted by unfavourable weather conditions. Accordingly, female mating frequency decreases towards the north along with the time available for reproduction (I, II). However, even in the north, females seem to be able to mate as many times as they want (I), and thus it is likely the case in more southern latitudes as well. On

the basis of a male biased operational sex ratio (Wiklund *et al.* 1998), the result may not be surprising at all. The life expectancy of pierids hardly exceeds 12 days in the wild (Chew 1981). In 2001, when weather conditions were exceptionally unfavourable, suitable weather conditions [20th June–15th July, 09.00 am.–07.00 pm., temperature $\geq 12^{\circ}$, wind ≤ 5 m/s, no rain] for reproductive activities during randomly selected 12-day periods lasted only 58 [± 18.37 (S.E.)] hours in northern Scandinavia, Kilpisjärvi (III). Nevertheless, even in that particular year, the mating frequency distributions did not differ between wild females and females in laboratory conditions (I). Therefore, the conclusion that females do not suffer from a lack of mates in the wild seems sustainable.

Interestingly, the benefits of polyandry are dependent on both females' chances to mate according to their genetic background (Wedell *et al.* 2002b) and the amount of received spermatophore material, even independent of the number of matings they perform (Kaitala & Wiklund 1994, Karlsson 1998, Wiklund *et al.* 1998). If females are primarily optimising the amount of spermatophore material, small ejaculates due to frequent matings of males may explain the reproductive depression of polyandrous females, and the maintenance of low mating frequencies. Unfortunately, I did not have any control over the mating history of males that wild females had mated with (I). However, females increase their mating frequency if their previous partner has recently mated, and is thus capable of delivering only a small spermatophore (Kaitala & Wiklund 1994). Hence, assuming free mating possibilities, the observed mating frequencies in the field should have been higher than in the laboratory if wild females had suffered from a lack of seminal fluid substances.

On the other hand, the conclusion that polyandrous females face neither a lack of mating opportunities, nor do they suffer from small male donations, may be applicable only to univoltine populations and the over-wintering generation within multivoltine populations. A short male lifespan (Wedell *et al.* 2002b), combined with protandry (Wiklund *et al.* 1991), suggests that females emerging late may actually face a lack of mating opportunities in the wild. The risk of suboptimal mating frequency in an additional summer generation may be substantial because males produced in spring are less likely to hatch during the same season than females, due to strong selection on size or protandry (Wiklund *et al.* 1991, Wiklund *et al.* 1992). At the very least, the risk of mating with an already mated male capable of delivering only a small spermatophore increases as the season proceeds. All things combined, the realised benefits of polyandry, if any, are almost certainly lower in the second generation in the wild than those

observed in optimal laboratory conditions. This is because polyandrous females hatch later than monandrous ones (V) and their matings are more dispersed in time.

3.4 Female mating tactics and conflicting interests of sexes

Male size correlates with ejaculate volume in *P. napi* (Forsberg & Wiklund 1989, Svärd & Wiklund 1989, Bissoondath & Wiklund 1996). The positive correlation between male size and female remating interval (II) suggests that, like in some other pierids, spermatophore size is one of the key factors affecting female remating behaviour in my study species as well (Sugawara 1979, Rutowski *et al.* 1981). Accordingly, Kaitala & Wiklund (1994) were able to increase mating frequency of *P. napi* females up to 11 by manipulating spermatophore size. Moreover, male ejaculates contain also anti-aphrodisiacs that render females unattractive to rival males (Andersson *et al.* 2000, Andersson *et al.* 2004). Whenever there is a risk that females mate with more than one male during a single breeding season, male adaptations that prevent or delay remating of their mates are favoured (Birkhead & Møller 1998). Hence, exaggerated butterfly ejaculates may be interpreted as male devices to reduce the risk of sperm competition rather than nuptial gifts in the strict sense, but due to reduced potential to achieve the benefits of polyandry, females have evolved resistance traits leading to an exploitation of male coercion (Boggs 1990, Stockley 1997, Vahed 1998, Arnqvist & Rowe 2005).

Females delayed remating for a longer time when mating with a larger male (II), which is consistent with the idea that males have some control over female behaviour (Bissoondath & Wiklund 1997). There was, however, no geographical variation in the level of sexual dimorphism, and the average female mating frequency was not affected by whether females mated with southern or northern males (II). Moreover, male manipulation should primarily manifest itself via an increased remating interval, which was not found to differ between southern and northern females (I). These results contradict the conjectures of sexually antagonistic co-evolution, predicting that male manipulative ability should be positively correlated with the degree of polyandry (Arnqvist & Rowe 2005), and females should exhibit effective counter-adaptations to males with whom they have co-evolved and show stronger resistance to males with a high manipulative ability (Clark *et al.* 1999, Gavrillets *et al.* 2001, Nilsson *et al.* 2002).

A correlation between mating frequency and the remating interval must exist to some extent, because it would be impossible for a female to have a very long unreceptive period after mating and exhibit a high degree of polyandry (Wedell 2001, I). Still, the fundamental issue of whether a male induced prolonged remating interval is costly for females remains questionable. Male mating attempts can be so intense that they may inflict various costs on females and, at least, interfere with essential activities such as egg-laying and foraging (Martens & Rehfeldt 1989, Stone 1995). Egg-laying of *P. napi* females peaks approximately three days after the previous mating (Wiklund *et al.* 1993) and recently mated females are quickly abandoned by a courting male due to a release of male-derived volatile anti-aphrodisiacs (Wiklund & Forsberg 1989, Andersson *et al.* 2000). Therefore, a remating interval of 4.21 ± 0.23 (S.E) days (I) may actually turn out to be beneficial for a female as well. Thus, even if large male ejaculates would have evolved to assure the paternity of a given male with negative side effects on female fitness, females seem to have achieved equilibrium between a male-induced prolonged remating interval and spermatophore depletion ability, which conceals possible implications of antagonistic co-evolution. Anyway, geographic variation in mating frequency distribution among the southern and northern populations is unlikely driven by a variation in the level of sexual conflict.

3.5 Adaptive significance of polyandry and monandry in variable conditions

3.5.1 Temporal variation in the reproductive rate among females

Both artificially selected and wild-type *P. napi* females with a low intrinsic mating frequency produced more eggs during the early days of reproduction than females with a high mating frequency (III). The benefits of polyandry arose after about one week from the first mating, by which time the reproductive rate of polyandrous females had exceeded that of females with a low mating frequency. Consequently, females with a high mating frequency had approximately 1.5 times higher lifetime fecundity than females with a low mating frequency, which is in concordance with the prevailing conception (Wiklund *et al.* 1993, Vahed 1998, Arnqvist & Nilsson 2000).

Mating is both time-consuming and mutually exclusive with egg-laying (e.g., Daly 1978). The low daily fecundity of polyandrous females that mated compared to that of polyandrous females that did not mate on those particular days indicates that the time cost of mating is biologically significant in *P. napi* (III). This was highlighted by the fact that monandrous females had more than twice the daily fecundity of mating polyandrous females during the early days of reproduction. It should be noted that the time cost of mating in my experiments include also post-mating processes such as spermatophore absorption and sperm migration to the spermatheca (Tschudi-Rein and Benz 1990). On the very first days of reproduction, monandrous females tended to lay more eggs than non-mating polyandrous females as well. This indicates that there may be physiological costs involved too, but this difference was statistically non-significant (III). Hence, the time costs of mating seem to constitute a great deal of the observed temporal variation in the reproductive rate between mating tactics.

This contradicts earlier findings of polyandrous females having a higher fecundity at all stages, suggesting that the time costs of mating are negligible in *P. napi* (Wiklund *et al.* 1993). The heritability of mating tactics was, however, not clear at the time of this earlier study. As a consequence, most randomly selected females in the “monandry” treatment were actually polyandrous by their genetic background, but forced to mate only once. Given that the benefits of polyandry will not materialise if females cannot mate according to their intrinsic mating frequency (Sauter *et al.* 2001, Wedell *et al.* 2002b, Kokko & Mappes 2005), the reproductive performance of true monandrous and polyandrous females was not explored properly.

The cost of mating increases if females mate with a recently mated male, both because mating duration is prolonged from two up to seven hours of suitable weather (Wiklund *et al.* 1998) and females will receive only a small ejaculate, and thus they have to remate sooner (Kaitala & Wiklund 1994). Because females are unable to discriminate between mated and unmated males (Kaitala & Wiklund 1995), and virgin males are no longer readily available late in the season, I probably have even underestimated the cost of remating for wild females. The time cost of mating (III) and the absence of female control over copula termination (Wickman 1985) points to the possible sexual conflict over mating duration, although sexually antagonistic co-evolution over mating rates do not seem to explain variation in female mating tactics among populations (II).

In *P. napi*, like in other species with wide geographic ranges, discrete populations face widely varying weather conditions. Sunny weather obligatory to

butterfly activity is frequently interrupted by cold and rainy periods in the northern latitudes. Making the reasonable assumption that the date of a butterfly female's first mating falls within a suitable weather period, her realised fitness will depend on the number of suitable days afterwards. From a butterfly perspective, the number of such days is highly unpredictable. Assuming that each day carries with it a constant risk (probability p) that the weather turns unsuitable, the fitness W of a female, whose mating tactic leads it to lay a cumulative sum of $F(i)$ eggs by the end of the i th day, equals

$$W = \sum_{i=1}^{\infty} (1-p)^{i-1} p F(i) \quad (1)$$

Applied to the data on females deriving from artificial selection lines (III), we can assume that egg-laying ceases after 13 days since the first mating, which means that $F(i)$ stays constant from that day on, and the equation (1) can be written as

$$W = \sum_{i=1}^{12} (1-p)^{i-1} p F(i) + (1-p)^{12} F(13) \quad (2)$$

A given value of p corresponds to a mean of

$$\sum_{i=1}^{\infty} i(1-p)^{i-1} p = 1/p \quad (3)$$

suitable consecutive days for reproductive activities. The average success of LMR and HMR females depends on the mean length of each suitable weather period. Given a day length of ten hours, the model shows that if the effective life spans of females last on average less than five days, monandry yields a higher fecundity than polyandry (Fig. 3, III). Interestingly, five days after the first mating, monandrous females still performed better in the experiments (III), but the model predicts for them an equal fitness with highly polyandrous ones. This emphasises the importance of unpredictability within a season: even if average flight periods are fairly short, weather patterns may stay constant for a number of days, allowing some polyandrous females to take advantage of their late-life benefits. Anyway, foregoing the chance of acquiring nutrients through multiple mating is beneficial for a female in terms of egg quantity, if time for reproduction is limited. Alternatively, monandry may be beneficial if polyandrous females suffer from a higher mortality than monandrous ones, which may arise, for

example, from an increased predation risk of mating pairs (Ward 1986, Wing 1988, Arnqvist 1989, Magnhagen 1991, Fairbairn 1993, Rowe 1994).

My results suggest that a co-existence of different mating tactics may be related to weather unpredictability: fitness as described in figure 3 is accumulated through all possible lengths of suitable weather conditions for butterfly activity and their associated probabilities. Although there are years when the selection pressure for polyandry is expected to be low, summer weather in Fennoscandia shows strong annual variation. As an indicator of this, the number of rainy days in July has varied between four and 25 in the last few decades (1952–2003) in Kilpisjärvi, and the average July temperature has varied between 4.2°C and 14.0°C during the same period. Moreover, the length of suitable weather conditions during the whole flight period of *P. napi* (20th June–15th July) during 2000–2004 has varied between 46 and 142 hours. Such annual variation in weather conditions creates obvious possibilities for temporally fluctuating selection, which decreases the geographic-mean fitness of the polyandrous mating tactic (see Seger & Brockmann 1987).

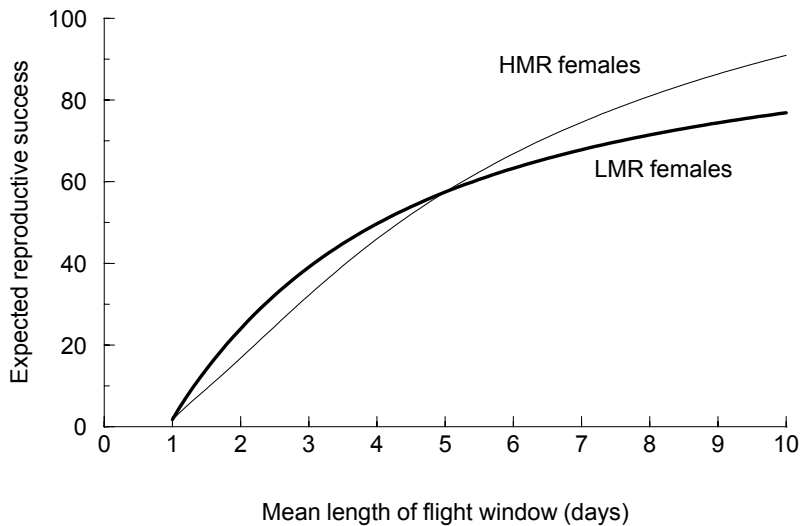


Fig. 3. Expected reproductive success for monandrous (LMR) and highly polyandrous (HMR) *P. napi* females as a function of the mean length of the flight window (*i.e.*, effective lifespan) assuming unpredictable weather (a constant probability of weather change, regardless of the number of suitable days experienced so far) (III).

3.5.2 The effects of high density and poor quality diet on larval performance

Larvae that faced a high density or poor quality diet performed worse than larvae reared on a high quality diet alone (IV). A commonly observed effect of low resource availability is that a decreased growth rate results in both prolonged development time and reduced size, which indicates non-adaptive variation in growth rate (Stearns & Koella 1986, Roff 1992, Stearns 1992). In study IV, only growth rate and pupal mass was affected, whereas the duration of the larval period was more or less constant across conditions. This indicates that there is strong selection in seasonal environments for being ready for pupation at the right time, even at the expense of size if a high growth rate is prevented by external factors. This is, of course, the case, because otherwise individuals would not reach the over-wintering stage in time. The positive correlation between the degree of polyandry and high growth rate (see 3.1) diminished when larvae were stressed (IV). This suggests that polyandry allows a more plastic size because polyandrous females may rely on nutrient compensation in the form of male ejaculates. Similar reasoning has been presented to explain sex-specific body size responses on diet quality (Leimar *et al.* 1994). Alternatively, polyandry is more prone to unfavourable conditions than monandry in terms of larval performance, but this could only be shown with more severe environmental stress than the larvae were exposed to in my experiment.

The plastic effects of poor diet or high density can undoubtedly be non-adaptive, but there may be adaptive plasticity in size as well, at least in species adapted to fluctuating resources (Banno 1990, Leimar *et al.* 1994). *P. napi* females lay their eggs on small crucifer rosettes (Forsberg 1987). Due to the small size of hosts in relation to larval needs and the fact that crucifers do not usually form dense growths, larvae of this species have to find several individual hosts to achieve full-size. In the mountains of northern Scandinavia, the only host of reasonable size, *Arabis alpina*, grows more or less singly, being highly scattered in space (own observation). The problem is emphasised by the notion that single rosettes have frequently more than one larva feeding on it. Therefore, wild larvae obviously face food shortage or resource competition from time to time. It is clear that if the costs of a high growth rate exceed the benefits, individuals benefit from the ability to change their growth rate accordingly, and thus plasticity may evolve (Sibly & Calow 1986, Werner & Ahnholt 1993, Abrams *et al.* 1996).

Monandrous females had a relatively low growth rate, which implies that the costs of growing faster are greater than the benefits of maturing at a larger size for them (IV). Evidently, a high growth rate is sometimes coupled with an increased mortality risk due to physiological requirements that would deplete stored resources quickly, if resources are in short supply (Clutton-Brock *et al.* 1985, Conover & Present 1990, Stockhoff 1991, Wiklund *et al.* 1991). In study IV, *P. napi* larvae suffered from high density and low food quality in terms of increased mortality. Although a high juvenile growth rate is associated with nutritional stress induced mortality in a variety of taxa (Arendt 1997), my experiment showed that it is not universal among Lepidoptera since offspring mortality appeared to be decoupled from the mother's mating tactic (see also Gotthard 1998). This is probably due to plasticity in growth rates that allows polyandrous females to modify their development in relation to the availability of resources. Hence, the physiological costs of having a high growth rate do not seem to explain the maintenance of genetic variation in the female mating tactics in *P. napi*. However, I did not take all the implications of high growth rate into account. A surplus allocation to growth may interfere with the capacity to store resources that could be used when food is not readily available (Chippindale *et al.* 1996). Thus, the costs of a high juvenile growth rate do not necessarily materialise until the adult stage. Juvenile growth rate may also interact with the immune function against parasitoids, parasites and pathogens (Rantala & Roff 2005), which may furthermore reflect upon starvation resistance at any stages of development (Kraaijeveld & Godfray 1997, Moret & Schmid-Hempel 2000, Hoang 2002). A high growth rate may also be associated with ecological costs such as higher predation risk (Werner 1986, Abrams & Rowe 1996, Moody *et al.* 1996, Gotthard 2000) and higher susceptibility to parasitoids (Sharpe & Detroy 1979, Clancy & Price 1987).

3.5.3 Variation in voltinism among female mating tactics

In partially bivoltine populations, the proportion of monandrous females increased from the first to the second generation ($G^2 = 6.692$, $df = 1$, $P < 0.01$), which explains a simultaneous decrease in average mating frequency (Table 2, V). Because polyandry yields a higher lifetime fecundity than monandry (Bergström & Wiklund 2002, Kaitala & Wiklund 1994, Karlsson, 1998, Wiklund *et al.* 1993, 1998, III), the observed pattern is understandable if a remarkable proportion of the offspring produced by polyandrous females in the first

generation developed into over-wintering pupae, whereas the offspring of monandrous ones were more likely to develop into directly breeding adults. This is most probably due to the facts that monandrous females have a higher egg-laying rate in the beginning of the reproductive period, and their reproduction is less dispersed in time than that of polyandrous ones (III). Hence, my results appear to be in good agreement with the ideas that only the first offspring produced in the spring will develop directly into adults within a single breeding season and females with a high early fecundity contribute relatively more to additional summer generation than females with delayed reproduction in seasonal environments (Vepsäläinen 1974, Seger & Brockmann 1987, Wiklund *et al.* 1991). Generally, individuals that are able to produce additional generations successfully within a given time are favoured by selection. Therefore, in regions where only a fraction of individuals develop directly into adults, a high early fecundity of monandrous females and the consequent change in voltinism causes a counter-selection against polyandry that is obviously strong enough to explain the maintenance of genetic variation in female mating tactics in *P. napi*.

Table 2. Proportions of *P. napi* females following each mating tactic and average female mating frequencies in bivoltine and partially bivoltine populations in different generations (mf for average mating frequency) (V).

Origin	Population	Gen.	Female mating tactics						Mf	N
			1	2	3	4	5	6		
Southern	Tammisaari	I	.17	.41	.28	.10	.04		2.41	29
Finland		II	.14	.36	.26	.13	.07	.07	2.84	31
(bivoltine)	Kirkkonummi	I	.19	.37	.30	.11	.04		2.44	27
		II	.16	.41	.25	.16	.03		2.50	32
	Helsinki	I	.16	.48	.23	.13			2.32	31
		II	.16	.34	.31	.16	.03		2.56	32
	Nurmijärvi	I	.20	.40	.27	.10	.03		2.37	30
		II	.17	.33	.27	.17	.03	.03	2.67	30
Central Finland	Kaakkuri	I	.17	.47	.20	.07	.07	.03	2.50	30
(partially		II	.27	.50	.17	.07			2.03	30
bivoltine)	Taskila	I	.14	.46	.27	.14			2.41	22
		II	.28	.31	.34	.06			2.19	32
	Rusko	I	.17	.46	.17	.17	.04		2.46	24
		II	.25	.24	.25	.09	.06		2.37	32
	Kiiminki	I	.13	.55	.23	.10			2.29	31
		II	.33	.30	.23	.10	.03		2.20	30

Due to the obvious direct benefits of polyandry for *P. napi* females, things are more complex in regions where complete bivoltinism prevail. Although the difference in the average female mating frequencies between generations was non-significant, the number of matings increased rather than decreased from the first to the second generation (Table 2, V), like Bergström *et al.* (2002) suggested. However, since the proportion of monandry was constant within populations across generations ($G^2 = 0.331$, $df = 1$, $P > 0.1$), this change was not as pronounced as expected based solely on the higher lifetime fecundity of polyandrous than monandrous females (Wiklund *et al.* 1993, 1998, Kaitala & Wiklund 1994, Karlsson 1998, Bergström & Wiklund 2002, III). This suggests that even in southern Finland, offspring of highly polyandrous females entered diapause in larger numbers than offspring of monandrous ones. Thus, increasing butterfly abundance across generations does not necessarily imply that all offspring of the first generation females hatch within the same season even if decreasing butterfly abundance from the first to the second generation indicates that only a fraction of individuals develop without diapause. It also seems relevant to point out that focusing only on average mating frequencies would have resulted in misleading conclusions, which emphasises the need to explore exact frequencies of each mating tactic rather than relying only on average mating frequencies.

In the partially bivoltine region (Oulu), thermal summer has started on average on the 30th of May (range: 6th of May–16th of June), and it has lasted until the 7th of September (21st of August–27th of September) during 1971–2000 (Finnish Meteorological Institute 2007). The average dates for the onset and the end of thermal summer in southern Finland (Helsinki) during the same period have been the 18th of May (26th of April–6th of June) and 23rd of September (3rd of September–16th of October), respectively. This suggest that there may occasionally be such years even in southern Finland that the duration of summer allows the production of only a partial second generation. Again, there are possibilities for temporally fluctuating selection, so that a high early fecundity (low mating frequency) results in a relatively constant reproductive output, whereas the adaptive significance of high lifetime fecundity (high mating frequency) is more dependent on environmental conditions in a particular year. Given that the variance of success is important in addition to the average success in the long-term (Dempster 1955; Gillespie 1977; Seger & Brockmann 1987), annual fluctuations may well promote the maintenance of seemingly maladaptive female mating tactics with low intrinsic mating frequencies.

The unexpectedly high prevalence of monandry in the summer generation may simply arise because offspring of monandrous females are laid earlier on average than those of polyandrous ones in the spring generation. The pattern may be further reinforced by variation in diapause propensity among mating tactics driven by implications of the temporal variation in reproductive rate. In populations with a bivoltine life cycle, monandrous females emerged earlier than polyandrous ones in the second generation (V). The sequential appearance of females with different mating tactics as such may result in diminishing rewards for polyandry, due to unobtainable male donations for late emerging females (see 3.3). Asynchronous hatching of offspring may also incur additional cost to polyandry. The average offspring of polyandrous females are laid about four days later than those of monandrous ones (III). Asynchrony in the hatching of larvae will be twice as pronounced in the second generation, assuming that there is no variation in growth rate among larvae in the wild, and monandrous females still do better in the early days of reproduction in the second generation. This may result in biased juvenile mortality, especially in the second generation, due to the competitive superiority of early-hatching larvae, or time limitations that do not allow late-hatching larvae to reach the over-wintering stage in time. In the seed beetle, *Callosobruchus maculatus*, even a two-day head start at hatching is enough to induce a change in competitive ability between larvae (Messina 1991, see also Begon 1984). In central Finland, the second generation of *P. napi* flies until mid August and juvenile development into the hibernating stage lasts 29.96 (95 % CI: 29.48–30.43) days in the wild (Välimäki & Kivelä, unpublished data). Because autumn frosts are common in early September, females that emerge relatively late or have a long reproductive period may lose some offspring due to the onset of winter. Thus, both unobtainable male donations and biased juvenile mortality may partly explain variation in diapause propensity among mating tactics.

The results of study V suggest that monandrous *P. napi* females contribute relatively more than expected based on the difference in reproductive potential among mating tactics to the following generations. If temporal variation in reproductive rate among females creates such an effective counter-selection against a high degree of polyandry, fast larval development associated with polyandry is expected. One possible reason why polyandrous individuals cannot achieve a synchronous emergence with monandrous ones by accelerated development comes from the trade-off between juvenile development time and size at maturity (Stearns & Koella 1986, Roff 1992, Stearns 1992). Although

body size is positively correlated with fecundity in many organisms (Bell 1980, Sibly & Calow 1986, Honěk 1993, Iyengar & Eisner 1999), this does not hold true in *P. napi*, because of the nutrient compensation provided by males (Leimar *et al.* 1994, Wiklund & Kaitala 1995, IV). In fact, polyandrous females that develop directly through juvenile stages into adults can complete development faster than monandrous ones in optimal conditions (Wedell *et al.* 2002b, IV). This seems not to be the case in the wild, probably because of constraints on resource availability and uptake that do not allow completing development within a very short time (Sibly & Calow 1986, Roff 1992, Stearns 1992). This is supported by the observations that a high growth rate of polyandrous females disappears if larvae are stressed (IV), and the correlation between female size and the degree of polyandry is less pronounced in the wild than in the laboratory conditions (Bergström *et al.* 2002).

4 Concluding remarks

Monandry and degrees of polyandry are distinct strategies with life history differences reaching beyond mating frequencies (Table 3). Both strategies may be maintained by selection even if the direct benefits of nuptial feeding are involved. Monandry, although coupled with low lifetime fecundity, may be beneficial if time for reproduction is limited severely enough or other female traits or behaviours associated with polyandry are traded off against longevity (III). Secondly, genetic variation in female mating tactics will prevail if environmental conditions do not allow all individuals to contribute evenly to the directly breeding generation within bivoltine populations, or if even the production of a single generation per year is time-limited (V). Moreover, annual variation in weather conditions and the duration of summer promote variation by creating possibilities for a temporally fluctuating selection so that a high early fecundity (low mating frequency) results in a relatively constant reproductive output, whereas the adaptive significance of high lifetime fecundity (high mating frequency) is more dependent on environmental conditions in a particular year (III, V). Yet, it is currently unclear if these fluctuations are sufficient for maintaining variation in mating tactics indefinitely.

Table 3. Life history differences between polyandrous and monandrous mating tactics.

Variable	Monandry	Polyandry
Juvenile growth rate (IV)	low	high
Early reproductive rate (III)	high	low
Relative contribution to additional summer generation (V)	high	low
Fertility (III, Wiklund <i>et al.</i> 1993)	low	high
Male dependence (Wedell <i>et al.</i> 2002b)	low	high

A low early egg-laying rate alone can outweigh the direct benefits of polyandry if the effective life spans of females last less than 50 hours (III). The northern environment is characterised by a short summer and low temperatures compared to more southern latitudes (Strathdee & Bale 1998). In northern Finland, Kilpisjärvi, the duration of suitable weather conditions for butterfly activity during the whole flight season of *P. napi* has varied between 46 and 142 hours during the period of 2000–2004. In the former case of a short season, selection for polyandry should relax (III). Even in the most unfavourable years, monandrous females can realise most of their reproductive potential, whereas

polyandry will yield a more variable reproductive output. Increasing variance of reproductive output decreases geometric-mean fitness, which may well promote co-existence of different female mating tactics in the long-term (see Seger & Brockmann 1987). Accordingly, the proportion of monandry increases with latitude, being almost three times higher in the northern edge-of-range populations than in southern Finland (I), although neither male availability (I) nor male properties with possibly sexually antagonistic implications (II) seem to restrict female mating frequency.

A high metabolic rate that allows for a fast depletion of male donations has been suggested to be responsible for the correlation between a high growth rate and the degree of polyandry (Wiklund *et al.* 1998, Wedell *et al.* 2002b), but due to a weak correlation between female mating frequency and the remating interval (I) this seems unlikely. This is the first study to offer an adaptive explanation for the high growth rate of polyandrous females (IV). Polyandrous females achieve a larger size or mature faster than monandrous ones, but pay no costs due to a trade off between the two variables, like a recent life history model suggests (Abrams *et al.* 1996). Although a high growth rate has been associated with severe physiological costs (Arendt 1997), this is not a rule among butterflies (Gotthard *et al.* 1998, IV). Thus, the high growth rate of polyandrous females may give them a double advantage over monandrous ones in the over-wintering cohort due to their larger size or minimise asynchrony at eclosion in the directly developing cohort. Polyandrous females can, however, develop at a high rate only under restricted conditions (IV) that may not always be applicable to the wild (Bergström *et al.* 2002, V).

Monandrous females are more likely to contribute to the additional summer generation than highly polyandrous ones, especially in areas with only a partial second generation (V). This seems applicable to the whole bivoltine region as well, because the proportion of monandrous females was constant across generations within more or less bivoltine populations (V). Generally, individuals capable of producing additional generations successfully within a given time are favoured by selection. Therefore, a variation in the relative contribution to summer generation between females with different mating tactics acts as a counter-selection against polyandry, and more generally, against high fertility if it is traded off against a low early reproduction rate in potentially multivoltine insects in seasonal environments. Although variation in mating tactics is not due to a lack of mating opportunities in univoltine populations (I), asynchrony at eclosion may increase the risk of unobtainable male donations for polyandrous

females in the second generation because (1) males are more likely to enter diapause than females (Wiklund *et al.* 1992), (2) males have a shorter lifespan than females (Wedell *et al.* 2002b), and (3) unmated males are not available late in the season.

Seasonality and an unpredictability of fitness in the wild seem to be sufficient reasons for the maintenance of variation in female mating frequencies, and life history variation within populations in general. In some reports reaching outside of my study species, the time costs of mating (Daly 1978, Thornhill & Alcock 1983, III), a risk of prolonged copulations (Svärd & Wiklund 1986), and an increased mating rate due to sperm depleted mates (Gromko *et al.* 1984, Savalli & Fox 1999, Jones 2001, Simmons 2001, Wedell *et al.* 2002a, Jones *et al.* 2006), suggest that temporal variation in the reproductive rate among females with a different mating pattern is a common phenomenon. As a consequence, spatial variation in female optimal mating tactics among populations is expected to be a rule rather than an exception. This may generate spatial variation both in the level of sperm competition and the females' chances for cryptic mate choice (see Parker 1970, Eberhard & Cordero 1995). Cryptic female choice increases female control over paternity, which is highly important in species with indiscriminate sexual interactions (Thornhill & Alcock 1983). Sperm competition and cryptic female choice may drive a variety of evolutionary changes in males with spatial patterns from genital morphology and the numbers of sperm ejaculated to ejaculate expenditure and the behaviour of individual sperm (Eberhard & Cordero 1995, Gage & Barnard 1996, Parker 1998, Wedell & Cook 1999, Wedell *et al.* 2002a, Hosken & Stockley 2004). If females perform substantial pre-copulatory mate choice, variation in the degree of polyandry among populations will generate spatial variation in the overall strength of sexual selection, which may have implications even on the most fundamental evolutionary events, such as speciation (Arnqvist *et al.* 2000, Panhuis *et al.* 2001).

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Original papers

- I Välimäki P & Kaitala A (2006) Does a lack of mating opportunities explain monandry in the green-veined white butterfly (*Pieris napi*)? – Oikos 115: 110–116.
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- IV Välimäki P & Kaitala A (2007) Life history trade-offs in relation to the degree of polyandry and developmental pathway in *Pieris napi* (Lepidoptera, Pieridae). – Oikos (In print).
- V Välimäki P, Jääskeläinen L, Kivelä S & Kaitala A (2007) Seasonality may promote polymorphism in female mating tactics in a bivoltine butterfly *Pieris napi* (Pieridae) (Manuscript).

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