Nordic Society Oikos

Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly, Pieris napi

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Wiklund, C., Nylin, S. and Forsberg, J. 1991. Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly, *Pieris napi*. – Oikos 60: 241–250.

This paper explores what factors influence size, development time and growth rate in a polyandrous and bivoltine butterfly, *Pieris napi* L. In butterflies male/female sexual size dimorphism has been shown to be positively correlated with female polygamy. Hence, males of *P. napi* should be selected for large size. Comparing time constraints between the directly developing and the diapause developing generations, it is obvious that the former is more pressed for time, having to complete two generation cycles in one season, whereas the latter only completes one life cycle. On top of this comes selection on males to emerge before females. Rearing larvae at the critical daylength, where part of the individuals develop directly and part diapause, a two-way ANOVA on growth rate shows that there is an interaction between sex and developmental pathway. This means that males repond to the selective pressure for large size and protandry by increasing their growth rate so that it is more accelerated relative to that of females under direct compared to diapause development.
Although growth rate is phenotypically plastic, it must have a physiological upper limit. Hence, it seems likely that directly developing males have to make a trade off between size and protandry. In general, selection for protandry should be strongest under monandry, whereas selection for large size should be strongest under polyandry. When reared at the critical daylength male size is largest under direct development, whereas protandry is less accentuated. This suggests that males of *P. napi* have to make a trade off, and favour the achievement of large size to protandry.

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Introduction

According to Harvey and Clutton-Brock (1985) G. Evelyn Hutchinson once argued that priorities for ecological research should include the questions "How big is it and how fast does it happen?". In agreement with this outlined "research programme" we focus in this paper on exploring what factors influence size and development time in a bivoltine butterfly, *Pieris napi* L., living in a seasonal environment. In particular we examine how selection for one, or both, of these parameters result in phenotypic plasticity in growth rate. In spite of the somewhat detailed development of predictions that follow below, which is necessitated by the fact that time

constraints affecting different life stages are particular to the specific life history of the study organism, we contend that our conclusions have general applicability. Essentially, the results emphasize growth rate as a life history variable in its own right which can be increased or decreased by natural selection, and not a parameter which is given passively by temperature or food availability in the environment. Hence, to name but one example, this will have consequences for life history calculations of optimal size and age at sexual maturity (cf. Stearns and Koella 1986), where optimal solutions in two-dimensional size-age space will need to take into account not only trade offs between size and age, but
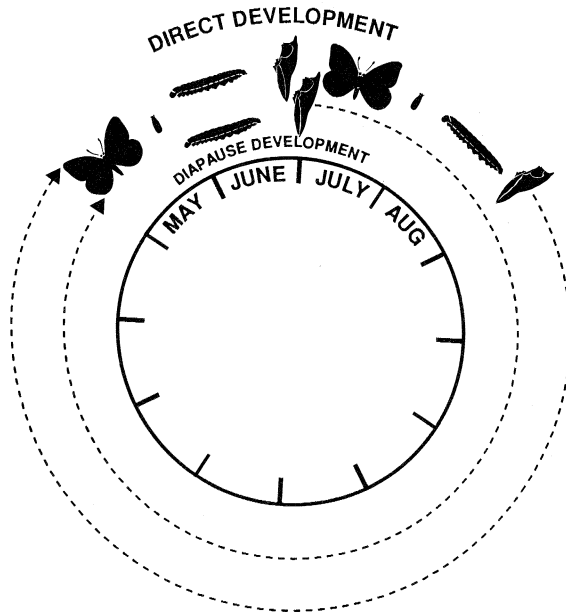
Fig. 1. A schematic representation of the phenology of *P. napi* in central Sweden, where some individuals follow a bivoltine life cycle and enter direct development early in the season, and others follow a univoltine life cycle and enter diapause development.

the triangular nature of trade offs between size-age- and growth rate.

Experimental rationale and predictions

Polyandry and size

Selection for large male size is reasonably well understood among mammals and other vertebrates, and seems to be associated with male polygamy and female monogamy (Clutton-Brock 1983, Greenwood and Wheeler 1985). Likewise, a comparative study of 23 Swedish butterfly species in the Pieridae and Satyridae has shown that male/female sexual size dimorphism is positively correlated with female polygamy (Wiklund and Forsberg 1991). Large male size can be selected for as a result of many processes. As a rule large individuals are competitively superior to smaller ones (Caldwell and Dingle 1979, Sigurjonsdottir and Parker 1981, Enquist and Leimar 1983, Thornhill 1984, 1987, Crespi 1986) and large males have been shown to have mating advantage in two butterfly species exhibiting female monogamy (Wickman 1985, Elgar and Pierce 1988). However, the fact that large male size has been shown to be associated with female polygamy, calls for some additional explanation that links large male size to polyandry. We believe that the answer is a sperm competition explanation. Firstly, it has been shown that the size of the ejaculate transferred to the female at mating is

positively correlated with male size in a number of butterflies (Svärd and Wiklund 1986, 1988, Forsberg and Wiklund 1989, Oberhauser 1988), and secondly females that have received large ejaculates seem to delay mating longer than those that have received small ejaculates (Labine 1964, Boggs 1981, Oberhauser 1989, Wiklund and Kaitala unpubl.). We contend that these processes result in sexual selection favouring large male size especially in species where females mate repeatedly.

Development time, growth rate and seasonality

Development time and growth rate of insects in temperate areas are influenced by (1) environmental seasonality, (2) selection for protandry, and (3) interactions between the two. In general insect development exhibits adaptations to the changing seasons which are especially obvious in species that are partially bivoltine and have two generations per year, like *P. napi*. This butterfly overwinters in the pupal stage, and adults of the overwintering generation eclose in May/June. The larvae hatching from the eggs laid in the beginning of the female flight period typically develop directly and produce a second generation of adults that eclose in July/August, whereas larvae hatching from eggs laid later enter the diapause developmental pathway and produce pupae that overwinter (see Fig. 1). In *P. napi*, as in the majority of insects, each individual responds to daylength and temperature and as a result enters either direct, or diapause, development (Wiklund et al. submitted). The daylength at which approximately half of the individuals develop directly and half diapause, is usually referred to as the "critical daylength" (Danilevski 1965, Tauber et al. 1986). If the switch is a threshold, this date marks the latest date at which individuals develop according to a bivoltine life cycle, and also the earliest date at which individuals develop according to a univoltine life cycle. Hence, time constraints on development time will be contingent to the developmental pathway entered, so that individuals entering diapause development at the critical daylength will have ample time available, whereas individuals that enter direct development will have little time available. The rationale is as follows: *P. napi* can only survive the winter in the pupal stage. Thus the problem for larvae entering diapause development is to have time to complete development and pupate before the winter, a problem which may be severe for larvae hatching late in the season (cf. Figs 1 and 2) but becomes increasingly less pressing the earlier in the season they hatch. Among the larvae entering diapause development those that hatch earliest in the season are those that enter this developmental pathway at the critical daylength. Thus, the size of individuals that enter diapause development at the critical daylength is little affected by time constraints related to the necessity of completing development before the winter.

242

The problem for individuals that develop directly is that they must complete a whole generation cycle extra compared to their diapausing sibs, and that not only they themselves but also their offspring must have time to complete development and pupate before the winter. Accordingly, time available to larvae that develop directly decreases as the season proceeds, and those that enter direct development at the critical daylength are the ones that have the least time available since these individuals are the ones that start their direct development latest in the season. Contingent to the different time constraints for individuals following the different developmental pathways, we predict that larval development time will be shorter under direct development than under diapause development. For the same reason we also predict that growth rate will be higher under direct development than under diapause development (see also Denlinger et al.'s (1988) general claim, when comparing neotropical insects that are characterized by the absence of diapause capacity with those that have the capacity, that a number of life history traits are associated with diapause capacity and that the development time of these under direct development is speeded up compared to the direct development of species that lack diapause capacity).

Development time, growth rate and protandry

Development time is also influenced by selection for males to emerge before females. This is known as protandry, and is found in the majority of insects with non-overlapping generations (Wiklund and Fagerström 1977). Theorists have attempted to account for protandry in terms of sexual selection acting either on males to maximize the expected number of matings (Wiklund and Fagerström 1977, Iwasa et al. 1983, Parker and Courtney 1983), or on females to minimize the prereproductive period (Fagerström and Wiklund 1982). There is incidental evidence that both are correct, and that protandry is not an incidental side-effect of some other process, but stems from sexual selection acting on both males and females (Wiklund and Solbreck 1982, Singer 1982; see also Elgar and Pierce (1988) for observational evidence of selection on early male emergence in *Jalmenus evagoras*). The time considerations leading to the expectation that the directly developing generation should have a shorter development time as a result of a higher growth rate is equally relevant to both sexes, but on top of this comes the selection pressure on males to be protandrous. Again the strength of this selection pressure is contingent on developmental pathway in *P. napi*. The reason is that protandry is accomplished differently in the two generations. In the directly developing summer generation development is uninterrupted, and protandry results from shorter development time, and higher growth rate, throughout the egg, larval and pupal stages. However, since the pupae overwinter in an undifferentiated stage

(as evidenced by the fact that post-diapause development of pupae takes longer than that of pupae developing without diapause at the same temperature, Forsberg and Wiklund 1988), protandry in the overwintering generation depends only on different post-diapause development rates of male and female pupae. Hence, larval growth rate and final size of individuals are decoupled from protandry in the diapausing generation. Accordingly, we predict not only that the directly developing generation will have a shorter development time than the diapausing one, but also that directly developing males will have shorter development time compared to females that develop directly. Moreover, since males are larger than females in *P. napi* (Wiklund and Forsberg 1991, Table 1), we predict that larval development of males under diapause development will be longer than that of females, on the assumption that growth rate of diapausing males and females are similar. Since *P. napi* is one of the most strongly polygamous butterflies in the Swedish fauna, males are also likely to be selected for large size. This leads us to predict that directly developing males will have a higher growth rate compared to directly developing females, both of which should have a higher growth rate compared to diapausing individuals.

Trade off between size and protandry

We have explained that selection should favour both protandry and large male size in the directly developing generation, but for obvious reasons the shorter development time of males should impair their ability to acquire large size. Indeed, Singer (1982) has stated that "If males are to emerge before females as a result of selection for protandry, they must have shorter development time than females, and hence will be smaller, if they grow at the same rate as larvae". According to Sibly and Calow (1986) "Growth processes may either be maximized to physiological/developmental limits or, on the assumption that high growth rates carry survival costs, be an optimum compromise between the fitness costs and benefits of different growth rates". Hence, growth rate should be regarded as a variable which is amenable to alteration by natural selection, a fact which has been demonstrated to apply to the speckled wood butterfly *Pararge aegeria*, where Nylin et al. (1989) have shown that larval growth rate among directly developing individuals are higher at daylengths close to the critical daylength which occurs in late July, compared to the longer daylengths characteristic of June or early July.

Although growth rate may be phenotypically plastic, it must have an upper limit. Hence, since directly developing males of *P. napi* seem to be selected both for large size and protandry, it seems reasonable to assume that they must make a trade off between the two. When both are not simultaneously achievable, the outcome of a trade off between protandry and large size will depend
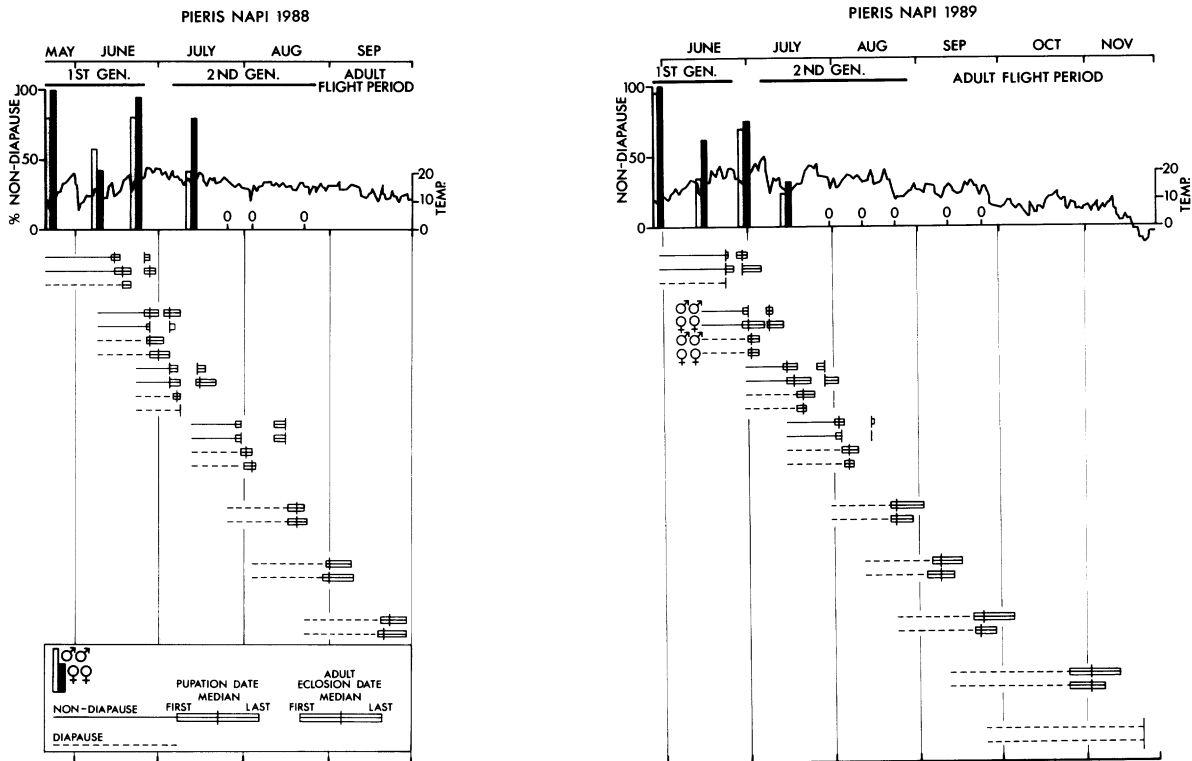
Fig. 2. The phenology of *P. napi* reared outdoors in central Sweden in 1988 and 1989. The percent of individuals developing without diapause for each cohort is indicated by vertical bars located on the date of larval hatching. The number of individuals in the cohorts were as follows: in 1988: 20 May– n = 16; 7 June – n = 19; 22 June – n = 36; 12 July – n = 39; 25 July – n = 37; 3 August – n = 32; 22 August – n = 39; and in 1989: 30 May – n = 32; 13 June 1 – n = 35; 29 June – n = 37; 14 July – n = 36; 30 July – n = 28; 11 August – n = 39; 23 August – n = 29; 11 September – n = 32 of which 10 individuals froze to death on 21 November. All of the 24 larvae that hatched on 24 September froze to death on 21 November at which time one was in the third instar, five were in the fourth instar and 18 were in the fifth instar.

critically on the strength of selection for these two traits. In general, selection for protandry should be strongest in species where females are monogamous (Wiklund and Fagerström 1977, Fagerström and Wiklund 1982). However, on the assumption that the latest male to mate with a female has sperm precedence, which seems to hold true in most butterflies (see review by Drummond 1984), protandry should become increasingly less important with increasing degree of polyandry. Conversely, selection for large male size is associated with polygamy (Wiklund and Forsberg 1991). Accordingly, we predict that in species where there is a trade off between protandry and large male size the balance should lean towards the achievement of protandry under female monogamy, and, conversely, towards the achievement of large male size under female polygamy. Since *P. napi* is one of the most strongly polyandrous species in the Swedish butterfly fauna, we predict that males will favour large size when forced to make a trade off between size and protandry.

In this paper we test the predictions advanced related to differences in development time and growth rate of males and females of *P. napi* under diapause and direct

development, and the prediction relating to the hypothesized trade off between protandry and size. We do this by comparing development time, pupal weight, and growth rate among seven replicates of rearings of larvae of *P. napi* under constant daylength and temperature conditions that produce split broods, i.e. where part of individuals develop directly and part diapause. Hence, all comparisons are made between individuals that are reared under identical temperature and daylength conditions on the same food in the same environmental chamber. In order to assess the natural phenology of *P. napi* in central Sweden, we also reared cohorts of larvae of *P. napi* started at hatching at approximately two week intervals, under outdoor conditions during two years.

Materials and methods

In order to assess how the proportion of directly developing individuals changes as the season progresses, we reared cohorts of approximately 40 larvae hatching on the same day throughout the season on a terrace (facing

Table 1. Mean development time (±S.E.), mean pupal weight (±S.E.) and developmental response of *P. napi* reared in a variety of constant conditions producing mixed broods where a fraction of individuals enter diapause, and another fraction enter direct development.

Daylength Temp.	Development	Larval development time (d)		Pupal weight (mg)		Sample size	
		Males	Females	Males	Females	Males	Females
22h	Direct	23.6±0.7	24.8±0.3	143±7	130±4	4	11
17°C	Diapause	27.7±0.4	26.0±0.5	140±3	130±3	16	16
22h	Direct	16.9±0.4	17.2±0.3	156±5	141±4	8	12
20°C	Diapause	18.9±0.3	18.0±0.6	144±5	134±8	11	3
19:00h	Direct	13.2±0.1	13.7±0.2	162±2	155±1	36	49
23°C	Diapause	15.3±0.6	14.8±0.8	158±3	154±3	6	4
18:45h	Direct	14.0±0.2	14.3±0.2	158±2	148±2	40	37
23°C	Diapause	17.8±0.4	16.3±1.0	157±2	154±4	8	6
18:30h	Direct	14.5±0.3	15.6±0.4	160±1	151±3	29	26
23°C	Diapause	17.3±0.4	17.1±0.5	153±3	152±3	15	7
18:15h	Direct	14.2±0.2	14.5±0.3	164±3	155±3	21	19
23°C	Diapause	16.8±0.2	16.6±0.3	157±2	149±3	27	14
18:00h	Direct	13.5±0.3	14.3±0.3	164±5	150±4	10	20
23°C	Diapause	17.0±0.3	16.7±0.3	161±1	154±3	36	23

west) of the Zoology building. Cohorts were started at approximately two week intervals. In 1988 cohorts were started between 20 May and 22 August, and in 1989 between 30 May and 24 September. Larvae were reared individually in plastic jars supplied with leaves of the natural host plant *Alliaria petiolata*. For each individual date of pupation was noted, and for directly developing ones also the day of adult eclosion. Directly developing individuals were sexed upon adult eclosion, whereas diapausing individuals were sexed by external morphological characters in the pupal stage.

Data on larval developmental times, pupal weight, and developmental pathway were assessed in 1986 and 1989. In 1986 larvae from eggs laid by six females that

Table 2. Mean growth rate (±S.E.), measured as percent weight increase per day from the date of larval hatch to the date of pupation, of male and female larvae of *P. napi* under diapause or direct development when reared at 23°C and daylengths that produce mixed broods.

Daylength (h)	Temp. (°C)	Direct development		Diapause development	
		Males	Females	Males	Females
22:00 N	17	34.9±0.40% 4	33.5±0.3% 11	30.0±0.5% 16	31.6±0.6% 16
22:00 N	20	54.8±1.4% 8	51.2±2.0% 12	47.0±0.8% 11	49.3±1.8% 3
19:00 N	23	75.4±1.0% 36	71.6±0.9% 49	61.8±3.2% 6	65.2±3.8% 4
18:45 N	23	69.9±1.5% 40	66.9±1.5% 37	51.6±1.4% 8	55.1±6.4% 6
18:30 N	23	67.2±1.5% 29	61.1±1.7% 26	53.4±1.7% 15	53.8±2.0% 7
18:15 N	23	68.7±1.5% 21	66.7±1.5% 19	55.3±0.8% 27	55.7±1.3% 14
18:00 N	23	73.5±1.9% 10	67.8±1.7% 20	54.8±1.5% 36	55.7±1.4% 23

Note that all values along the horizontal rows are perfectly comparable, as all individuals are sibs reared in one environmental chamber. Although all individuals reared at 23°C are pooled sibs from eggs laid by 12 females on the same day, values between individuals reared in daylengths 19:00, 18:45, 18:30, 18:15, and 18:00 are not perfectly comparable as individuals were reared in five separate environmental chambers and possible small differences in temperature between chambers will preclude comparison of values between rows.
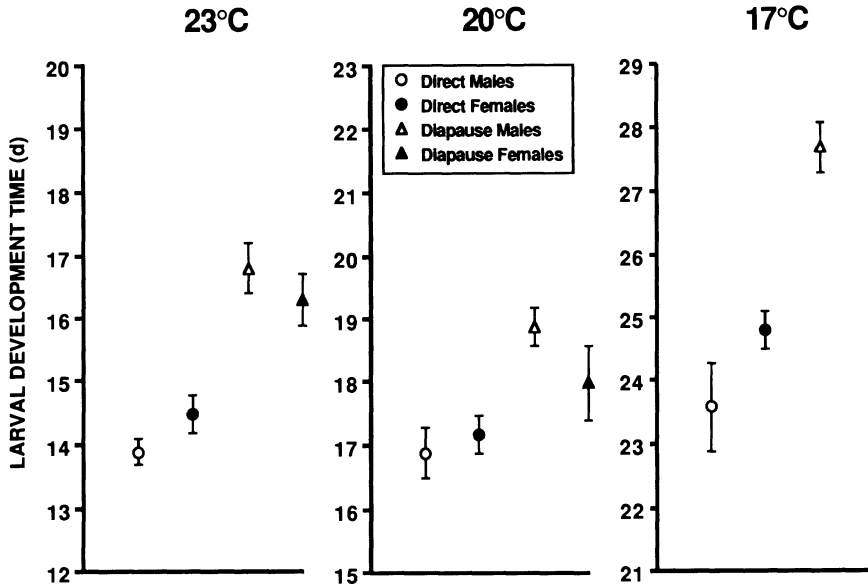
Fig. 3. Larval development time of males and females under direct and diapause development, respectively, at 17°C and a 22 h daylength, at 20°C and a 22 h daylength, and pooled results for larvae reared at 23°C and 18:00, 18:15, 18:30, 18:45 and 19:00 h daylengths.

were caught in the vicinity of Stockholm, Sweden, were reared at 17 and 20°C, respectively, under a L:D 22:2 cycle. As in the outdoor experiment larvae were reared individually in plastic jars where their host plant, *A. petiolata*, was cultured in ample supply. Age and weight at pupation were recorded. The numbers developing directly and the numbers diapausing were recorded. Diapausing individuals were kept at 4°C for 5 months, which is known to break diapause in all individuals of *P. napi* from the Stockholm area (Forsberg and Wiklund 1988), and then returned to their initial regime. In 1989, the same data were assessed from larvae from some 500 eggs laid on the same day by 12 females caught in the

vicinity of Stockholm. These eggs were pooled and some 440 larvae were reared at 23°C at five different daylengths, 18:00, 18:15, 18:30, 18:45 and 19:00 h.

The individual growth rate of each of the 514 larvae used in the experiments was calculated according to the formula for exponential growth

$$\% \text{ weight increase} = ((m_p/m_l)^{1/t} - 1) \times 100,$$

where m_p = pupal weight, m_l = larval weight at hatching, and t = time from hatching of the larva to pupation. To assess the weight of newly hatched larvae, a sample of 25 eggs were removed from the leaf on which they
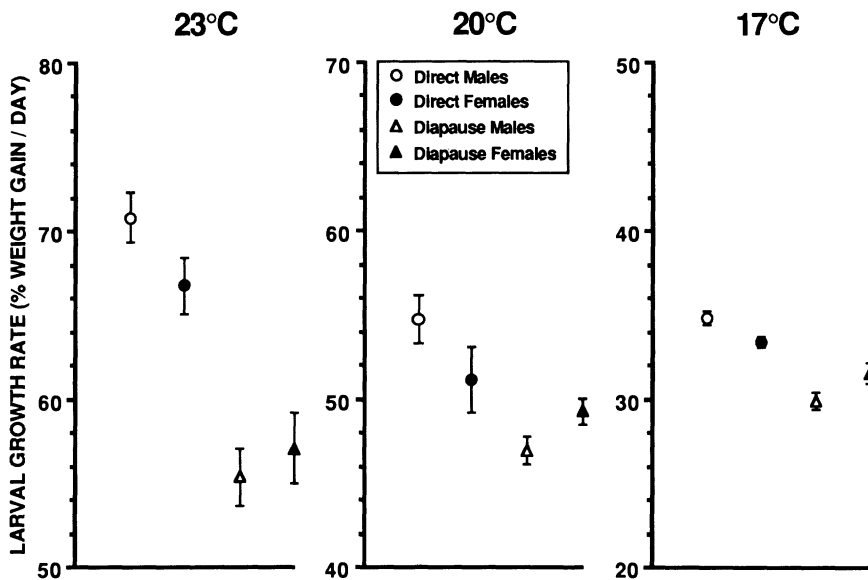

Fig. 4. Larval growth rate of males and females under direct and diapause development, respectively, at 17°C and a 22 h daylength, at 20°C and a 22 h daylength, and pooled results for larvae reared at 23°C and 18:00, 18:15, 18:30, 18:45 and 19:00 h daylengths.

Table 3. Analysis of variance for larval growth rates in relation to sex and developmental pathway, i.e. diapause or direct development.

Source	DF	Seq SS	F	P
Developmental pathway	1	1.85	261.12	0.000
Sex	1	0.04	1.86	0.174
Dev. Pathway × Sex	1	0.05	7.55	0.006
Error	429	2.88		
Total	432	4.82		

were glued and transferred to a moistened filter paper kept in a petri dish. The larvae were weighed on the day of hatching and their weight was 0.109 ± 0.004 mg (mean ±S.E.). Variance in egg weight is very small in pierids (Jones et al. 1982, Wiklund unpubl.), and since a newly hatched larva can increase its weight some 50% after a few hours of feeding, a standardized weight for newly hatched larvae of 0.100 mg was used when calculating the growth rate for each individual.

Protandry for individuals developing directly was assessed by rearing larvae from the same population at 17, 20 and 23°C under a L:D 22:2 cycle. Protandry for diapausing individuals from the same population was assessed by rearing larvae at the same three temperatures under L:D 16:8 cycle, after which post-diapause development times were recorded when pupae were brought back to initial conditions after spending between 4 to 8 months at 4°C to break their diapause.

Results

Under outdoor conditions some of the larvae that hatch from May to mid-July develop directly and produce pupae from which adult butterflies eclose after one to two weeks (Fig. 2). In both 1988 and 1989 all of the female larvae in the May cohorts developed directly, whereas at least some males entered diapause development in all cohorts. Larval development time was shortest during June/July, where some of the larvae in the 22 June cohort completed development in 12 d in 1988. Larval development time increased with the progression of the season as temperatures decreased and the median larval development time for larvae hatching on 11 September in 1989 was 52 d. Out of the 32 larvae hatching on this date, only 22 completed development and survived, whereas 10 individuals were killed by frost on 21 November (four were killed as V instar larvae, three as prepupae and three as newly formed pupae). In the same year all of the 24 larvae hatching on 24 September were also killed by frost on 21 November, by which time the larvae ranged between the third and fifth instar.

Qualitatively, the results from the seven replicates of rearings in the laboratory are identical regarding larval development time and growth rate, and almost identical regarding pupal weigth (Tables 1 and 2; Figs 3 and 4). Larval development time was invariably shorter under direct than under diapause development (Table 1; Fig. 3). This is in agreement with the hypothesis that the directly developing generation is under a more severe time constraint than the diapausing generation. The probability that this result should be replicated by chance in the predicted direction seven times equals $(1/2)^7 = 0.008$ for both males and females.

Moreover, as predicted by the hypothesis that males are selected to emerge before females, larval development time was shorter than that of females under direct development in all seven replicates. However, in the diapausing generation, where larval development time is decoupled from protandry by the intervening winter, larval development time of males was longer than that of females in all seven replicates, as was predicted by the fact that male pupae are heavier than female pupae. Again the probability that this difference in larval development time should be replicated in the predicted direction by chance is $(1/2)^7 = 0.008$.

Most interestingly, the shorter development time of directly developing males was not accompanied by loss of weigth (Table 1). Not only was the mean pupal weight of males greater under direct than under diapause development in all seven replicates (the overall mean values being 158 ± 3 mg (±S.E.) under direct and 147 ± 3 mg under diapause development), but also the difference in pupal weight between the sexes (the overall mean difference between male and female pupal weights being 11 ± 1 mg under direct, and 6 ± 1 mg under diapause development in the seven replicates). The probability that these weight differences should point in the same direction in these seven replicates is $2 \times (1/2)^7 = 0.015$ for each of these two comparisons which shows that the shorter development time by males under direct development is accompanied by a relative increase in size (Table 1).

Naturally, this can only be achieved by means of an increase in growth rate on the part of the directly developing males, which is indeed the case (Table 2, Fig. 4). Since size is important to females as well, we earlier predicted that growth rate should be higher under direct than under diapause development, as a result of the former generation developing under a more severe time constraint. On top of this comes the selective pressure on males to emerge before females, which led us to predict that directly developing males should exhibit the highest growth rate of all. The empirical data confirm this prediction in all seven replicates. The probability that this pattern should appear due to chance is $(1/6)^7 = 3.6 \times 10^{-6}$. In fact, the pattern of growth rate replicates that of development time, so that directly developing males exhibit the highest rate, followed by directly developing females, followed by diapause developing females, which are followed by diapause developing males. Moreover, a two-way ANOVA on growth rate

Table 4. Protandry, measured as the number of days males emerge before females, for directly developing and diapausing generations of *P. napi* reared at 17, 20 and 23°C, and a L:D 22:2, or a L:D 16:8 cycle.

Development	Protandry (d) (mean ±S.E.)	Number of	
		experiments	individuals
Direct	0.65±0.16	4	201
Diapause	1.39±0.14	17	336

shows that there is a significant interaction between sex and developmental pathway (Table 3), which means that males in the directly developing generation have an accelerated growth rate relative to females compared to the diapausing generation. This is in agreement with the predictions from the hypothesis that males are selected to emerge before females, a selective pressure which is relevant only in the directly developing generation since larval growth rate and protandry are decoupled in the diapausing generation.

In the treatment designed to assess protandry at 17, 20 and 23°C, development times were influenced by temperature, but the difference between the sexes was not. The same holds true for post-diapause development times for pupae that had spent different time periods at 4°C (cf. Forsberg and Wiklund 1988). Therefore, data on protandry are pooled for diapausing and directly developing individuals, respectively. Males emerged on average 1.39 d before females in the overwintering generation, whereas the mean difference was only 0.65 d in the directly developing generation (Table 4). This difference was statistically significant (Table 4: t = 2.67; df = 17; p < 0.02). Hence, protandry is less pronounced in the directly developing generation which lives under more severe time constraints than the diapausing generation. Since the size of directly developing males is as great as that of diapausing males, the evidence suggests that males of *P. napi* have to make a trade off between size and protandry under direct development, and that both cannot be achieved in spite of the fact that directly developing males exhibit accelerated growth rate.

Discussion

The results show that the directly developing generation of *P. napi* lives under a more severe time constraint than the diapausing generation, and suggests the interpretation that this results in a shortening of the larval development time which is made possible by an increase in growth rate. The results also demonstrate that the growth rate of males is accelerated relative to females in the directly developing generation, which is in agreement with our predictions based on the hypothesis that

this results from selection on males to emerge before females. Moreover, the fact that protandry is less accentuated under direct than under diapause development, whereas the size of directly developing males is not reduced, suggests that males trade off protandry for size under direct development. This is consistent with our predictions based on the hypothesis that polyandry selects for large male size, whereas monandry primarily selects for protandry.

Seasonality and time constraint

The reason why the directly developing generation is time constrained can be illustrated by Fig. 2. In 1989 all of the larvae hatching on 11 September pupated before the autumn frosts, but 11 of the 35 larvae hatching on 24 September died in the first cold spell of the autumn on 21 November. The latest cohort to produce directly developing individuals hatched on 14 July, eclosing as adults on 14 and 15 August. If we estimate that the duration of the egg stage is some 10 d, the first laid eggs from the females would hatch in mid-August, which means that they would have time to complete development and pupate before the frosts occurred in 1989. However, since female *P. napi* can live up to three weeks (Wiklund, unpubl.) eggs laid by two week old females would not hatch until late September, which means that a portion of them would be killed as larvae by the first autumn frosts. Moreover, the actual date on which the lethal autumn frosts appear varies drastically between years, and in 1988 the first frosts occurred almost a whole month earlier, on 24 October. If the cold period had occurred on this date in 1989, it is likely that both cohorts that hatched in September would have been killed. Two conclusions may be drawn from the data on the natural phenology of *P. napi* illustrated in Figs 1 and 2. Firstly, the directly developing generation is time constrained because of the risk that the offspring will not have time to complete development and pupate before the autumn frosts. Secondly, the mechanism for producing directly, or diapause, developing individuals seems well adapted to the local environment with the second generation flying at a time period when the majority of the offspring should have time to complete development and pupate before the winter.

Phenotypic plasticity in growth rate

As a result of the time constraint on the generation that develops directly, growth rate is increased under direct compared to diapause development. Moreover, selection on directly developing males to emerge before females comes on top of the seasonal time constraint, and this results in a still more accelerated growth rate in non-diapausing males. These findings, in conjunction with Nylin et al.'s (1989) observations on the extreme

248

variability in growth rate of *Pararge aegeria* at constant temperature under different daylength regimes, emphasize that insects exhibit adaptive plasticity in growth rate that we feel is unexpected in an ectothermic animal. This capacity to "choose" growth rate may appear surprising and can only be understood in the light of physiological theory which assumes that increased growth rate among juveniles is associated with survival costs (Sibly and Calow 1986). This assumption has considerable empirical support from mammals and birds (Clutton-Brock et al. 1985), fish (Beverton and Holt 1959), echinoderms (Ebert 1985), and insects (Sharpe and Detroy 1979). What survival costs can conceivably be associated with increased growth rate in larvae of *P. napi*? In this butterfly ovipositing females often lay eggs on small crucifer rosettes (Forsberg 1987a), which means that the larvae often have to find at least one new host plant to become fully grown. It seems reasonable to assume that a higher metabolic rate decreases the capacity of larvae to endure starvation. Moreover, it seems generally true among animals that males have a higher growth rate and as a result suffer higher mortality (cf. Clutton-Brock et al. 1982, Sherman and Morton 1984, Trivers 1985, Sibly and Calow 1986). In this context it is also relevant to note the lower propensity of males to develop directly at the critical daylength (Table 1). The observation that males have a different reaction norm for direct development compared with females, so that males enter diapause development earlier in the season than females, has been explained as a result of selection for protandry (Wiklund et al. 1991). ESS models show that late emerging males are penalized in terms of fewer mating opportunities, which means that males have to increase their growth rate quite drastically to emerge before females in the time constrained directly developing generation (Parker and Courtney 1983, Iwasa et al. 1983). Hence, the high growth rate necessary for males to be able to realize protandry under direct development might be associated with so high a cost, that delaying emergence until next year by entering diapause development may be more profitable. It seems also relevant to point out that the assumed survival cost associated with increased growth rate makes it unimportant, in the present context, to decide if direct development in itself affects growth rate, or if only individuals capable of increasing their growth rate enter the pathway of direct development at the critical daylength.

Male trade off between size and protandry

Although males that develop directly increase their growth rate, protandry among the directly developing individuals was only half of that in the diapausing generation. Does this indicate that protandry was suboptimal in one of the generations? According to theory, protandry should increase with male longevity and the du-

ration of the eclosion period (Wiklund and Fagerström 1977, Fagerström and Wiklund 1982). When comparing the duration of the flight periods (which gives a combined tentative measure of both longevity and the duration of the eclosion period) of the two generations of *P. napi* in the Stockholm area, it is apparent that the duration of the flight period of the directly developing second generation is somewhat longer than that of the overwintering first generation (Forsberg 1987b). Hence there is little reason to believe that the more pronounced protandry that we found in the overwintering generation should be an adaptive response, since theory would predict protandry to be at least as profound in the directly developing generation. On the contrary, the fact that protandry was less pronounced in the directly developing generation suggests that protandry was suboptimal under direct development.

Conversely, males developing directly under severe time constraints became as large as males under diapause development (Table 1). Hence, large size appears to be favoured by *P. napi*. Why is this so? A comparative study of 23 species of Swedish butterflies in the Pieridae and Satyridae has shown that male/female sexual size dimorphism is positively correlated with female polygamy (Wiklund and Forsberg submitted). Spermatophore counts on females of *P. napi* caught in the Stockholm area has shown that they mate up to five times, and that females mated on average 2.03 times (Forsberg and Wiklund 1989). Thus *P. napi* is one of the most polyandrous butterflies out of the odd twenty species of Swedish butterflies that have hitherto been studied (Svärd and Wiklund 1989), and in agreement with the pattern outlined above males of *P. napi* should be expected to be strongly selected for large size.

Hence, we argue that sexual selection favours both protandry and large male size in *P. napi*. Unless both ends can be achieved by increased growth rate, we contend that the outcome of a trade off between protandry and size will depend critically on the strength of selection on these two "characters", so that large male size will be favoured under polyandry, and protandry (i.e. short development time) will be favoured under monandry. The results in this study suggest a trade off in the predicted direction in *P. napi*, but a rigorous test of the above hypothesis demands a comparative study of several species that have variable mating systems.

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