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A SEX DIFFERENCE IN THE PROPENSITY TO ENTER DIRECT/DIAPAUSE DEVELOPMENT: A RESULT OF SELECTION FOR PROTANDRY

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Abstract.—In monandrous mating systems with discrete nonoverlapping generations males should maximize the expected number of matings by starting to emerge before females. This is known as protandry. Moreover, Evolutionarily Stable Strategies (ESS) models show that the male emergence curve should be abruptly truncated before female emergence has ceased. In temperate areas where many insects have partial second generations, we accordingly predict that males should enter diapause development at an earlier date than should females, as a result of late-emerging males being penalized in terms of fewer mating opportunities. The decision to diapause or to develop directly is usually mediated by response to environmental stimuli of which day length is the most important. Hence we predict that the mechanism by which males enter diapause at an earlier date than females will be that of the male reaction norm for diapause development being shifted towards longer day lengths when compared to that of females. As a result of the greater tendency of males to enter diapause development, partial second generations that develop directly should be female biased. As a corollary, first generations should be male biased because some males of the first generation are from the previous year. The prediction that males should enter diapause development earlier in the season, i.e., at longer day lengths, as compared to females was corroborated by rearing *Pieris napi* under a variety of critical day length regimes producing mixed broods of directly developing and diapausing individuals, and by outdoor rearings of cohorts of larvae of *P. napi* and *P. rapae* initiated throughout the season. The prediction that partial second generations should be female biased was corroborated by laboratory rearings at constant temperature of *P. napi* (Pieridae), *Polygonia c-album* (Nymphalidae), and *Pararge aegeria* (Satyridae) under critical day length conditions, producing female-biased sex ratio under direct, and male-biased sex ratio under diapause development.

Key words.—Butterflies, development, diapause, protandry, reaction norms, sex difference, sexual selection.

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In monandrous mating systems with discrete nonoverlapping generations males should maximize the expected number of matings by starting to emerge before females (Wiklund and Fagerström, 1977; Fagerström and Wiklund, 1982). This is known as protandry. Moreover, Evolutionarily Stable Strategy (ESS) models show that not only should males start to emerge before females but also cease to emerge before females (Bulmer, 1983; Iwasa et al., 1983; Parker and Courtney, 1983). More specifically, even if the female eclosion curve is smooth with one peak, the male eclosion curve should be abruptly truncated before female emergence has ceased (cf. Fig. 1 in Iwasa et al., 1983). In temperate areas many insects have a partial second generation that is due to season length not being long enough to support complete bivoltinism. In partial second generations we predict that males should enter diapause development at an

earlier date than should females, as a result of late emerging males being penalized in terms of fewer mating opportunities, and so postpone emergence until next season. This prediction follows logically from theories on optimal timing of eclosion of males relative to females when applied to partially bivoltine populations but has not been realized before.

The decision to diapause or to develop directly is usually mediated by response to environmental stimuli of which day length is the most important but also temperature can play a role (Danielvskii, 1965; Tauber et al., 1986; Danks, 1987). Hence, we predict that the mechanism by which males enter diapause development at an earlier date than females will be that of the male propensity to enter diapause development being shifted towards longer day lengths when compared to that of females (see Fig. 1). More specifically, we predict that the

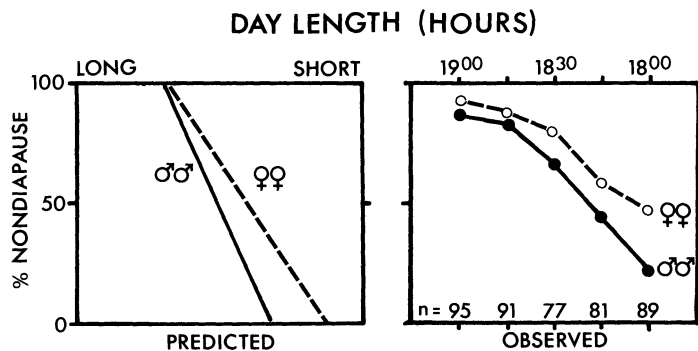


FIG. 1. The difference between males and females in the propensity to develop directly in response to photoperiod, (left) as predicted by theory, and (right) as shown by *P. napi* reared at 23°C and the day lengths 18:00, 18:15, 18:30, 18:45, and 19:00 hr. The number of individuals reared in each day length is shown at the bottom of the figure.

difference in diapause propensity between the sexes should increase when approaching the point where all individuals enter diapause development, because directly developing males will be most severely penalized when few, or no, females develop directly. This means that a higher percentage of females should develop directly at any given photoperiod during the interval of day lengths that produce mixed broods, i.e., broods in which some of the individuals develop directly and others enter diapause development. As a result, partial second generations should be female biased, on the assumption that the primary sex ratio is unity. As a corollary, first generations of populations exhibiting partial bivoltinism should be male biased because some males of the first generation are from the previous year. In this paper we test for a difference between the sexes in the propensity to enter direct/diapause development in the predicted direction by rearing larvae of the green-veined white butterfly, *Pieris napi* L., in a variety of photoperiods in the critical day length interval, i.e., day lengths producing mixed broods. We also test for a difference between the sexes in the propensity to develop directly under seminatural conditions by rearing cohorts of larvae of *P. napi* and *P. rapae* hatching at approximately two-week intervals throughout the season, and noting the respective proportion of males and females that enter direct development. Moreover we test for a female bias under direct development, and a male

bias under diapause development, for the butterflies *P. napi* (Pieridae), *Polygonia c-album* (Nymphalidae), and *Pararge aegeria* (Satyridae), when reared at constant temperature in the laboratory under critical day length regimes. All of the four butterflies used in the experiments are generally protandrous, as are indeed the majority of insects (Wiklund and Fagerström, 1977; Forsberg and Wiklund, 1988; Nylin et al. 1989; Wiklund and Forsberg, 1991; Nylin and Wiklund, unpubl. data).

MATERIALS AND METHODS

Life History of the Studied Species

The two pierid butterflies, *P. rapae* and *P. napi*, have similar life histories. Both spend the winter in the pupal stage and the first generation of adults flies in May/June. Eggs are laid throughout the female flight period and a second generation of adults flies in July/August, resulting from individuals that have developed directly through the egg, larval, and pupal stages. Typically, abundance of adults is greater in the second generation of both of these butterflies (cf. Heath et al., 1984). The nymphalid butterfly *Polygonia c-album* usually emerges in June/July and overwinters as an adult, before maturing sexually in the following spring. Mating and egg laying take place from late April to early June. In some years part of the adults that emerge in June/July may mature sexually within a week after emergence and produce a new generation of adults that

emerge in late August/September, before hibernating as adults. The satyrid *P. aegeria* has a rather complicated life cycle, but is bivoltine in southern Sweden (Nylin et al., 1989; Wiklund et al., in prep.). Winter can be spent in the pupal stage, and the adults of the first generation fly from late April to early June. The offspring from this generation produce a second generation of adults that is on the wing in July/August. *P. aegeria* can also hibernate as half-grown larvae that produce a first generation of adults that fly in June. The offspring of this generation produce a second generation of adults that fly in August/September. Hence, all four butterflies used in our experiments generally seem to have nonoverlapping generations in nature.

*Laboratory Experiments to Assess
Diapause Propensity in
Relation to Sex*

To establish the propensity to enter direct/diapause development of males and females of *P. napi*, we collected 12 females on one day in the vicinity of Stockholm, Sweden, pooled the eggs laid by the females on the day of their capture, and reared a total of 433 larvae to pupation at 23°C at five different day lengths, 18:00, 18:15, 18:30, 18:45, and 19:00 hr. All larvae were reared individually in plastic jars in which leaves of the natural host plant *Alliaria petiolata* were cultured in ample supply. Pupae were allowed to remain at 23°C for three months, and pupae that had not produced adults by then were classified as diapausing. A total of 287 pupae produced adult butterflies after 9 to 15 days after pupation, whereas none of the remaining 146 pupae produced adult butterflies between the 16th and 90th day after pupation before being brought to a cold room to break the diapause. Directly developing individuals were sexed upon eclosion, whereas diapausing individuals were sexed as pupae.

*Outdoor Experiments to Assess
Diapause Propensity in
Relation to Sex*

To study the phenology of *P. napi* and *P. rapae* under seminatural conditions, and to assess the diapause propensity in relation to sex, we reared cohorts of larvae hatching at

approximately two-week intervals throughout the season in 1988 for both species, and in 1989 for *P. napi* alone (cf. Fig. 2). Larvae were reared individually in plastic jars on leaves of the natural host plant *A. petiolata*. Approximately 40 larvae were reared in each cohort and in total 204 larvae of *P. rapae* were reared in 1988, whereas 186 and 207 larvae of *P. napi* were reared in 1988 and 1989, respectively. Some pupae produced adults within three weeks of formation, whereas part of the pupae had not produced adults when they were brought to the laboratory in the beginning of December. Directly developing individuals were sexed upon eclosion, whereas pupae remaining intact by the beginning of December were sexed as pupae and judged to be diapausing.

*Sex Ratio in Second Generations in
Laboratory Experiments*

Mixed broods of *P. napi*, *P. c-album*, and *P. aegeria* were produced by rearing them in environmental cabinets at constant temperatures in a variety of day lengths. In *P. napi* mixed broods were produced by rearing larvae individually in plastic jars on their natural host plant *A. petiolata* in constant day lengths ranging between 18 hr to 19 hr at a constant temperature of 17, 20, or 23°C. In *P. c-album*, mixed broods were produced by rearing larvae individually in plastic jars where the natural host plant *Urtica dioica* was cultured in ample supply at a constant temperature of 20 or 23°C, and by moving larvae from a shorter constant day length to a longer constant day length, usually from 18 hr to 20 hr, when the larvae were 4, 6, or 8 days old (cf. Nylin, 1989). Mixed broods of *P. aegeria* were produced by rearing larvae individually in plastic jars in which the grass *Poa annua* was cultured in ample supply, at a constant temperature of 17°C, and constant day lengths of 16:00, 16:30, and 17:00 hr.

RESULTS

The propensity to enter diapause/direct development in *P. napi* differed between sexes as predicted and the proportion of males that entered direct development was lower than that of females when all five day lengths were considered together (Table 1; Fig. 1; 2 × 2 Analysis, $\chi^2 = 9.47$, $P = 0.002$).

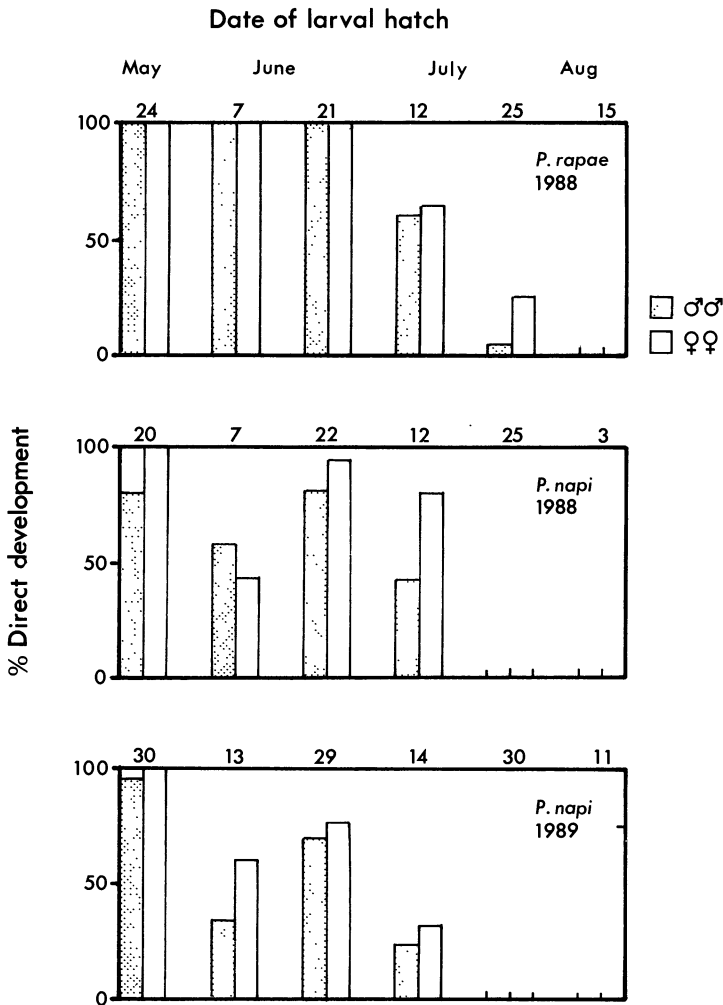


FIG. 2. Percent directly developing males and females of *P. rapae* and *P. napi* reared outdoors throughout the season. Cohorts of approximately 40 larvae were reared, and the hatching date of each cohort is shown above the bars. The number of individuals in each cohort reared is shown in Table 3.

The results from the laboratory experiments on *P. napi* allow tentative quantification of the time difference in the propensity to enter diapause development between the sexes. The assessment of the percentage of diapausing males and females at 15-minute intervals at 23°C between 19:00 to 18:00 hr day lengths, can be used to calculate a regression for each sex. This yields r^2 values of 0.948 and 0.955 for males and females ($P < 0.01$ for both sexes), respectively. Solving for the time difference when 50, 75, and 100% of the members of each sex enter diapause, shows that the time difference between the two regression lines in-

creases from 19 over 27 to 36 minutes (Table 2; Fig. 3). The regression shows that all males should enter diapause at a day length of 17:36 hr and all females should do the same at a day length of 17:00 hr. Just as the difference in time increases towards the point where all individuals enter diapause development, so does the difference in terms of number of days that separate the regression lines. However, this goes at a slower pace as a consequence of the fact that change in day length is minimal at summer solstice, which is on June 22, and then increases towards autumn equinox. Hence, according to the regressions, the difference in photo-

TABLE 1. Number of males and females of *P. napi* that enter direct or diapause development when reared at 23°C and five different day lengths.

Day length (hr)	Male development		Female development		Number of individuals		
	Direct	Diapause	Direct	Diapause	Males	Females	All
19:00	36	6	49	4	42	53	95
18:45	40	8	37	6	48	43	91
18:30	29	15	26	7	44	33	77
18:15	21	27	19	14	48	33	81
18:00	10	36	20	23	46	43	89
Total	136	92	151	54	228	205	433

periods for the diapause propensity of males and females of 19, 27, and 36 minutes, translates to a difference in terms of days to 6, 7, and 8 days, respectively, when translated to actual calendar dates at the Stockholm latitude (Table 2; Fig. 3).

Although the regression lines for the two sexes appear to diverge, as predicted by theory, the difference in slope was not quite statistically significant (ANCOVA, MINITAB 7 (1989), $P = 0.07$, one-tailed analysis). Hence we have been unable to get strong experimental support for our theory that the difference between the sexes in propensity to enter diapause development should increase towards the day length where all individuals diapause. However, apart from the above tendency for the regression lines to diverge, circumstantial evidence in support of our theory is furnished by the observation that the only day length for which there was statistical significance for the higher tendency of males to enter diapause was at the 18:00 day length (2×2 Analysis, $\chi^2 = 6.10$, $P < 0.05$), i.e., the day length closest to the point where all individuals are expected to enter diapause (Table 1).

The results of the outdoor rearings differ somewhat between the two species studied

(Table 3; Fig. 2). In *P. rapae* all individuals hatching as larvae in May and June developed directly to produce a second generation of adults that emerged later the same season. Larvae hatching in July had a mixed response and some individuals developed directly and others entered diapause development. The proportion of individuals developing directly decreased from 63% to 14%, for the two cohorts of larvae that hatched on July 12 and 25, respectively, and it is noteworthy that a higher proportion of females developed directly in both of these mixed brood cohorts. All of the larvae that hatched on August 15 produced diapausing pupae. This seasonal change from direct to diapause development as a function of hatching date strongly resembles the gradual decrease in the proportion of individuals that enter direct development as produced at different day lengths under laboratory conditions in *P. napi* (Fig. 1). In *P. napi*, the pattern of seasonal development was similar, but all cohorts were mixed broods although all of the females in the first cohorts developed directly both in 1988 and 1989. Essentially, most larvae hatching in May and June developed directly, although a peculiar decrease in the proportion of direct

TABLE 2. Propensity of males and females of *P. napi* to enter diapause development in terms of day length and translated to calendar dates from the Stockholm latitude as calculated from regressions for males and females derived from laboratory data shown in Table 1.

Diapause %	Day length (hr and min)			Calendar date ¹		
	Males	Females	Difference (min)	Males	Females	Difference (d)
0	19:06	19:04	2	—	—	—
25	18:44	18:34	10	—	—	—
50	18:21	18:02	19	July 5	July 11	6
75	17:58	17:31	27	July 12	July 19	7
100	17:36	17:00	36	July 18	July 26	8

¹ Because the maximum day length at summer solstice is 18:31 at the Stockholm latitude, day lengths longer than that cannot be translated into calendar dates.

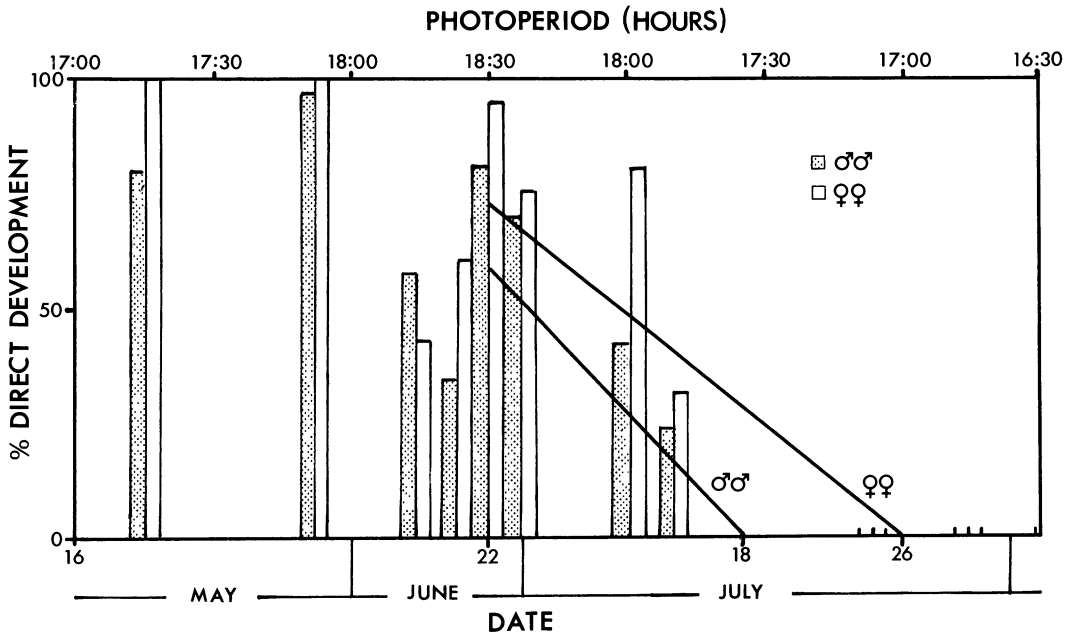


FIG. 3. Regression lines for the propensity to develop directly of males and females of *P. napi* as calculated from the empirical results obtained at 23°C and day lengths from 18:00 to 19:00 hr (data shown in Table 1). The bars show the empirical values from outdoor rearings in 1988 and 1989 (data shown in Table 3). Photoperiods are shown above the figure and the corresponding calendar dates are shown below the figure. Note that changes in day length are smallest close to summer solstice, which occurs on June 22, and that no males or females developed directly in the cohorts hatching on July 25, 1988 or July 30, 1989, as indicated by short vertical lines on the horizontal line indicating calendar dates.

development occurred in early June cohorts both years, and the latest cohorts to produce mixed broods were the ones that hatched early in July. Cohorts hatching in late July or later produced only diapausing pupae. Because our theory predicts that males should have a higher tendency to enter diapause than females, all of the mixed brood cohorts can be used as a test. In 9 of the 10 mixed brood cohorts of *P. rapae* and *P. napi* a higher proportion of males entered diapause when compared to females. The probability that the sex ratio should be in the predicted direction in 9 cases out of 10 is $11/1024 = 0.01$. It may also be relevant to point out that the only cohort in which the higher tendency for males to enter diapause development was statistically significant was that of *P. napi* larvae hatching on July 12, 1989, i.e., the date closest to the day length when all individuals enter diapause development (Table 3; Fig. 2; 2×2 Analysis, $\chi^2 = 5.9$, $P < 0.05$). Hence, both patterns observed in the laboratory experiments, viz.

that of males having a higher tendency to enter diapause development compared to females, and this tendency becoming more pronounced towards the day length where all individuals diapause, were supported by the outdoor experiments.

As predicted by theory the sex ratio was female biased under direct development, which corresponds to the partial second generation in the field, and male biased under diapause development for *P. napi*, *P. c-album*, and *P. aegeria* when reared under laboratory conditions that produced mixed broods (Table 4).

DISCUSSION

The results show that males tend to enter diapause development at longer day lengths than do females (Fig. 1), and as a result the sex ratio is female biased in the generation that develops directly. This result is observed both under controlled constant conditions in the laboratory (Table 1), and under outdoor conditions where the animals

TABLE 3. Number of males and females of *P. rapae* and *P. napi* that enter direct or diapause development in relation to time of larval hatch when reared under outdoor conditions.

Species	Year	Hatch date	Males		Females		Number of individuals		
			Direct	Diapause	Direct	Diapause	Males	Females	All
<i>P. rapae</i>	1988	24.v	17	0	16	0	17	15	32
		7.vi	21	0	17	0	21	17	38
		21.vi	20	0	14	0	20	14	34
		12.vii	11	7	11	6	18	17	35
		25.vii	1	18	4	12	19	16	35
		22.viii	0	18	0	18	18	18	36
<i>P. napi</i>	1988	20.v	8	2	6	0	10	6	16
		7.vi	7	5	3	4	12	7	19
		22.vi	13	3	19	1	16	20	36
		12.vii	8	11	16	4	19	20	39
		25.vii	0	19	0	18	19	18	37
		3.viii	0	15	0	17	15	17	32
		22.viii	0	17	0	22	17	22	39
<i>P. napi</i>	1989	30.v	22	1	9	0	23	9	32
		13.vi	6	11	11	7	17	18	35
		29.vi	14	6	13	4	20	17	37
		14.vii	4	13	6	13	17	19	36
		30.vii	0	16	0	12	16	12	28
		11.viii	0	20	0	19	20	19	39

experience natural temperatures and day lengths (Fig. 2). These results were predicted as a consequence of selection for protandry, as a result of selection against late emerging males in terms of fewer mating opportunities. We have analyzed the difference between the sexes in their respective propensity to enter diapause development on the population level, and hypothesize that the effect we have observed is brought about by males and females having different norms of reaction for direct/diapause development with respect to day length. Moreover, we contend that the pattern of the reaction norm for males to enter diapause development earlier in the season as a result of selection for protandry, has wide generality. The quantitative separation between the reaction norms of males and females will be contingent on a variety of factors, as will be

the magnitude of the female bias in the sex ratio of the partial second generation.

The existence of partial bivoltinism in temperate areas is likely to result from lack of time for offspring from late-developing individuals in the second generation to have time to reach the species-specific hibernating stage before the winter (Wiklund et al., 1991). Hence, selection should favor female offspring of the first generation that can respond to seasonal cues so that they enter diapause and emerge next season instead of eclosing too late the same season in terms of offspring survival. This means that males should also be selected to react to seasonal cues so that they do not emerge suboptimally late in terms of fewer mating opportunities. Since ESS models show that male emergence should be abruptly truncated before female emergence has ceased (cf. Iwasa

TABLE 4. Number of males and females that enter direct or diapause development under constant temperature and photoperiod conditions that produce mixed broods in three species of butterfly.

Species	Development				Number of individuals			p^1
	Direct		Diapause		Males	Females	All	
	Males	Females	Males	Females				
<i>P. napi</i>	189	295	152	86	341	381	722	<0.001
<i>P. c-album</i>	141	155	91	43	232	198	430	<0.001
<i>P. aegeria</i>	64	95	56	34	120	129	249	<0.001

¹ Chi-square 2 × 2 Analysis.

et al., 1983), males should accordingly start to enter diapause at an earlier date than females on the assumption that the development times of the sexes are equal from the time when the decision whether to diapause or not is made. Obviously the magnitude of the difference between the reaction norms of the sexes will decrease with the ability of males to shorten their development time, and the earlier during larval development the decision whether to diapause or develop directly is taken.

Data from the outdoor rearings of *P. napi* also appear to be in reasonably good agreement with the difference between the sexes in diapause propensity derived from the laboratory rearings when the percent direct/diapause developing individuals are mapped on the time scale using the date of larval hatch (Fig. 3). This suggests that the decision to develop directly or to enter diapause development is taken relatively early in larval development. (The decrease in direct development for cohorts hatching in early June is surprising. A tentative explanation may be that the day lengths at that time are confused with the identical day lengths in early July, at which time a decrease in direct development would be appropriate. Perhaps the relatively small changes in day length during this time of the year is also responsible, because a large proportion of individuals enter direct development when hatching in May, and accordingly do not mistake the relatively short day lengths for similar day lengths that occur in late July, when few individuals develop directly.)

Recent studies have shown that larval growth rate can be highly variable, both between sexes and developmental pathways, i.e., direct or diapause development, (Nylin et al., 1989; Wiklund et al., 1991; Nylin, 1992.). For instance, at 23°C growth rate in larvae of *P. napi*, measured as percent weight gain per day, varied from 71 ± 1 to $67 \pm 1\%$ (mean \pm SE) between directly developing male and female larvae, and between 56 ± 1 to $57 \pm 1\%$ between male and female larvae destined to diapause in the pupal stage. Not only was this difference significant between developmental pathways, but there was also a significant interaction between sex and pathway, showing that directly developing males increased their

growth rate relative to females (Wiklund et al., 1991). The corresponding development times were 13.9 ± 0.2 to 14.5 ± 0.3 days for males and females under direct development, and 16.8 ± 0.4 to 16.3 ± 0.4 days for males and females that later diapaused in the pupal stage. Hence, although male larvae of *P. napi* are able to increase their growth rate under direct development relative to females, and the decision whether to diapause or not appears to be made relatively early in the early larval instars, it appears that the decrease in development time that males can achieve does not fully compensate for the required time difference between the sexes which appears to be in the order of some six to eight days (Table 2).

As a result of the difference in reaction norms between the sexes, partial second generations will be female biased. The magnitude of this bias in nature will be contingent on the temporal distribution of eggs laid by first generation females. Specifically the female bias will depend on the proportion of directly developing offspring that develop at the interval of critical day lengths, and will be smaller the fewer the offspring that develop during that interval. This is obvious, because species that exhibit complete bivoltinism, in which all of the offspring develop before the critical day lengths, should not be female biased, on the assumption of a primary sex ratio of unity.

Because reaction norms can be observed only under controlled conditions when animals are reared in captivity, the relevance for our theory in nature can be assessed only by investigation of whether first generations are male biased and second generations are female biased. To our knowledge, male biased first generations have not been subject to much theoretical or empirical exploration. This may be so because the overwhelming majority of butterfly populations in the field appear to be male biased, although the primary sex ratio is supposed to be equal. The experienced male-biased sex ratio is accordingly largely ascribed to the higher flight activity, and general higher visibility of male butterflies (Ehrlich et al., 1984).

However, female-biased sex ratios in the second generation of partially bivoltine in-

sects have been observed. Denlinger (1981) described such a situation in the flesh fly *Sarcophaga crassipalpis*, and hypothesized that it resulted from a demonstrated impaired fecundity among females that had diapaused, which should select for a tendency of females to refrain from entering diapause. Although Denlinger's data may apply to *S. crassipalpis*, there is no indication that diapause in any way impairs fecundity in butterflies. Hence, the pattern that we observe seems not to result from the explanation advanced by Denlinger.

Female-biased sex ratios have also been observed in second generations of partially bivoltine Hymenoptera. According to theory developed by Werren and Charnov (1978) and Seger (1983), this phenomenon should be associated with the ability of males of the first generation to survive well into the eclosion period of the second generation. This theory is based on the assumption that the sex ratio of the offspring is controlled by the ovipositing female, and shows that investment in male offspring in the first generation is favored, as a result of the opportunity for first generation males to mate with both generations of females. Lepidoptera are female-heterogametic, which means that the avenue of maternal ability to control the sex of offspring is possible. However, we are not aware of any evidence in support of this possibility, and in the data presented in this paper binomial tests show that only 1 out of the 27 sex ratios shown in Tables 1, 3, and 4 departs significantly from unity, viz. the relatively small 30 May sample of *P. napi* in 1989 (Table 3). Hence, we feel that closer exploration of the consequences of an eventual maternal ability to control the sex of offspring in the Lepidoptera is not warranted now.

Although Denlinger's, Werren and Charnov's, and Seger's theories are sound per se, clearly they do not apply to species with discrete generations. The explanation for female-biased sex ratios in second generations of partially bivoltine insects as a result of selection for protandry provides an alternative explanation of considerable general applicability. Although existing models that show protandry to be an adaptive strategy for maximizing the number of matings all assume female monogamy, mating with

virgin females is beneficial also under female polygamy, and so protandry is favored under a variety of mating systems (Forsberg and Wiklund, 1988; Wiklund and Forsberg, 1991). Hence, protandry is prevalent in the majority of insects. Because the reaction norm for direct/diapause development should differ between the sexes as a result of selection for protandry, the prevalence of protandry leads to the prediction that biased sex ratios under partial bivoltinism should be common in nature. Moreover, we contend that the second generation of most bivoltine insects in temperate areas consists partly of individuals that have developed at the critical day length, and so we predict that biased sex ratios in different generations will be found in the majority of bivoltine insects. Because female bias in partial second generations means that male mating success may be higher, on average, for second generation males, this may generate a selective pressure against "drastic" female bias. However, mating success does not necessarily equal fitness, and because the ESS approach (cf. Bulmer, 1983; Iwasa et al., 1983; and Parker and Courtney, 1983) takes into account the selective pressure above, the emergence times of males represent a mixed ESS, which means that each component strategy must have the same fitness. This means that the fitness of first and second generation males will be balanced in spite of different sex ratios in the two generations.

In summary, we hypothesize that selection for protandry is the causal factor underlying the difference between the sexes in propensity to enter diapause/direct development so that males enter diapause at an earlier date than do females, which in turn leads to biased sex ratios under partial bivoltinism. Hence, a corollary to our theory would be that the difference between the sexes for diapause/direct development will be reversed under protogyny. Recently, Kato (1989) described the unusual biology of the pierid *Eurema hecabe* in Japan. This butterfly is multivoltine and has two morphs, a summer morph and an autumn morph, which are regulated by photoperiod and temperature. Only adults of the autumn morph survive the winter. Interestingly, overwintering autumn morph females mate

with summer morph males before hibernation, whereas overwintering autumn morph males mate only after hibernation. Hence, the overwintering generation of this butterfly is (from a reproductive viewpoint) effectively protogynous. In *E. hecabe* autumn morph females appear in the field before males, and the propensity to enter direct/diapause development differs between the sexes, and is reversed, relative to *P. napi*, *P. c-album* and *P. aegeria*. This is consistent with the predictions above, and may be viewed as a corroboration of our theory.

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