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ABSENCE OF TRADE-OFFS BETWEEN SEXUAL SIZE DIMORPHISM AND EARLY MALE EMERGENCE IN A BUTTERFLY[1]

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Abstract. Protandry, here defined as the earlier emergence of males, is a common feature in life histories and could be the result of sexual selection on males to maximize matings, or alternatively an incidental by-product of other selection pressures on the sexes. If protandry is selected for per se, theory predicts that it should be associated with seasonal environments where there is little overlap between generations. The degree of protandry should be insensitive to environmental conditions. Moreover, on the assumption that males and females grow at the same rate as larvae, a trade-off between development time and size is expected to result in a strong association between protandry and female-biased sexual size dimorphism. These predictions were tested by a combination of comparative and experimental studies on five populations of the speckled wood butterfly, *Pararge aegeria,* from central and south Sweden, England, Spain, and the island of Madeira. Protandry was associated with seasonal environments, as it was only exhibited in the three northernmost populations. Protandry in these populations remained largely constant in a variety of temperatures, both under direct development, when protandry results from a sex difference in development time through the egg, larval, and pupal stages, and under diapause development, when it results from a sex difference in pupal development time only. These results indicate that protandry is selected for per se through sexual selection in seasonal environments. Similar female-biased size dimorphism occurred in protandrous and non-protandrous populations alike, and hence sexual size dimorphism in *P. aegeria* is not a result of selection for protandry, nor the causal factor behind protandry. Protandry and sexual size dimorphism appear to be largely decoupled traits in the life history evolution of *P. aegeria.* This is achieved by means of variation in pupal developmental time and variation in the relative growth rates of the sexes. Variation in growth rates is likely to be a general phenomenon and may make possible independent optimization of size and development time (age at sexual maturity), and accordingly influence expected patterns of size-related trade-offs.

Key words: coadaptation; Lepidoptera; life histories; Pararge aegeria; *protandry; Satyrinae; seasonality; sexual selection; sexual size dimorphism; trade-offs.*

INTRODUCTION

An organism's life history (e.g., Cole 1954, Stearns 1976) is generally depicted as a whole suite of traits, adapted to characteristics of the environment (Southwood 1977) but also to each other, thus forming a complex "strategy" made up of coadapted traits (Pianka 1970, Horn 1978). The direction and strength of such coadaptation, i.e., what is cause and what is effect in a particular association of traits typical of a strategy, or how obligatory is a particular association, is poorly known at best. Also, the existence of different strategies is generally assumed to be a result of trade-offs between traits, with different outcomes of trade-offs being favored in different environments. Recently, it has become increasingly clear that there are a number of reasons why the expected trade-offs may not always be observed (van Noordwijk and de Jong 1986, Pease and Bull 1988, Stearns 1989, Charlesworth 1990, Wiklund et al. 1991, Nylin 1992).

Untangling the webs of causality in coadaptation and obtaining an understanding of the nature and generality of specific trade-offs should consequently have high priority in life history studies. A combination of experimental and comparative studies on individuals and populations experiencing different environments is a powerful means to this end. This combination of techniques was used in the present study on butterfly protandry and sexual size dimorphism, a potential association between life history traits for which both directions of causality have been proposed (Fig. 1).

In butterflies and other insects male adults generally emerge and enter the population before females, a very common life history phenomenon known as protandry (Wiklund and Fagerström 1977; note that this term is also used for the different phenomenon of sequential

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hermaphroditism). It has been shown on theoretical grounds that protandry, thus defined, may be best explained as a result of sexual selection, as originally proposed by Darwin (1981:260). In modern terms, males may be under stabilizing selection for a degree of protandry that maximizes the number of females mated or, in polyandrous mating systems, the number of virgin females mated (Wiklund and Fagerström 1977, Bulmer 1983, Iwasa et al. 1983, Parker and Courtney 1983, Zonneveld 1992). Simultaneous selection on females to minimize the prereproductive adult period may contribute to protandry (Fagerström and Wiklund 1982, Wiklund and Solbreck 1982).

Assuming a trade-off between short development time and large adult size, selection on adult size may also affect protandry (Wiklund and Solbreck 1982, Wiklund and Forsberg 1991, Wiklund et al. 1991). Thus, sexual dimorphism in development time, as indeed in any trait (Ralls 1976, Arak 1988), is essentially the sum of several selection pressures acting on one or both sexes. However, a contrast can be made between explanations of protandry granting an important role to selection for protandry per se (invoking sexual selection, e.g., Darwin 1981, Wiklund and Fagerström 1977), on one hand, and explanations viewing protandry mainly as an incidental result of natural selection acting differently on the sexes on the other hand (Fig. 1).

Singer (1982), who advocated the sexual selection explanation for early male emergence, linked protandry to sexual size dimorphism. He made several important inferences: (1) If males are to emerge before females, they will be smaller, if they grow at the same rate as larvae. (2) Selection for protandry per se can only occur when generations are discrete, since, if there is overlap between generations, males cannot be selected to emerge before females. As a consequence, protandry should be restricted to seasonal habitats where generations are discrete. Also, female-biased sexual dimorphism in mass/size should be more common in seasonal habitats, as a result of protandry. (3) There is no advantage of early male emergence when reproduction is delayed by, e.g., adult reproductive diapause. In such cases protandry and size dimorphism should be less accentuated than when adults mate soon after emergence.

Singer's third inference can be extended to the prediction that when there is a diapause in any stage, there will be a less accentuated sexual difference in development time up to that stage as compared to individuals developing directly to sexual maturation. This applies to the typical case, when diapause occurs in a very specific developmental stage and thus synchronizes populations so that individual males with short prediapause development times do not benefit in sexual selection by emerging early in spring. Instead, we expect protandry in diapausing individuals to be caused by differences in diapause and postdiapause development. Hence, when diapause occurs in the pupal or adult stage, there should be less difference in larval development time between the sexes (and, as a consequence, less sexual size dimorphism) in diapausing generations as compared to directly developing generations.

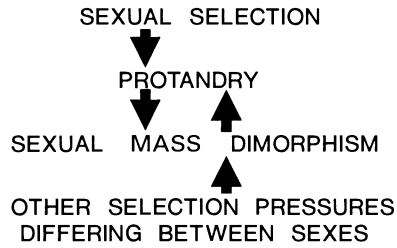

FIG. 1. A schematic illustration of two different hypotheses regarding causality in a life history strategy including both protandry and female-biased sexual mass dimorphism.

One example of the "incidental effects" category of hypotheses is the "developmental constraints" hypothesis mentioned by Thornhill and Alcock (1983: 103). Like Singer's (1982), this hypothesis also links protandry to sexual size dimorphism, but with the causality reversed (Fig. 1). According to this hypothesis, large size can only be achieved at the expense of prolonging the larval stage. Protandry would accordingly be expected when large females enjoy greatly increased fecundity whereas large males do not secure disproportionate reproductive success. Protandry is thus predicted to occur as a *result* of female-biased size dimorphism.

In the present study a number of predictions concerning protandry and its relation to seasonality and sexual size dimorphism are tested. The first set of predictions are aimed at assessing whether protandry is selected for per se, or an incidental by-product of other selection processes. First, we test Singer's (1982) prediction that protandry should be associated with seasonality and only occur in areas where there is little overlap between generations. Second, we test the prediction that there should be less difference in development time between the sexes under diapause development (but before diapause) than under direct development. Third, we test the prediction that the degree of protandry, if it has been driven by sexual selection to an optimal or evolutionarily stable sexual difference in development time, should be insensitive to environmental conditions.

The second set of predictions is aimed at assessing whether there is a trade-off between development time and size, i.e., whether protandry and female-biased size dimorphism are associated according to one or the other of the two opposing hypotheses mentioned above. The hypotheses above are all tested by comparing life history data, assessed at a range of day lengths and temperatures, from five populations of the speckled wood butterfly, *Pararge aegeria* (Fig. 2): one popula-

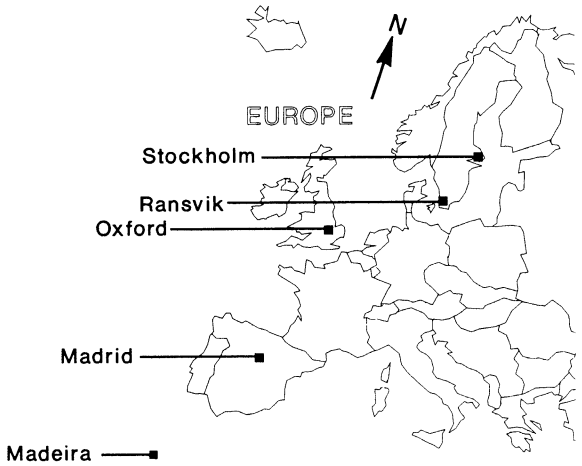

FIG. 2. The sites where the five studied populations of *Pararge aegeria* were sampled. The closely related species *Pararge xiphia*, coexisting with *P. aegeria* on the island of Madeira, was also studied.

tion is univoltine (central Sweden), two are bi-multivoltine with little overlap between generations (south Sweden and England), one is multivoltine with considerable overlap between generations (Spain), and one is multivoltine with no apparent seasonality and generations merging into one another (the island of Madeira).

MATERIALS AND METHODS

Study organism

The speckled wood butterfly, *Pararge aegeria* L., has a wide distribution in Europe and Asia. Two subspecies are recognized in Europe: the northern *P. aegeria tircis* (north of the Alps and north of a zone through France and Greece) and the southern *P. aegeria aegeria* (south of this range, and including the Mediterranean islands and Northern Africa). Relatively recently (1970s; Higgins 1977), *P. aegeria aegeria* colonized the Atlantic island of Madeira from an unknown Mediterranean source. An expanding population now coexists with the similar but larger sized endemic *P. xiphia* (Owen et al. 1986).

Climate and phenology

The five populations of *P. aegeria* sampled were from five latitudes (Fig. 2): Stockholm (central Sweden, 59.5° N), Ransvik (south Sweden, 56° N), Oxford (England, 52° N), Madrid (Spain, 40° N) and Madeira (33° N). The first three sites, inhabited by *P. aegeria tircis*, are characterized by similar "oceanic temperate" climates with strong seasonality (Table 1). Summer is generally warm and wet and thus beneficial to growth and development of both butterflies and host plants (grasses), whereas the winter is generally too cold for butterfly development (temperatures below 6°C prevent development in larvae; Lees 1962). One generation of all three populations consequently hibernates in a diapause, which can take place in either the pupal stage or as half-grown larvae (cf., e.g., Shreeve 1986, Nylin et al. 1989). This makes for a complicated phenology south of central Sweden, where there is a single adult peak in May–June (C. Wiklund, *personal observation*). Adults of the bi-multivoltine populations of south Sweden and England fly in 4–5 peaks from about April to September (Thomas 1986; C. Wiklund, *personal observation*). These flights have been synchronized by diapause (only third instar larvae and pupae survive winter; Shreeve 1986), and are relatively discrete.

The area of Madrid is characterized by a "Mediterranean" climate (Table 1). Summers are dry and warm, winters are relatively mild. Adults of *P. aegeria aegeria* fly from about March to October, occurring continuously throughout summer in an unknown number of generations, but with a decline during the warm and dry midsummer. There are peaks in adult density, but they are not discrete (E. Garcia-Barros, *unpublished data*). It seems possible that this could partly be because a fraction of this population survives winter in several developmental stages, without true hibernation diapause. This suggestion is based more on the observation of large overlap between generations and on the fact that evidence for diapause is lacking (this study) than on differences in winter conditions, which are not

TABLE 1. Climatic data (averages) from the five source regions* according to statistics from the Swedish Meteorological and Hydrological Institute.

Region	Day temp. (°C)	Night temp. (°C)	Rain/snow (mm)
Central Sweden (Stockholm)			
January	−1	−5	45
April	8	1	30
July	22	14	60
October	9	5	50
Southern Sweden (Malmö)			
January	2	−3	50
April	10	2	35
July	22	13	65
October	12	6	55
England (London)			
January	6	2	60
April	13	6	40
July	22	14	60
October	14	8	60
Spain (Madrid)			
January	9	2	40
April	18	7	50
July	31	17	10
October	19	10	55
Madeira (Funchal)			
January	19	13	65
April	20	14	35
July	24	18	0
October	22	16	90

* These are data from meteorological stations that were closest to locations of the sampled populations.

very dramatic, especially between England and Spain (Table 1). Some differences between areas may consequently be better described as differences in phenology than in seasonality per se.

The island of Madeira has a mild "oceanic" climate with temperatures beneficial for butterfly development all year round; seasonality is evident only in the typical lack of rain in July–August in the southern part of the island (Table 1). All developmental stages of *P. aegeria* can be found simultaneously (S. Nylin and P.-O. Wickman, *personal observation*), and adults of both *P. aegeria aegeria* and *P. xiphia* seem to fly more or less continuously all year round, at least at lower elevations (Higgins and Hargreaves 1983, Owen et al. 1986).

Protandry and mass dimorphism at a standard day length

A temperature of 17°C and a day length of 20 h were chosen as "standard" conditions for a comparison of protandry and mass dimorphism between populations. This choice was rather arbitrary, but 17°C is within the range of normal daily mean field temperatures at all of the geographical sites where specimens were collected, at least during some part of the year when growth and development is occurring. A day length of 20 h was chosen because at 17°C this promotes direct development in all populations of *P. aegeria.* However, all populations were also tested in a range of day lengths (see next section). One of the two replicates at 20 h stems from this larger experiment.

For each experiment, several females were caught in the wild and their offspring pooled. Larvae were reared to adults in environmental cabinets, individually in plastic jars where the grass *Poa annua* was cultivated. All populations seemed to thrive on this host plant. In most experiments, data were collected on development time in the larval and pupal stages, hatchling mass, mass of pupa on the 2nd and 9th d after pupation, respectively, and adult mass as measured after release of the meconium but before feeding or mating. These measurements were combined to calculate growth rates according to a formula assuming exponential growth:

$$\log(\text{growth rate}) = [\log(M_f) - \log(M_0)]/D,$$

where M_f is final (pupal) mass, M_0 hatchling mass, and D development time in days from hatchling to pupa. This formula returns a growth figure such as 1.20, corresponding to a daily increase in mass to 120% of the mass recorded the previous day. In the text and tables following this is referred to as a 20% mass increase.

Protandry and mass dimorphism at a range of conditions

If protandry is selected for per se, it is predicted to be achieved differently in directly developing and diapausing generations. This hypothesis, and the possibility that patterns of protandry and mass dimorphisms could differ between day lengths to the extent of making "standard" comparisons irrelevant, was tested by exposing individuals of the five populations of *P. aegeria* to a wide range of day lengths at 17°C. For each experiment the offspring of 7–10 females were pooled and divided randomly across day lengths, thus ensuring that any variation among day lengths was due to phenotypic plasticity rather than genetic differences or maternal effects. Individuals were cultivated and data collected and calculated as described above.

If protandry is selected for, we would also expect stabilizing selection on emergence dates to result in a degree of protandry (i.e., numerical rather than proportional sexual difference in development time) that is buffered against environmental variation. This was tested in two ways, regarding protandry under direct and diapause development, respectively:

1) Offspring of several females of the south Swedish population were pooled and divided randomly across a wide range of biologically relevant temperatures. This was done in two experiments (using different stock) at photoperiods of 22 h and 20 h, respectively, where direct development is ensured. For comparison, the procedure was repeated for the Madeiran population at a day length of 15 h. Larvae were reared as described above and data on protandry were collected.

2) Offspring of several females of the univoltine central Swedish population were reared under conditions promoting pupal diapause (17°C and short photoperiod). The resulting pupae were pooled and divided among 15 experimental treatments: all combinations of the experimental temperatures 14°C, 17°C, and 20°C with periods spent in cold storage (4°C) of 0, 1, 2, 3, or 4 mo, representing different lengths of winters and springtime temperatures. They were subsequently brought out of cold storage and the development time to adult measured at the experimental temperature and a photoperiod of 22 h.

Results

Protandry and mass dimorphism at a standard day length

Protandry.—Comparisons of protandry in cohorts (measured as sexual dimorphism in total development time from egg to adult, under standard conditions promoting direct development), between the four populations of *Pararge aegeria* where direct development occurs naturally, were in good general agreement with the prediction that protandry should be most strongly developed in seasonal (temperate) environments where generations are discrete (Fig. 3). There was statistically significant protandry (ANOVA) in all four experiments on the northern subspecies *P. a. tircis* from south Sweden ($P < .01$, $N = 54$ and $P < .001$, $N = 23$, respectively) and England ($P < .001$, $N = 58$ and $P < .001$, $N = 24$, respectively), whereas none of the four experiments on the southern subspecies *P. a. aegeria* resulted in statistically significant protandry. This was true for

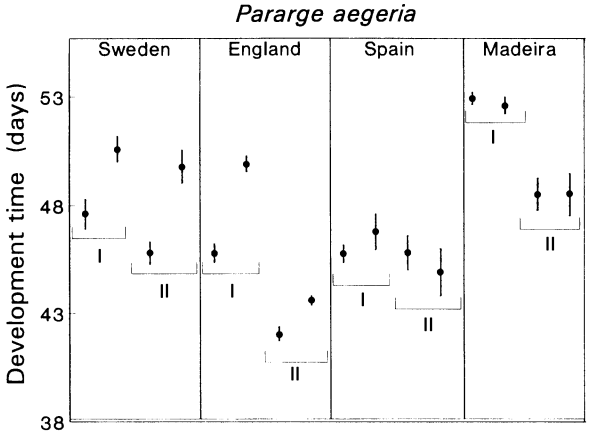

FIG. 3. Total development time (mean ± 1 SE) for the sexes in four potentially multivoltine populations of *Pararge aegeria*, as measured in two replicates. Males shown to the left in each pair (cohort) and the differences between sexes show the degree of protandry. South Sweden and England represent more strongly seasonal environments than Spain or Madeira, and here protandry was significant. See *Results: Protandry and mass dimorphism at a standard day length* and Table 3 for statistics and sample sizes.

cohorts originating from Spain ($P = .313$, $N = 44$ and $P = .472$, $N = 19$, respectively) or Madeira ($P = .503$, $N = 44$ and $P = .531$, $N = 26$, respectively). A two-way ANOVA (MINITAB general linear model) showed the interaction between sex and source region to be statistically significant ($P < .01$).

The univoltine population of *P. aegeria* from central Sweden is a special case. There was significant protandry under direct development in one replicate (data from Table 3: central Sweden I; males 39.0 ± 0.5 d, $N = 15$; females 41.4 ± 0.5 d, $N = 20$; ANOVA, $P < .01$) but not the other (central Sweden II; males 48.6 ± 0.8 d, $N = 14$; females 46.4 ± 0.6 d, $N = 9$; ANOVA, $P = .06$; note the reversed sexual difference). Evidently, individuals of this univoltine population do not display the strong and consistent protandry under direct development seen in the other northern populations in which direct development occurs naturally.

Mass dimorphism.—Despite the positive results concerning protandry in *P. aegeria*, comparisons of sexual body-mass dimorphism in the pupal stage (Table 2) did not support the prediction that greater dimorphism should be seen in more seasonal habitats where protandry prevails. For instance, the least dimorphic pupal masses were found in the most strongly protandrous cohort (south Sweden II; Fig. 3; Table 2). Both pupal and adult mass dimorphism was in fact similar for all populations, female pupae being ≈15–25% heavier than male pupae (Table 2).

The mass dimorphism was very similar in a given experiment for pupae weighed on the 2nd and 9th d after pupation, respectively, whereas mass dimorphism unexpectedly was substantially more accentuated in newly eclosed adults (30–50%; Table 2).

Larval and pupal development times.—A potential reason for the lack of a correlation between sexual di-

TABLE 2. Sexual differences in mass (mean ± 1 SE) at different developmental stages in cohorts of five populations of *Pararge aegeria*. Dimorphism in mass (ratio between female and male mass) given below each comparison.*

Cohort		*N*	Pupa day 2 (mg)	Pupa day 9 (mg)	Adult (mg)
Central Sweden I	♂♂	15	140.7 ± 2.9	...	...
	♀♀	20	173.0 ± 1.9	...	...
	♀/♂		1.23	...	...
Southern Sweden I	♂♂	24	137.9 ± 3.2	130.7 ± 2.9	48.6 ± 1.7
	♀♀	30	165.7 ± 3.2	157.9 ± 3.3	71.9 ± 2.0
	♀/♂		1.20	1.21	1.45
Southern Sweden II	♂♂	13	153.5 ± 3.7	...	...
	♀♀	10	172.0 ± 3.8	...	...
	♀/♂		1.12	...	...
England I	♂♂	34	148.9 ± 1.5	141.6 ± 1.5	59.2 ± 1.1
	♀♀	24	185.5 ± 2.8	177.8 ± 2.8	88.9 ± 2.0
	♀/♂		1.25	1.26	1.50
England II	♂♂	10	137.3 ± 1.3	...	...
	♀♀	14	163.6 ± 2.0	...	...
	♀/♂		1.19	...	...
Spain I	♂♂	20	134.4 ± 2.4	125.4 ± 2.3	55.5 ± 1.4
	♀♀	25	169.1 ± 3.2	155.0 ± 2.6	78.5 ± 1.9
	♀/♂		1.25	1.24	1.41
Spain II	♂♂	12	142.6 ± 3.3	...	...
	♀♀	7	170.1 ± 5.2	...	...
	♀/♂		1.19	...	...
Madeira I	♂♂	24	132.7 ± 2.0	126.9 ± 2.0	55.3 ± 1.6
	♀♀	20	153.1 ± 2.1	146.7 ± 2.0	72.7 ± 1.2
	♀/♂		1.15	1.16	1.31

* Sexual dimorphism in mass was highly significant ($P < .01$–$P < .001$; ANOVA) in all experiments and at all developmental stages.

TABLE 3. Sexual differences in development time and larval body-mass growth rates (both mean ± 1 SE) in cohorts of *Pararge aegeria*. *P* = statistical significance of male–female difference (ANOVA).

Cohort		*N*	Larval time (d)	Pupal time (d)	Growth rate (%/d)
Central Sweden I†	♂♂	15	25.3 ± 0.5	13.7 ± 0.2	27.5 ± 0.6
	♀♀	20	28.2 ± 0.6	13.2 ± 0.4	25.4 ± 0.6
	P		**	NS	**
Central Sweden II‡	♂♂	14	33.7 ± 1.0	14.9 ± 0.3	...
	♀♀	9	32.3 ± 0.8	14.1 ± 0.4	...
	P		NS	NS	...
Southern Sweden I	♂♂	24	32.8 ± 0.7	14.8 ± 0.2	20.2 ± 0.5
	♀♀	30	35.7 ± 0.5	14.9 ± 0.2	18.9 ± 0.3
	P		**	NS	*
Southern Sweden II†	♂♂	13	30.4 ± 0.4	15.4 ± 0.6	22.5 ± 0.3
	♀♀	10	34.8 ± 0.7	15.4 ± 0.2	19.5 ± 0.4
	P		***	NS	***
England I	♂♂	34	29.8 ± 0.3	15.9 ± 0.2	21.6 ± 0.3
	♀♀	24	33.2 ± 0.3	16.8 ± 0.1	19.7 ± 0.3
	P		***	**	***
England II	♂♂	10	27.0 ± 0.4	15.0 ± 0.3	25.2 ± 0.4
	♀♀	14	29.6 ± 0.3	14.0 ± 0.2	23.5 ± 0.2
	P		***	**	**
Spain I	♂♂	20	30.2 ± 0.4	15.5 ± 0.1	22.1 ± 1.5
	♀♀	25	31.8 ± 0.7	14.9 ± 0.2	21.7 ± 0.4
	P		NS	*	NS
Spain II	♂♂	12	29.3 ± 0.6	17.3 ± 0.4	22.5 ± 0.5
	♀♀	7	30.1 ± 1.1	16.1 ± 0.5	23.0 ± 0.8
	P		NS	NS	NS
Madeira I	♂♂	24	34.9 ± 0.3	18.0 ± 0.3	19.6 ± 1.0
	♀♀	20	35.1 ± 0.4	17.5 ± 0.2	20.0 ± 0.3
	P		NS	NS	NS
Madeira II‡	♂♂	12	30.2 ± 0.6	18.3 ± 0.6	...
	♀♀	14	31.9 ± 0.8	16.6 ± 0.5	...
	P		NS	*	...

* = $P < .05$, ** = $P < .01$, *** = $P < .001$.

† Hatchling masses were not recorded in this cohort. Growth rates were approximated from recorded pupal masses and the mean hatchling mass for other cohorts.

‡ No masses recorded.

morphism in development time and pupal mass, respectively, can be seen when total development time is divided into its components: larval and pupal development time (Table 3). Only variation in the former trait is relevant in causing pupal mass dimorphism. It can be noted that, protandry or not, males in fact did pupate in a shorter time under direct development in all experiments (interestingly enough with the exception of the already-mentioned non-protandrous cohort from the normally univoltine central Swedish population of *P. aegeria*; central Sweden II), although the sexual differences were not statistically significant in the experiments on the southern subspecies *P. a. aegeria* (Table 3).

Sexual differences in pupal development times were much more variable (Table 3). In the three northern populations of *P. aegeria*, pupal times were similar for the sexes and in individual experiments could add to or detract slightly from protandry. The lack of significant protandry in the populations of *P. aegeria* from Spain and Madeira resulted from slightly shorter larval development times for males, which were combined with shorter pupal development times for females (Table 3). A similar reversal of the sexual differences in development time from larvae to pupae, although much more strongly accentuated, was found in the Madeiran endemic *P. xiphia* (S. Nylin, C. Wiklund, and P.-O. Wickman, *unpublished data*). In this case, strongly significant sexual differences in development time in opposing directions combined to cause nonsignificant protandry.

Growth rates.—Investigating the role of sexual differences in larval growth rate reveals that in the south Swedish and English populations of *P. aegeria*, where direct development normally occurs, males grew faster than females under conditions promoting direct development (Table 3). This was also the case in the protandrous cohort of the central Swedish population, where masses were recorded (central Sweden I). Larval growth rates were more similar between sexes in the less protandrous southern populations of *P. aegeria*. Thus, the stronger protandry in the northern populations of *P. aegeria* was to a certain extent coupled with higher relative male growth rates rather than with lower

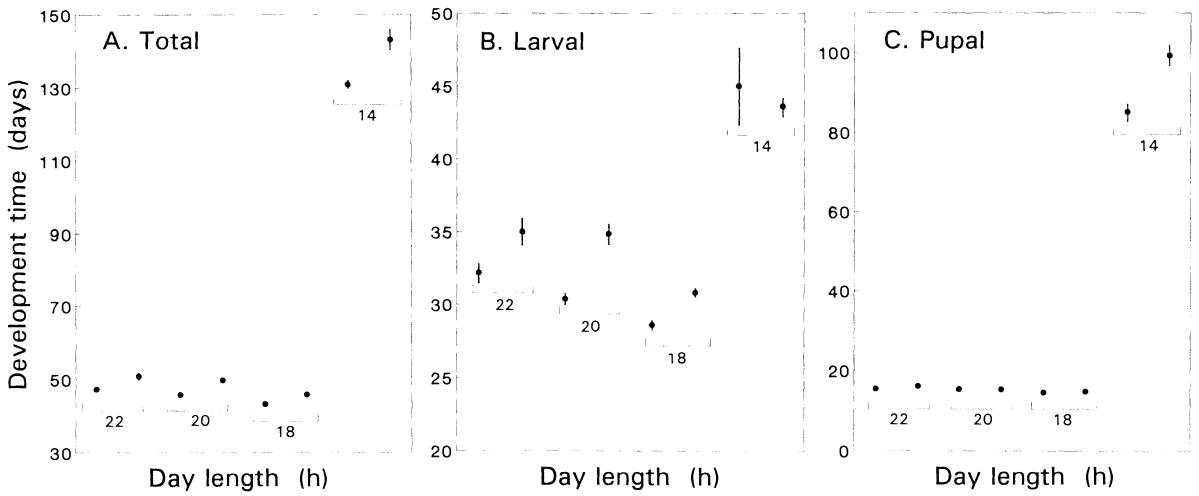

FIG. 4. Development time (mean ± 1 SE) for the sexes at different photoperiods in the south Swedish population of *Pararge aegeria*. Males to the left in each cohort. (A) Total development time and protandry. There was significant protandry at all day lengths (ANOVA), but this was achieved differently at different photoperiods as shown by (B) larval time and (C) pupal time. Direct development occurred at long day lengths, and here larval but not pupal times differed. At 14-h day length, where pupal diapause occurred, pupal but not larval times differed. See Table 4 for sample sizes.

relative male pupal masses, so that sexual body-mass dimorphism was not stronger in these populations despite stronger protandry (Tables 2 and 3). Variation in the relative growth rates of the sexes thus represents a second reason why the degree of protandry was not coupled with the degree of mass dimorphism among populations and species.

Protandry and mass dimorphism at a range of day lengths

Protandry.—A full discussion of the results concerning life cycle regulation and response to day length in the five populations of *P. aegeria* is outside the scope of the present paper, but some general aspects concerning protandry can be seen in Figs. 4 through 7. As predicted by our extension of Singer's hypothesis (1982), in the northern populations of *P. aegeria* sexual differences in larval and pupal development time varied across a range of day lengths at 17°C, according to whether pupal diapause followed or not at a particular constant day length (Figs. 4 and 5).

In the experiment on the population from south Sweden, males spent a significantly shorter time than females as larvae at day lengths of 22, 20, and 18 h (Fig. 4B; ANOVA, $P < .05$–$P < .001$), where all individuals developed directly to adults. The durations of the pupal

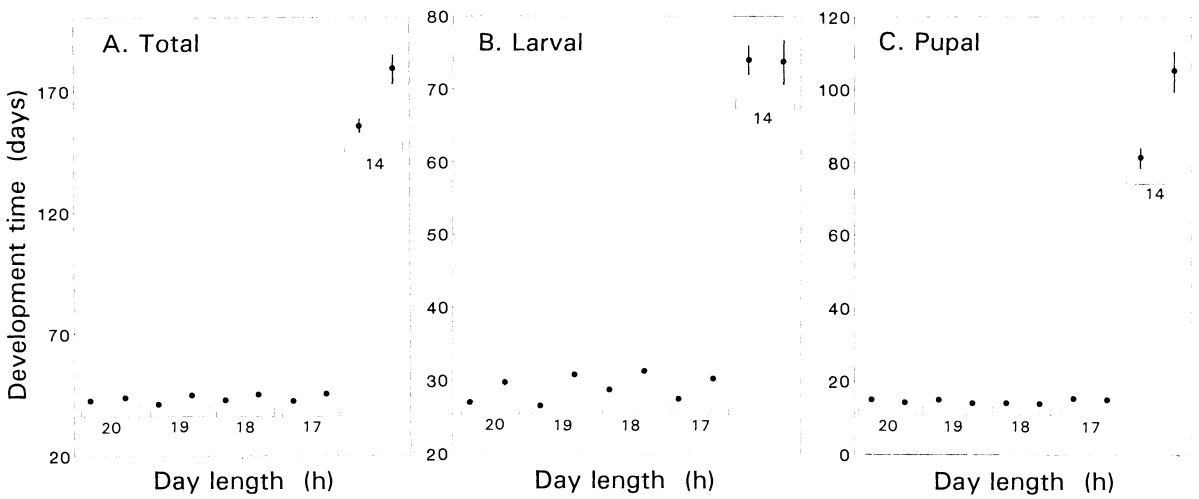

FIG. 5. Development time (mean ± 1 SE) for the sexes at different photoperiods in the English population of *Pararge aegeria*. Males to the left in each cohort. (A) Total development time and protandry, (B) larval times and (C) pupal times. For interpretation see legend to Fig. 4. See Table 4 for sample sizes.

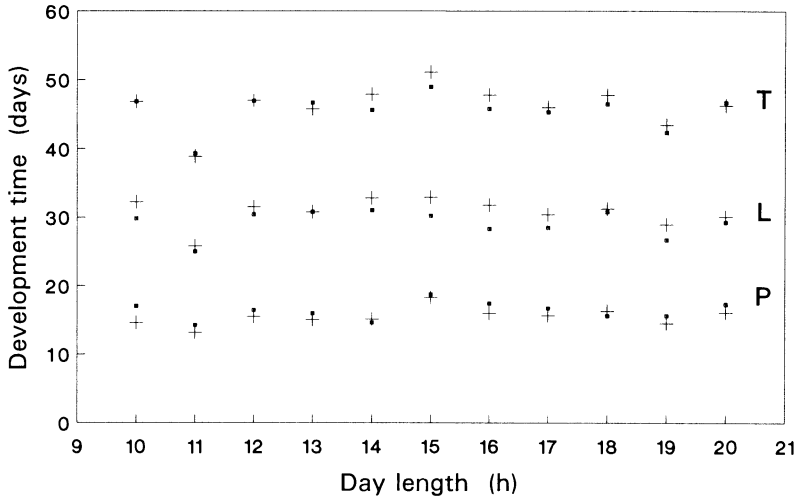

FIG. 6. Total development time for the sexes at different photoperiods in the Spanish population of *Pararge aegeria*. ■ means for males; + means for females (total *N* in each condition 15–20). For clarity no measure of variation is shown. T = total development time and protandry. There was significant protandry at some day lengths. L = larval times, P = pupal times.

stages were similar in the sexes (Fig. 4C; ANOVA, NS), which added up to protandry under these conditions (as can be seen by comparing total development time for the sexes; Fig. 4A). This can be contrasted with a day length of 14 h where all individuals diapaused in the pupal stage. Under these conditions there was no difference in larval development time between the sexes (Fig. 4B; ANOVA, NS). Instead, male pupae had shorter development times (including diapause and postdiapause development, Fig. 4C; ANOVA, $P < .001$), again resulting in protandry (Fig. 4A) but accomplished differently, as predicted. At the remaining day lengths studied there was either larval diapause or only partial pupal diapause, which complicates interpretation because the sexes differ in their propensity to enter diapause (Wiklund et al. 1992). These day lengths were consequently omitted from Fig. 4.

Similarly, in the experiment on the Oxford population the durations of the larval stage were shorter for males than for females under direct development, i.e., at day lengths of 20, 19, 18, and 17 h (Fig. 5B; ANOVA, $P < .001$). Pupal times were similar for the sexes or slightly shorter for females (Fig. 5C; significant at 20 and 19 h, ANOVA) in all cases, however, adding up to protandry (Fig. 5A). In contrast, larval times were similar for the sexes at a day length of 14 h (where all individuals diapaused in the pupal stage; Fig. 5B) but again males spent shorter times in the pupa under these conditions (Fig. 5C; ANOVA, $P < .001$), resulting in protandry (Fig. 5A). The experiments made at other day lengths resulted in partial responses and are not dealt with in the present paper.

In the Spanish and Madeiran populations of *P. aegeria* there was no evident diapause under any of the conditions studied (day lengths of 10–20 h at 17°C). Consequently, all studied day lengths are represented in Figs. 6 and 7. In both experiments the general pattern that has already been reported from standard conditions, i.e., sexual differences in larval development times that were balanced by reverse differences in pupal times, held true over a range of day lengths. Thus, in the experiment on the Spanish population males spent numerically (but not always significantly) shorter times than females as larvae at most day lengths, but this was balanced to some extent by females spending shorter times than males as pupae at most day lengths (Fig. 6). As a result, there was protandry at some day lengths but not all (including the "standard" day length of 20 h). A similar pattern could be seen in the experiment on the Madeiran population (Fig. 7), but in this case sexual differences in larval times were balanced by differences in pupal times to the degree that there was protogyny as often as protandry (Fig. 6).

The univoltine central Swedish population was also exposed to a range of day lengths (10–20 h at 17°C). As reported above, at the "standard" day length of 20 h direct development occurred, but there was no protandry in the cohort that formed part of this larger experiment. All individuals of this population normally undergo a pupal diapause, however, and at the day length where the greatest proportion of individuals entered pupal diapause (16 h) there was clear protandry. At this day length males did not spend shorter times in the larval stage (males 51.5 ± 2.4 d, $N = 10$; females 47.8 ± 2.4 d, $N = 12$; ANOVA, NS) but did so in the pupal stage (males 77.4 ± 5.4 d; females 103.2 ± 7.4 d; ANOVA, $P < .001$). Again, then, protandry was not accomplished *before* an intervening diapause.

Mass dimorphism.—As could be expected from the above investigation at standard conditions, patterns in pupal mass dimorphism over a range of day lengths did not closely mirror patterns in degrees of protandry.

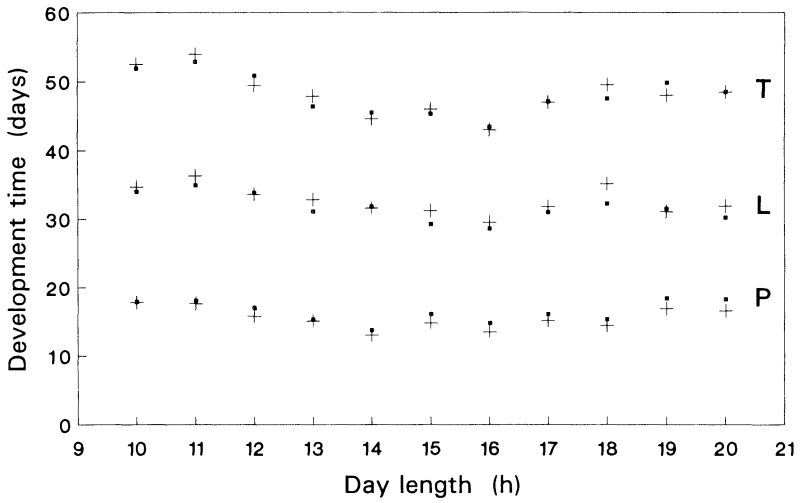

FIG. 7. Total development time for the sexes at different photoperiods in the Madeiran population of *Pararge aegeria*. ■ means for males; + means for females (total *N* in each condition 15–20). For clarity no measure of variation is shown. T = total development time and protandry. There was no significant protandry. L = larval times, P = pupal times.

This was in part because variation in total development time was strongly affected by variation in pupal times (not affecting pupal mass), as reported in the previous section. It could still be asked, however, whether the difference in how protandry was achieved under direct development and diapause development, respectively, affected mass dimorphism. Were the sexes more similar in mass under development to diapause in the pupal stage, where larval times were similar for the sexes (Figs. 4B, 5B)? This can be studied in the south Swedish and English populations of *P. aegeria* by comparing the mass dimorphism observed at day lengths of 14 h (pupal diapause) with that seen at day lengths promoting direct development (Table 4).

The expected pattern was found in the experiment on the English population, but not in the south Swedish experiment (Table 4). In the English population, mass dimorphism varied from female : male pupal mass ratios of 1.00–1.22. The least dimorphic measurement at any day length was from 14 h, where the greatest fraction of individuals entered pupal diapause. Mass dimorphism was female-biased and similar at all day lengths in the south Swedish experiment. The range of female : male mass ratios was 1.04–1.20 in day lengths from 22 to 9 h, without any pattern in relation to relative development time of the sexes.

Similarly, in the experiment on the central Swedish population, the sexes were similar in larval development time at most day lengths and any differences varied direction between day lengths. Despite this, mass dimorphism in the pupa was female-biased at all day lengths where masses were taken (day lengths from 10 to 18 h) and ranged from female : male ratios of 1.12–1.26 without any correlation with the relative development times of the sexes. These results suggest that overall, and especially in the Swedish populations, variation in the relative larval growth rates of the sexes, rather than in relative mass, was the main proximate cause of the observed differences in relative larval development times.

Growth rates.—In both the south Swedish and the English experiments, larval growth rates under direct development were higher for males (Table 4). However, at a day length of 14 h, where pupal diapause was induced, males did not display higher growth rates, in accordance with predictions from explanations of protandry invoking sexual selection. As noted above, together with the similar larval times for the sexes at 14-h day length (Figs. 4B, 5B), this should result in low mass dimorphism in diapausing generations compared to generations developing directly, as was indeed the case in the English experiment. This was not so in the Swedish experiment, apparently a result of slightly higher growth rates for females at 14-h day length (Table 4; NS). Approximations of growth rates in the central Swedish population showed that, with the exception of the protandrous cohort at 20 h and 17°C (Table 3; direct development), growth rates were similar for the sexes or lower for males in this population. At several day lengths males spent longer times in the larval stage yet ended up with lower pupal masses due to a tendency towards lower growth rates. For instance, at 16 h (where pupal diapause peaked) males grew slower (12.4 ± 0.6 %/d, $N = 10$) than females (14.2 ± 1.0 %/d, $N = 12$), but there was strong variation and the difference was not significant (ANOVA, $P = .15$).

Protandry at a range of temperatures

Total development time from egg to adult under direct development (22 and 20 h, respectively) in the south Swedish population was strongly dependent on temperature (Fig. 8). In the first experiment (Fig. 8A),

TABLE 4. Sexual differences in pupal mass (day 2) and larval body-mass growth rates (both means ± 1 SE) in cohorts of two potentially multivoltine populations of *Pararge aegeria* at a range of day lengths. Dimorphism in mass (ratio between female and male mass) given below each mass comparison.

Population	Day length		*N*	Pupal mass (mg)	Growth rate (%/d)
Southern Sweden†	22 h	♂♂	16	144.9 ± 1.5	21.1 ± 0.5
		♀♀	8	174.0 ± 8.3	19.3 ± 0.5
		♀:♂		1.20	*
	20 h	♂♂	13	153.5 ± 3.7	22.5 ± 0.3
		♀♀	10	172.0 ± 3.8	19.4 ± 0.4
		♀:♂		1.12	***
	18 h	♂♂	22	149.3 ± 2.5	24.0 ± 0.3
		♀♀	20	170.1 ± 2.7	22.1 ± 0.3
		♀:♂		1.19	***
	14 h	♂♂	13	153.1 ± 2.0	15.1 ± 0.6
		♀♀	7	183.9 ± 4.4	15.4 ± 0.2
		♀:♂		1.20	NS
England	20 h	♂♂	10	137.3 ± 1.3	25.2 ± 0.4
		♀♀	14	163.6 ± 2.0	23.5 ± 0.2
		♀:♂		1.19	**
	19 h†	♂♂	17	137.6 ± 1.3	25.7 ± 0.4
		♀♀	8	161.0 ± 3.1	22.4 ± 0.4
		♀:♂		1.17	**
	18 h†	♂♂	13	139.2 ± 1.7	23.5 ± 0.3
		♀♀	12	166.6 ± 1.6	22.1 ± 0.2
		♀:♂		1.20	***
	17 h†	♂♂	15	136.0 ± 1.3	24.6 ± 0.3
		♀♀	10	165.9 ± 1.6	22.9 ± 0.2
		♀:♂		1.22	**
	14 h	♂♂	16	151.2 ± 2.3	8.70 ± 0.2
		♀♀	7	150.7 ± 2.7	8.70 ± 0.4
		♀:♂		1.00	NS

* = $P < .05$, ** = $P < .01$, *** = $P < .001$.

† Hatchling masses were not recorded in these experiments. Growth rates were approximated from recorded pupal masses and the mean hatchling mass for each sex in other cohorts.

total development time increased threefold between 23°C and 11°C, from just >30 d to ≈100 d. However, the reaction norms of the sexes for development time in response to photoperiod were almost parallel, and as a result protandry was achieved at all temperatures, and only varied from 2.3 to 4.0 d (Fig. 8A). In the second experiment (Fig. 8B), the results were very similar. Thus, protandry was very constant over a great range of temperatures, despite strong variation in total development time. This can be contrasted with the experiment on the Madeiran population (Fig. 8C), where the sexual differences in development time varied both in direction and strength.

Protandry after varying periods of cold storage

Pupal development times in the central Swedish population varied strongly in response to temperature and to the period of chilling at 4°C before exposure to the experimental temperature and 22-h day length (Fig. 9). Development time to adult decreased with higher temperature and with longer periods of cold storage.

The sexual difference in pupal development time was large and variable after no cold storage or only short periods of chilling, but was relatively constant at 2–3 d protandry after at least 2 mo (or at 14°C for 3 mo) of chilling (Fig. 9). Evidently the variation after short periods of chilling occurred because not all individuals had broken diapause and because the sexes differed so that males broke diapause after a shorter period. Cold periods of such short duration are not experienced by this population in the field.

DISCUSSION

Protandry may be beneficial for both sexes in insect populations (Darwin 1981, Fagerström and Wiklund 1982). At the same time, insect females are often heavier than males, perhaps as a result of more strongly mass-dependent reproductive success in females than in males, as assumed by the "developmental constraints" hypothesis (Thornhill and Alcock 1983). Protandry should tend to reinforce such dimorphism (given any trade-off between short development time and large final mass) and vice versa. We would consequently expect both protandry and female-biased mass dimorphism to be very common life history phenomena in insect populations, and this seems to be the case. They should also tend to occur together, and form a coadapted life history strategy in which causality is not evident. This is demonstrated by the two opposing

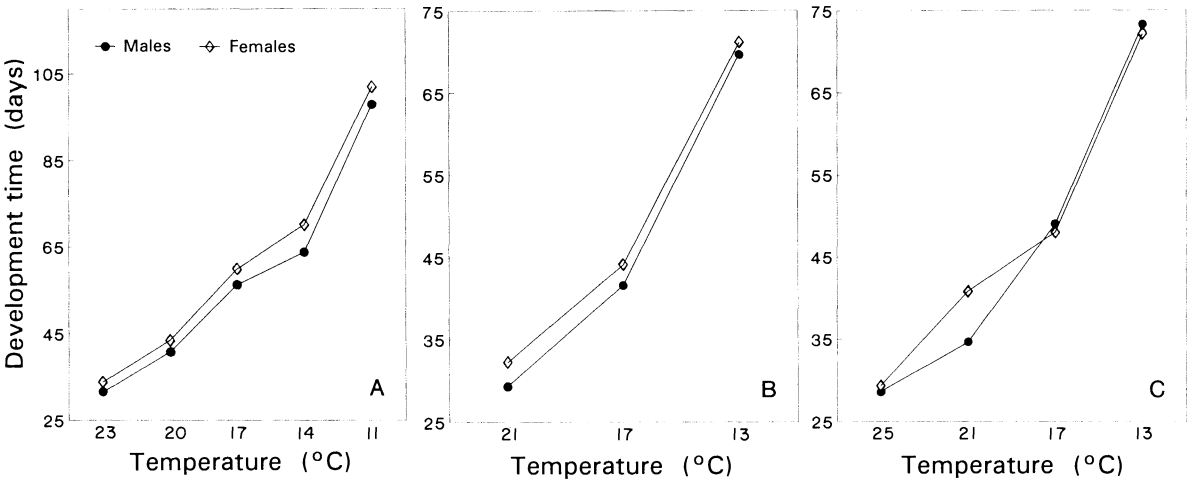

FIG. 8. Total development time (means) and protandry under direct development at different temperatures in *Pararge aegeria*. (A) and (B) show two replicates made on the south Swedish population, (C) shows an experiment on the Madeiran population. N = 15–20 individuals in each condition.

hypotheses (Fig. 1), which in part date back to a discussion between Darwin (1981) and Wallace (cited in Darwin 1981:346). The results of the present study concerning causality can be summarized as in Fig. 10.

There is strong support for selection for protandry per se through sexual selection. In particular, the results support Singer's prediction (1982; based on the assumption that sexual selection causes protandry) that the degree of protandry in a population should be a function of the degree of overlap between generations and therefore of the degree of seasonality of the environment. There is strong protandry in the strongly seasonal northern habitats, where generations are few and discrete, weak protandry in the mildly seasonal habitat of Spain where generations overlap to a high degree, and total lack of protandry in the nonseasonal environment of Madeira.

We also found support for our extension of Singer's hypothesis (1982; again assuming sexual selection for protandry) that protandry should not be accomplished *before* an intervening diapause. The pattern found in both of the potentially bivoltine northern populations of *P. aegeria* (south Sweden and England) was that protandry is achieved through sexual differences in larval development time (resulting mainly from differences in growth rate) at photoperiods where individuals developed directly, but through differences in pupal development time when individuals diapaused in the pupal stage (for similar results see Wiklund and Forsberg 1991, Wiklund et al. 1991, Nylin 1992).

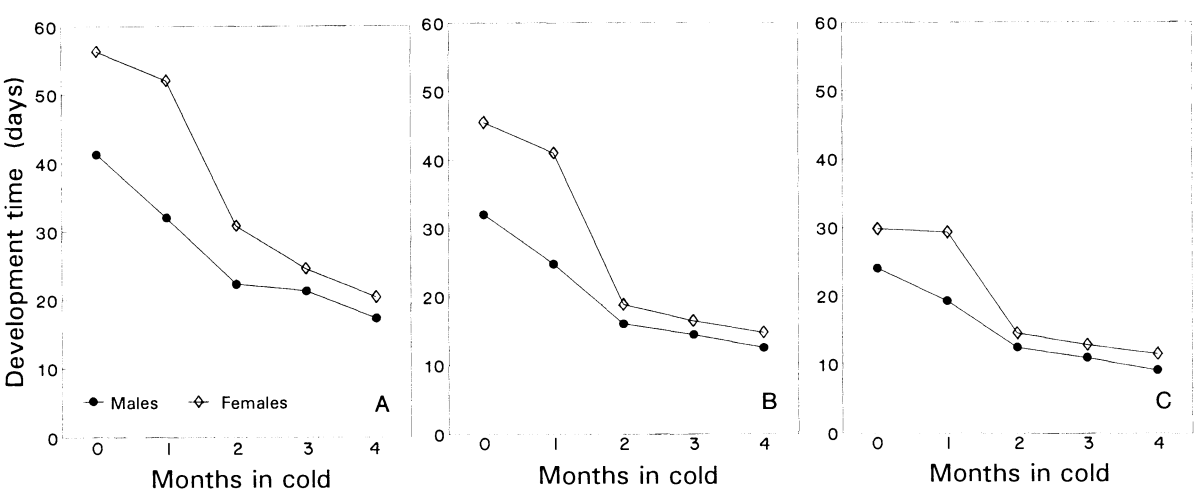

FIG. 9. Development time to adult (means) and protandry when pupae of the central Swedish population of *Pararge aegeria* had spent varying periods of time in cold storage and subsequently were exposed to different experimental temperatures (A: 14°C; B: 17°C; C: 20°C).

The hypothesis of continuous sexual selection for protandry per se is also supported by the fact that protandry in directly developing individuals is relatively constant in the south Swedish population, but not the Madeiran population, within a wide range of temperatures. Protandry is also constant in diapausing individuals of the univoltine central Swedish population, in different experimental conditions mimicking the biologically relevant portion of variation in winter length and spring temperatures. We suggest that, without stabilizing selection for protandry, there is no a priori reason to expect the numerical rather than proportional sexual differences in development time to be held constant when environmental conditions strongly affect development time for both sexes. The observed protandry of 2–4 d must be assumed to represent either the optimum for both sexes (cf. Fagerström and Wiklund 1982), the result of a conflict between different optima for the sexes, or the difference between peaks in evolutionarily stable distributions of emergence dates for the sexes (cf. Bulmer 1983, Iwasa et al. 1983, Parker and Courtney 1983). In a field study of *Euphydryas editha,* Baughman (1991) found equal mating success for males emerging at different dates, a result which may be seen as supporting the hypothesis that males emerge according to an evolutionarily stable strategy with equal fitness for all emergence dates.

This brings us to the next link in the hypothetical chains of causality (cf. Fig. 10). Singer (1982) suggested stronger sexual size dimorphism in more strongly protandrous generations, populations, and species. He also reported some evidence of such associations in butterflies, and some results of the present study (the pupal mass dimorphism seen in English directly developing, but not diapausing, pupae of *P. aegeria*) and results presented elsewhere (Wiklund et al. 1991, Nylin 1992) also suggest that the two traits may be associated to a certain extent (thin arrow in Fig. 10). However, the most general result from our studies on *P. aegeria* and other butterfly species is that of a surprisingly high degree of *non*-association between protandry and sexual body-mass dimorphism in the pupal and adult stages, as a result of (1) variation in pupal development time (which does not affect pupal masses) and (2) variation in the relative growth rates of the sexes.

The "developmental constraints" hypothesis (Thornhill and Alcock 1983) also predicts an association between protandry and sexual size dimorphism; in particular it predicts no protandry in species without female-biased size dimorphism. This is refuted in butterflies (Wiklund and Solbreck 1982, Wiklund and Forsberg 1991, Wiklund et al. 1991, Nylin 1992; this study), in a spider (Gunnarsson and Johnsson 1990), and in water striders (Fairbairn 1990). Thus, female-biased size dimorphism does not seem to be the cause of protandry in any general sense. Sexual size dimorphism is probably set by a complex interaction between selection pressures, including those favoring large size

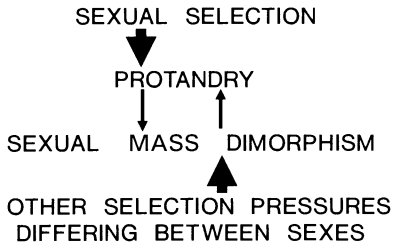

FIG. 10. A schematic illustration of the results of the present study and other investigations reported in the *Discussion,* regarding the two different hypotheses for causality in a life history strategy with protandry and female-biased sexual body-mass dimorphism. Thick arrows show links of causality that have strong support, thin arrows show weakly supported links.

in females (Wiklund and Solbreck 1982, Thornhill and Alcock 1983) and in males, e.g., through sperm competition (Wiklund and Forsberg 1991, Wiklund et al. 1991) or territorial disputes (*P. aegeria* is a territorial species; Wickman and Wiklund 1983).

Besides variation in pupal development times and growth rates, the dramatic change in mass dimorphism seen between the pupal and the adult stage could, if it is a general phenomenon, also decouple protandry from adult size dimorphism in a holometabolous insect or in any organism with some kind of metamorphosis, although in the particular case of *P. aegeria* the association between the two traits is not affected. The reason for the increase in mass dimorphism is not known, and it can only be speculated that the fact that males tend to lose relatively more of their mass at metamorphosis somehow reflects a sexual difference in larval growth patterns where males grow potentially faster but less efficiently.

Of the factors contributing to a lack of strong association between protandry and mass dimorphism in *P. aegeria,* one is relatively straightforward. Adaptive variation in growth rates (through plasticity or genetic differentiation) has been shown to be an important phenomenon in butterflies (Nylin et al. 1989, Wiklund et al. 1991, Nylin 1992). Typical of these results are the observation that growth and developmental rates vary adaptively, suggesting that they are not normally maximized. This parallels the development in vertebrate life history studies, where growth rates earlier were assumed to be maximized (Ricklefs 1969). More recently high growth rates have been seen to be associated with costs, and thus optimized rather than maximized among vertebrate species (Case 1978). Variation in growth rates has the general effect of complicating the expected simple relationship between development time and final mass (a two-dimensional association) by adding a third dimension, growth rate variation (cf. Pease and Bull 1988, concerning the general problem of dimensionality in studies on trade-offs). The present study is another indication that variation in growth rates should be given more prominence in life history theory, and that in many cases it may be profitable to

view an organism's growth rate as "chosen" rather than passively given by the environment.

The role of variation in pupal development time (also cf. Nylin 1992) is more intriguing. The general pattern in *P. aegeria* inhabiting relatively nonseasonal environments (Spain and Madeira) revealed by the present study is that sexual differences in larval development time associated with female-biased mass dimorphism (upwards-directed thin arrow in Fig. 10) is lost or reduced later in development, through a reversal of the difference in pupal development time between sexes. Why does this happen in a relatively nonseasonal environment, where the date of emergence should not matter? Tentative explanations could involve selection towards similar total development times of the sexes. First, selection in favor of synchronous emergence is possible. Second, there are aspects of development which continue throughout the larval and pupal stages. This means that the optimal pupal development times for females in a nonseasonal environment could well be shorter than for males. When growth rates are similar, they display longer larval development times (because of their greater masses) and thus have already completed a larger fraction of their total development to adults.

Conclusions

Several lines of evidence indicate that protandry is selected for per se and not merely a side effect of other selection pressures. It is thus a potential causal agent in life history coadaptation as suggested by Singer (1982). However, female-biased size dimorphism does not as a rule seem to be caused by protandry in butterflies, the group for which this hypothesis was proposed by Singer. Likewise, there is little evidence that the opposite causality is of any importance, and protandry does not seem to be caused by female-biased size dimorphism. Rather, the two traits seem to be associated only loosely in *P. aegeria* and many other arthropods, largely behaving like independent traits in life history evolution. Although the two traits are intimately functionally related, they are in effect largely decoupled by variation in pupal development time and larval growth rate between the sexes. Of general importance may be the observation that variation in growth rates can make possible independent optimization of size and development time, and accordingly influence patterns of size-related trade-offs in life history evolution.

Acknowledgments

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