# GEOGRAPHICAL VARIATION IN LARVAL HOST-PLANT USE BY *Heliconius erato* (LEPIDOPTERA: NYMPHALIDAE) AND CONSEQUENCES FOR ADULT LIFE HISTORY

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## ABSTRACT

Adult body size, one of the most important life-history components, varies strongly within and between *Heliconius erato phyllis* (Lepidoptera: Nymphalidae) populations. This study determines if this variation is caused by geographical changes in host-plant used by the larval stage, whose reproductive parameters are influenced by female body size, with estimates of the corresponding heritability. The variation in adult body size was determined together with a survey of passion vine species (Passifloraceae) used by the larvae in seven localities in Rio Grande do Sul State: three located in the urban area of Porto Alegre and Triunfo Counties, two within *Eucalyptus* plantations (Barba Negra Forest, Barra do Ribeiro County, and Águas Belas Experimental Station – Viamão County), one in a Myrtaceae Forest (Itapuã State Park – Itapuã County) and one in the Atlantic Rain Forest (Maquiné Experimental Station – Maquiné County). Effects of female body size on fecundity, egg size and egg viability were determined in an outdoor insectary. Size heritability was estimated by rearing in the laboratory offspring of individuals maintained in an insectary. The data showed that adults from populations where larvae feed only upon *Passiflora suberosa* are smaller than those that feed on *Passiflora misera*. The larvae prefer *P. misera* even when the dominant passion vine in a given place is *P. suberosa*. Fecundity increases linearly with the increase in size of females, but there is no size effect on egg size or viability. Size heritability is null for the adult size range occurring in the field. Thus, the geographical variation of *H. erato phyllis* adult size is primarily determined by the type, corresponding availability and quality of host-plants used by the larval stage. Within the natural size range of *H. erato phyllis*, the variation related to this caracter is not genetically based, thus being part of *H. erato phyllis* phenotypic plasticity.

*Key words*: body size, passion vines, heliconian butterflies, reproductive success, heritability.

## RESUMO

### Variação espacial no uso de plantas hospedeiras e conseqüências na história de vida de *Heliconius erato* (Lepidoptera: Nymphalidae)

Os adultos de *Heliconius erato phyllis* (Lepidoptera: Nymphalidae) variam acentuadamente em relação ao tamanho corporal. Neste trabalho, avalia-se a hipótese de que tal variação se deva em parte a diferenças qualitativas do recurso alimentar da fase larval (passifloráceas) existentes em campo. Em adição, identifica-se como a performance reprodutiva das fêmeas é influenciada pelo tamanho, sendo também estimada a herdabilidade dessa característica. Determina-se a variação espacial do tamanho corporal em sete populações de *H. erato phyllis* do Estado do Rio Grande do Sul (RS), situadas em ambientes urbanos (3), matas de *Eucalyptus* (2), mata de Mirtáceas (1) e Mata Atlântica (1), e relaciona-se tal variação ao recurso larval utilizado. Em insetário, quantifica-se a influência do tamanho das fêmeas nos parâmetros fecundidade, viabilidade e tamanho do ovo. A herdabilidade do tamanho foi estimada por intermédio da criação, em laboratório, da prole de indivíduos mantidos em insetário. Os adultos das populações cujas larvas utilizaram unicamente *Passiflora suberosa* foram significativamente menores em relação às que utilizaram *Passiflora misera*. As larvas foram encontradas preponderantemente sobre *P. misera*, mesmo quando *P. suberosa* foi a espécie predominante em um dado local. Dentre os parâmetros de performance reprodutiva estudados, apenas a fecundidade teve relação direta com o tamanho. A estimativa da herdabilidade para o tamanho foi zero. Assim, confirma-se a importância do recurso alimentar larval na determinação da variabilidade do tamanho dos adultos. Tal variação é parte da plasticidade fenotípica das populações naturais de *H. erato*, sendo a contribuição genotípica pouco expressiva neste caso.

*Palavras-chave*: tamanho corporal, maracujás, heliconíneos, sucesso reprodutivo, herdabilidade.

## INTRODUCTION

Body size is recognized as one of the most important life-history components for many animal species (e.g., Peters, 1983; LaBarbera, 1989; Roff, 1992; Stearns, 1992). Several studies focusing on insects (e.g., Honek, 1993; Klingenberg & Spence, 1997; Nylin & Gotthard, 1998; but see Leather, 1988), including Lepidoptera (e.g., Labine, 1968; Dunlap-Pianka, 1979; Elgar & Pierce, 1988; but see Boggs, 1986), have pointed out the existence of a positive correlation between body size and fecundity. In nymphalid butterflies, Dunlap-Pianka (1979) showed that there is a positive correlation between body size and fecundity in *Heliconius charitonia* (Linnaeus), and between body size and oviposition rate in *H. erato* (Linnaeus). In this study, we examine the effects of larval host-plant use on adult size in *H. erato phyllis* (Fabricius), and the corresponding consequences for female reproductive success.

Heliconiine butterflies are closely associated with their larval host-plants, the passion vines (Passifloraceae) (for reviews, see Benson *et al.*, 1976; Brown, 1981; Turner, 1981; Gilbert, 1991). Larvae of some species, as for example those of *H. erato*, feed upon a wide range of passion vine species. Physical and chemical properties, such as leaf toughness, concentration of nutrients and secondary metabolities, vary both intra- and interspecifically in such host-plants (Benson *et al.*, 1976; Smiley, 1978; Brown, 1979; Brown, 1981). Variation in host plant properties is expected to produce changes in the adult life history of *H. erato*, as has been demonstrated for many herbivorous insects (see Derr *et al.*, 1981; Scriber & Slansky, 1981; Slansky, 1993; Bernays & Chapman, 1994; Fernandes, 1994).

Both larval host plant species and plant part consumed influence larval development of *H. erato phyllis*. Tests perfomed in an enclosed insectary demonstrated that ovipositing females prefer *P. misera* over *P. suberosa* (S. M. Kerpel, UFRGS, unpublished data), and Menna-Barrreto & Araújo (1985) and Périco (1995) showed that pupae of *Heliconius erato phyllis* are heavier when larvae feed on *Passiflora misera* Humboldt, Bonpland et Kunth as compared to those reared on *Passiflora suberosa* Linnaeus. In addition, studies carried out in our laboratory demonstrated that larvae prefer feeding on *P. misera* over *P. suberosa*, and that feeding preference can not be induced in the larval stage (S. M. Kerpel, UFRGS, unpublished data). *H. erato* females preferentially oviposit on intact, apical *Passiflora* shoots compared to damaged ones (Mugrabi-Oliveira & Moreira, 1996b). On a given intact *Passiflora* shoot, a newly hatched larva typically selects the youngest tissue for feeding, which allows it to achieve greater survivorship and development rate compared to those that feed on mature leaves, but not necessarily a larger pupal size (Rodrigues & Moreira, 1999).

*H. erato* larvae have a solitary feeding habit and are cannibalistic (Benson *et al*., 1976), supposedly an adaptation to limiting plant tissue (Gilbert, 1991; Brower, 1997). In Viamão Municipality, Rio Grande do Sul State, a substantial number of *H. erato* eggs are laid on plants whose total leaf area is less than what is needed to complete larval development (Mugrabi-Oliveira & Moreira, 1996a). In addition, Rodrigues (1999) found that food shortage during the fifth instar has profound effects on survivorship and size attained in the adult stage. It is unknown whether adult size influences reproductive performance, which is also investigated in this study.

In *H. erato*, it has been documented that adult size varies both within and between populations (Benson *et al.*, 1976) (Fig. 1). Given that host plant use by larvae can affect adult size, we examine here the hypothesis that geographical variation in *H. erato* adult size is caused at least in part by host-plant shifts among populations in the field. To test for this hypothesis, we documented *H. erato phyllis* adult size for different passion vine species used by the larval stage in several localities in Rio Grande do Sul State. We also examined the importance of size on female life history characteristics, by evaluating fecundity, egg size and viability, and determined size heritability, to evaluate whether the variation in adult size observed for *H. erato* is genetically based or simply phenotypic plasticity.

## MATERIAL AND METHODS

### *Geographical variation in host-plant use and adult size*

The possibility of a correlation between larval host-plant use and adult size was examined in seven areas in Rio Grande do Sul State: 1) Parque Estadual de Itapuã (30º23'S; 50º55'W), predominantly a Myrtaceae forest; 2) Estação Experimental de Maquiné (29º39'S; 50º12'W), part of the Atlantic Rain Forest; 3) Estação Experimental de Águas Belas (30º05'S; 51º02'W) and 4) Horto Florestal Barba Negra (30º23'S; 51º12'W), both old *Eucalyptus* plantations; and three urban areas: 5) Fundação Zoobotânica and 6) Instituto de Pesquisas Hidráulicas/UFRGS (City of Porto Alegre – 30º05'S; 51º10'W), and 7) Parque COPESUL (29º56'S; 51º43'W). Sampling was done from April 22 to May 22, 1998, during the heliconian population peak (Saalfeld & Araújo, 1981). For each locality, the sampling area consisted of a 250-m long, 3-m wide trail section.

For each locality, trails were sampled once, during early morning (samples lasted at most three hours). All *Passiflora* individuals in the trail were surveyed, counting branches with intact apical buds (apical meristem, leaf primordia and unopened leaves), and *H. erato phyllis* immatures per branch.

Forewing length is considered to be a good predictor of body size for Lepidoptera in general (Miller, 1977; Haukioja, 1993), being highly correlated with pupal size in *H. erato phyllis* (Rodrigues, 1999). Thus, concomitantly with examination of plants, adults found along the trail were captured with an insect net and their forewing length (base to apex) measured to the nearest 0.05 mm with a pair of calipers. Measured butterflies were numbered on the forewing red patch with a felt-tipped pen, and then released.

### *Female reproductive performance in relation to size*

Examination of reproductive performance was based on 23 *H. erato phyllis* females (wing length varying from 29.55 to 40.45 mm) captured at the Fundação Zoobotânica and the Instituto de Pesquisas Hidráulicas/UFRGS. They were individually kept in outdoor insectaries of the Zoology Department of the Universidade Federal do Rio Grande do Sul, following methods described in Dunlap-Pianka (1979). Adults were fed daily with a mixture of commercially available honeybee pollen (AGA®), honey (AGA®) and distilled water (ratio 2:1:7) (details in Mugrabi-Oliveira & Moreira, 1996a).

In each insectary three potted *Passiflora suberosa* Linnaeus plants were available for oviposition. They were inspected daily for presence of eggs, which were removed from the plants by using a fine, moist brush, and individually placed in Petri dishes, lined with moist filter paper. Eggs were kept in a large laboratory chamber (14 hours of light: 10 hours of darkness; 25 ± 1ºC), and checked daily for newly hatched larvae.

Females were monitored for daily oviposition rate during a time interval that varied from 10 to 20 days (average 18.4 days per female). Estimates of egg volume were based on the first eggs laid by females, varying from 15 to 30 per female. By using a stereomicroscope equiped with a micrometric scale, egg height and maximum diameter were measured, and then used to estimate egg volume. In average, 25.95 eggs were used to estimate the egg volume produced by a given female. Egg viability corresponded to the larval hatching rate of undamaged eggs.

### *Size heritability*

Size heritability was determined by crossing newly emerged females (n = 10), reared from adults collected at the Fundação Zoobotânica and the Instituto de Pesquisas Hidráulicas, with males collected from the same places. This procedure was justified by the fact that *H. erato* females are monogamous, and in most cases mate during or immediately after emergence. In contrast, males achieve sexual maturity later in life (Alexander, 1961). Paired males and females (parents = P) had similar forewing length, which varied from 33.02 to 39.67 mm per pair. Mating pairs were maintained in individual outdoor insectaries, following the methodology described above. The procedure for collection and incubation of eggs was as described above. Newly hatched larvae (offspring = $F_1$) were individually transferred to branches of *P. suberosa* in water-filled, plastic bottles. The branches came from potted plants that were transplanted at an early stage from the Estação de Águas Belas population (Mugrabi-Oliveira & Moreira, 1996a), and maintained under cultivation in outdoor enclosures. Food was offered *ad libitum*, with *P. suberosa* branches replaced whenever necessary. Plants were covered with a fine mesh cloth, and kept in the laboratory chamber until adult emergence. The forewing length of freshly emerged adults (the 30 first offspring of each couple) was also measured with calipers as described above.

### *Statistical analysis*

Adult size frequency distributions for each area were evaluated for normality and homocedasticity of variances through Kolmogorov-Smirnov and Bartlett tests. When analyses of variance were significant, differences among localities were compared by using Tukey's multiple comparison tests. Size effects were evaluated through regression analyses using all reproductive parameters. Heritability was estimated by regressing the average size of parents in relation to that of their offsprings, with $h^2$ corresponding to the slope of the resulting regression line (Falconer, 1989; Stearns, 1992; Beiguelman, 1994). Parametric and non-parametric tests followed procedures described in Sokal & Rohlf (1981) and Conover (1980), respectively. Unless noted measurements are given as mean ± standard error.

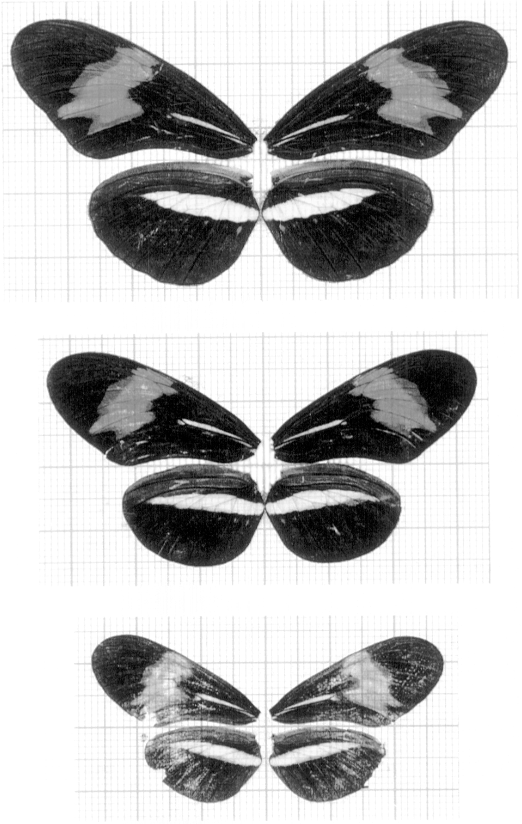

**Fig. 1 —** Variation in *H. erato phyllis* forewing length. Large squares = 0.5 cm.

## RESULTS

### *Geographical variation on host-plant use and adult size*

Eight passion vine species were found in the seven study sites: *P. suberosa* Linnaeus, *P. misera* Linnaeus, *P. caerulea* Linnaeus, *P. elegans* Masters, *P. alata* Dryander, *P. tenuifila* Killip, *P. actinia* Hooker and *P. capsularis* Linnaeus (Fig. 2).

Species composition of passion vine communities varied among localities. *P. suberosa* or *P. misera* were present at all sites, with the main host-plants being used, except at Estação Experimental de Maquiné.

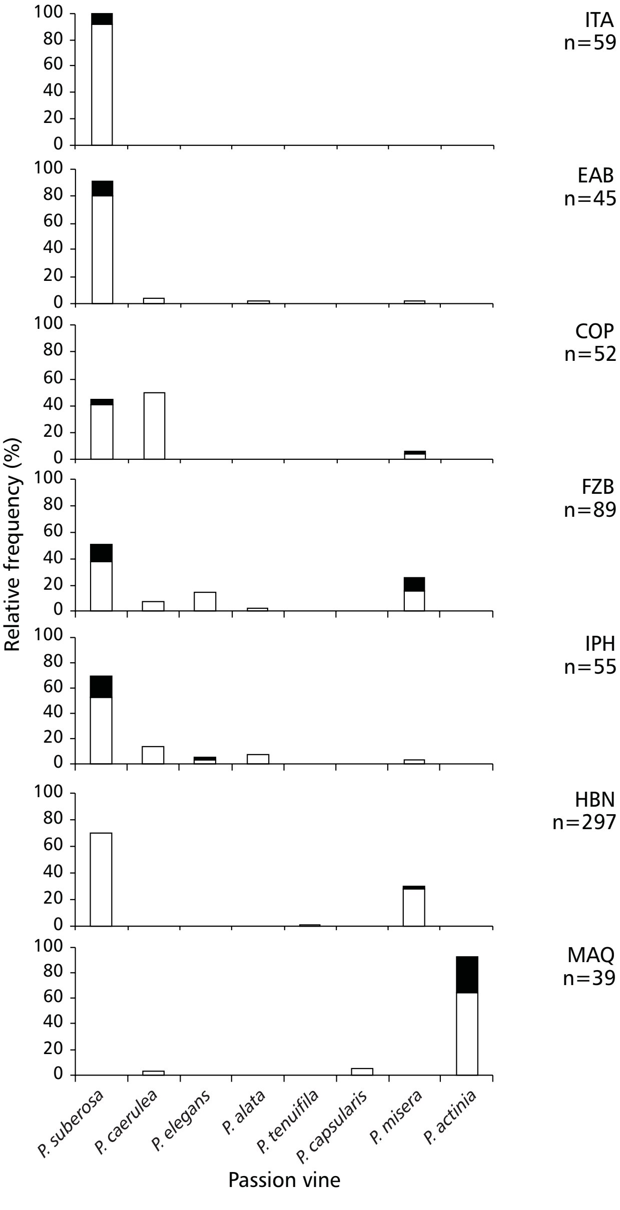

**Fig. 2** — Relative abundance of passion vine species among localities. Dark portions of bars correspond to relative frequencies of shoots with immatures of *H. erato phyllis*. ITA, Parque Estadual de Itapuã; EAB, Estação Experimental de Águas Belas; COP, Parque Copesul; FZB, Fundação Zoobotânica; IPH, Instituto de Pesquisas Hidráulicas/Campus do Vale, UFRGS; HBN, Horto Florestal Barba Negra; MAQ, Estação Experimental de Maquiné. n = total number of passion vine shoots sampled per locality.

At Maquiné, *P. actinia* was the most abundant passion vine species and the one predominatly used by the immatures of *H. erato phyllis*.

A progressive increase on *H. erato phyllis* forewing length was found in the sites, concurrent with a shift in host plant used from *P. suberosa* to *P. misera* or *P. actinia* (Figs. 2-3).

The smallest forewing lengths were in the Parque Estadual de Itapuã and Estação Experimental de Águas Belas (Fig. 3). These were the sites where *P. suberosa* was the most abundant and the unique host-plant species used by *H. erato phyllis* immatures (Fig. 2).

Forewing lengths were intermediate at Parque COPESUL and Fundação Zoobotânica, places where both *P. suberosa* and *P. misera* were used as host-plants. They were larger at Horto Florestal Barba Negra, where *P. misera* was the only host-plant used in spite of the predominance of *P. suberosa*. The largest forewing length values were found at Estação de Maquiné, where both these host-plant species were absent.

### *Female reproductive performance in relation to size*

Daily oviposition rate increased significantly with increase in female forewing length (F = 10.217; p < 0.0048; Fig. 4A). Minimal and maximum rates were 0.52 and 4.92 eggs, for females with forewing length of 29.55 and 38 mm, respectively. On the average, females laid 2.28 eggs per day.

Egg viability was not correlated with female forewing length (F = 0.3696, p > 0.55; Fig. 4B), nor was egg volume (F = 0.1521, p > 0.70; Fig. 4C). Egg viability per female varied from 44% to 82.8% (average = 65.42%), and egg volume from 0.53 to 0.88 mm$^3$ (average = 0.8 mm$^3$).

### *Size heritability*

The slope of the regression for offspring forewing length versus that of their parents was essentially zero (slope = – 0.0115, F = 0.030, p = 0.8661; Fig. 5). Thus, the heritability (h$^2$) estimated for body size in *H. erato phyllis* was null. The offspring forewing length varied from 30.15 to 41.35 mm (average = 37.56 mm; n = 294).

Development time from egg to pupa for the F1 averaged 21.65 ± 0.12 days. There was a significant negative correlation between development time and adult size for F1 individuals (n = 294; F = 65.475; p < 0.0001).

The few individuals with development time greater than 25 days emerged with greatly reduced body size (Fig. 6).

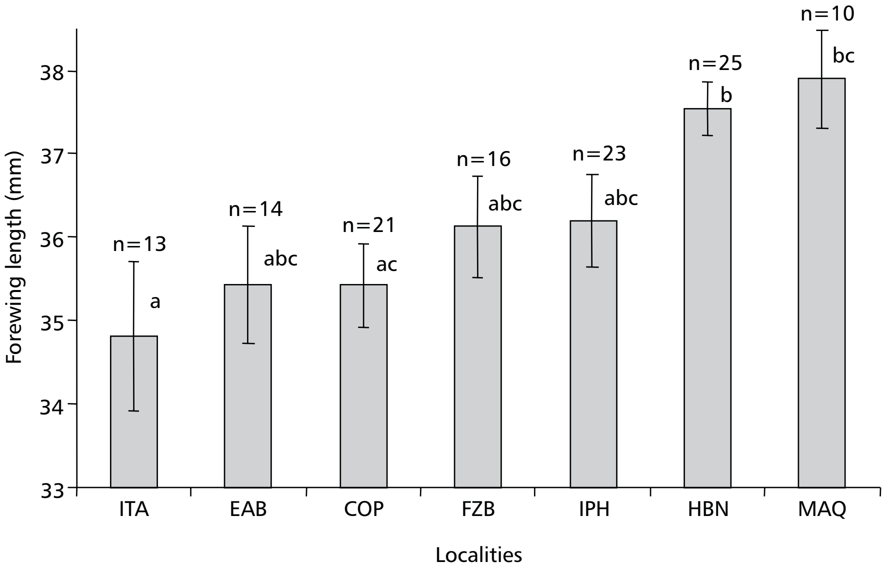

**Fig. 3** — Variation in *H. erato phyllis* adult body size (mean ± standard error) among localities. ITA, Parque Estadual de Itapuã; EAB, Estação Experimental de Águas Belas; COP, Parque Copesul; FZB, Fundação Zoobotânica; IPH, Instituto de Pesquisas Hidráulicas/Campus do Vale, UFRGS; HBN, Horto Florestal Barba Negra; MAQ, Estação Experimental de Maquiné. n = total number of adults sampled per locality. Bars followed by the same letter are not significantly different (ANOVA, alpha = 0.05; Tukey multiple comparison tests, alpha = 0.05).

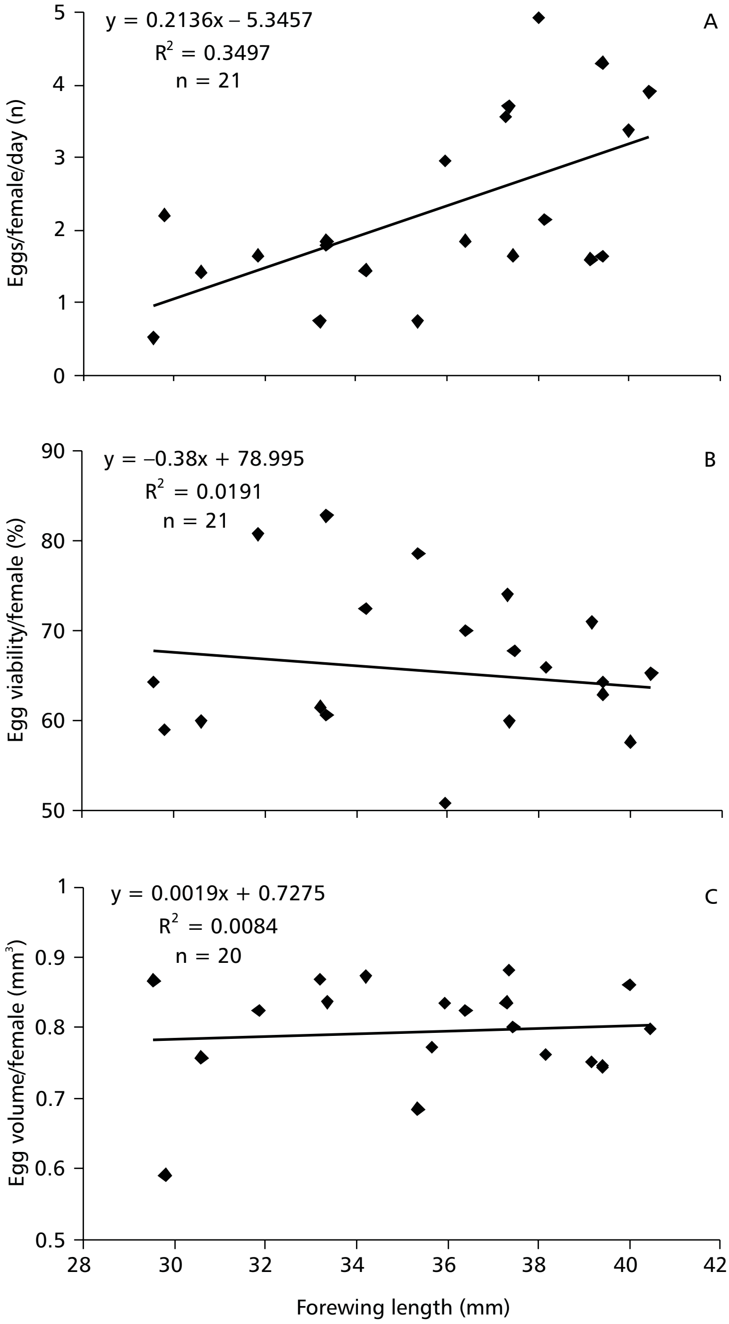

**Fig. 4** — Daily oviposition rate (A), egg viability (B) and egg size (C) in relation to *H. erato phyllis* female body size.

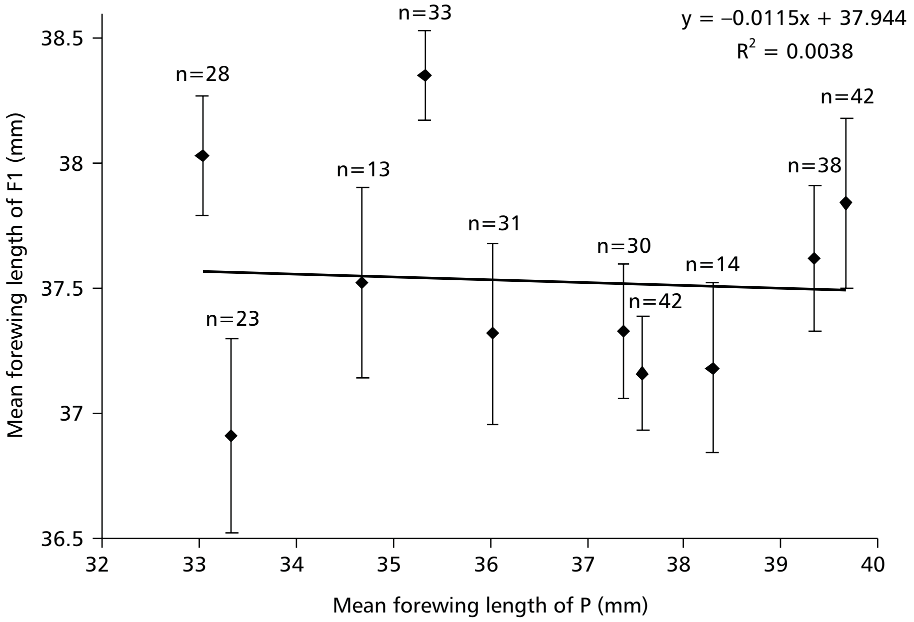

**Fig. 5** — Size (mean ± standard error) of offspring (F1) in relation to adult body size of parents (P) in *H. erato phyllis*. Data correspond to ten crossed pairs. n = number of adults obtained per cross.

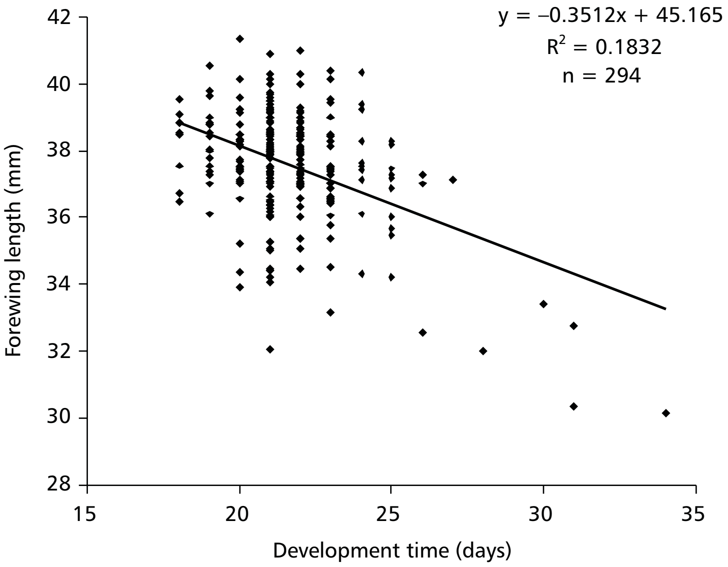

**Fig. 6** — Adult size of *H. erato phyllis* in relation to larval and pupal development time.

## DISCUSSION

Our study indicates that *H. erato phyllis* varies in body size from place to place according to the passion vine species used as feeding resource by the larval stage. Where larvae fed basically on *P. suberosa*, adults averaged smaller than those where *P. misera* was used. In fact, Rodrigues (1999) demonstrated under controlled laboratory conditions that adults reared on *P. misera* are significantly larger than those reared on *P. suberosa*, independent of temperature. In one site (Horto Florestal Barba Negra), where *P. misera* occurred at low densities in this study, but high enough to support some larvae, *P. suberosa* was not used in spite of its greater abundance. *H. erato phyllis* females select *P. misera* over *P. suberosa* for oviposition, under field and insectary conditions, even when abundance and quality of the former species is lower (S. M. Kerpel, UFRGS, unpublished data). Nevertheless, females will lay eggs on *P. suberosa* when *P. misera* shoots are defoliated or deprived of terminal buds and those of *P. suberosa* are abundant and intact. Adults in the Horto Florestal Barba Negra are smaller during the winter, when *P. misera* is completely defoliated and *P. suberosa* is used as host. When immatures were reared under laboratory conditions, adults obtained from larvae that fed on *P. misera* were significantly larger than those obtained from larvae on *P. suberosa* (Rodrigues, 1999).

In the populations studied, we could not detect any influence on adult body size of abiotic or biotic factors other than host-plant use. The study sites are less than 100 km from each other and have similar altitudes. Samples were taken practically at the same time, and thus there is no indication that abiotic factors, such as temperature, could play a major role in determining the observed variation in body size. Furthermore, competition could not account for the size trend in this case, since the greatest body size values, contrary to what would be expected, were achieved when larvae fed on *P. misera*, the only potentially limited food resource. Parasitism is negligible in these *H. erato phyllis* populations, and there is no indication that other biotic factors, such as the existence of differential predation rates among study sites, could be an alternative explanation for the observed variation in size (G. R. P. Moreira, UFRGS, unpublished data).

The patterns of host-plant use in the field reported in this paper are in agreement with some previous studies (e.g. Romanowsky *et al*., 1985), however, not with other ones. Menna-Barreto & Araujo (1985) found an oviposition preference of *H. erato phyllis* for *P. capsularis*, which was not confirmed by Périco (1995) nor was it confirmed in this study. We believe that such discrepancies can be attributed to differences in the abundance and relative quality of host-plants, a factor that was not taken into account in their studies. In general, host-plant attributes can significantly affect oviposition choices in Insecta (see Cates, 1980; Singer, 1983), including *H. erato phyllis* (Mugrabi-Oliveira & Moreira, 1996a,b). Although occurring at low densities compared to *P. suberosa* in the Horto Florestal Barba Negra, the population of *P. misera* is large enough to entirely support the *H. erato phyllis* larvae, unlike the other sites in this study.

To our knowledge, this paper presents the first documented evidence supporting the influence of geographical changes in host plant use on the variation of adult size in Lepidoptera. The effect of larval environment on adult body size in Lepidoptera was demonstrated by Cook (1961) in a pioneer study on field variation on body size among southern populations of *Panaxia dominula* (Arctiidae) in the British Island. In this case, wingspan strongly varied among several localities, along size with differences between males and females in some regions. When they were reared under the same conditions in the laboratory, this variation could not be detected. However, the author did not mention the corresponding larval food sources.

The existence of a positive correlation between nutrient levels of a given host-plant and body size is widely accepted for Insecta (Wickman & Karlsson, 1989; Slansky, 1993). Within the heliconiines, this relationship has been demonstrated for *Dryas iulia* and *Heliconius charitonia* (Boggs, 1981), and for *H. ismenius* and *H. melpomene* (Smiley & Wisdom, 1985). Although biochemical and physiological studies have not been done for the *H. erato phyllis*-*Passiflora* system, our data suggest that *P. misera* represents a higher quality larval food resource than *P. suberosa*, yielding a larger size to adults.

We found that body size had an effect on egg production, but not on egg size or viability. The insectary data clearly demonstrate that fecundity increases linearly with increase in female body size. Unlike fecundity, egg size and fertility were not associated with female body size in *H. erato phyllis*. The size of eggs and that of newly hatched larvae is highly correlated in Lepidoptera (Reavey, 1992), and small first instar larvae may take a longer time to complete development (Wright & Clarke, 1981; Happ, 1984). Inasmuch as egg size and viability were comparable for small and large *H. erato* females, our observations suggest that offspring development and competitive potential are independent of the mother's size. Wiklund *et al.* (1987) found that egg size may or may not be correlated with female body size depending on environmental conditions, under which the species is adapted to withstand. Independence between adapted withstand these parameters has been pointed out for several nymphalid butterflies (Boggs, 1986) and for some Diptera (Roff, 1981).

The null result for size heritability indicates low genotypic determination of this trait, which should be valid only for the size range of *H. erato phyllis* in the field. Thus in these populations, the potential size of offspring is practically the same for either small or large parents, when reared under the same conditions. The small females of *H. erato phyllis* could have a smaller reproductive apparatus, that produces and stores a lesser amount of eggs (Dunlap-Pianka, 1979); but the egg allocation in terms of size and fertility is similar to greater females. Thus, we consider the body size variation in *H. erato phyllis* as part of its high phenotypic plasticity (see Nylin & Gotthard, 1998; Ramos & Freitas, 1999; Correa *et al*., 2001). In this case, it benefits *H. erato phyllis*, by allowing this species to explore a wide range of host-plants as larval food resource, which can vary in abundance not only in space but also in time (Rodrigues, 1999). Size is a trait considered as more plastic in insects adapted to situations where larval resources fluctuate (Nylin & Gotthard, 1998).

There are at least three reasons for explaining the absence of heritability for body size in wild *H. erato phyllis* populations. First, genetic additive effects for this trait may act on parent sizes outside the range included in the experiment. All mating attempts using females with forewing length below 33.35 mm were unsuccessful, independent of male size. This suggests the existence of a size threshold, which needs further study. Also, our methods do not exclude dominance effects, including those of maternal origin (see Falconer, 1989). In fact, the smallest offspring were obtained from one of the two smallest females in the experiment. Second, the absence of additive genetic variance may reflect the correlation of body size with other important life-history components (see Hegman & Dingle, 1982; Roff, 1992), like larval development rate and fecundity. Third, it is possible that some degree of inbreeding had occurred among parents. This is less likely, however, since males and females used in the experiment came from different populations.

The absence of body size heritability has been also found for the bug *Nezara viridula*, where an intricate relation between size and larval development rate was observed (McLain, 1991). In this study, the offspring larval development rates were negatively correlated with larval size. This effect was stronger among the few larvae that had extremely reduced size. These individuals probably came from eggs, which were also smaller, since the size of eggs and that of newly hatched larvae are highly correlated in Lepidoptera (Reavey, 1992). The fact that these individuals were in low frequency in the F1 population represents another evidence for low genotypic influence on size. By being smaller since their conception, these individuals may require more time to attain the size threshold for moulting (Wright & Clarke, 1981; Happ, 1984). The existence of a trade-off between development time and adult size has been found for many insects (e.g. Reavey & Lawton, 1991; Klingenberg & Spence, 1997; Nylin & Gotthard, 1998).

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