



## Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea)

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*Received 24 November 1998; accepted for publication 5 July 1999*

The interspecific relationships between egg size and body size in butterflies (Papilionoidea and Hesperioidea), and between size and egg and larval development time, larval trophic specificity, foodplant structure, climate, and phenology were investigated based on a sample of more than 1180 species. The independent contrasts method was used to avoid taxonomy-dependent results. Egg size is allometrically related to adult wing length by a slope of 0.43. Based on a subset of species, fecundity is correlated to adult body size, and there is evidence for a compromise between egg number and egg size (relative to adult size) across species. Butterfly size increases in correlation to the mean annual temperature of the species geographic range, but decreases in relation to increased aridity (or the length of the dry season). Larger butterflies tend to have longer larval development times, use large or structurally complex host plants, and are more likely to lay their eggs in batches, irrespective of climate. Larger eggs tend to develop more slowly, and give rise to larvae with longer developmental periods that will result in larger adults. No evidence was found to support a relationship between butterfly body size and polyphagy. A complex pattern of interrelationships links body size (and egg size) to other traits, although correlations other than that between egg size and body size are generally low. The results suggest the necessity of separating climate and seasonality into components that are relevant to insect life histories in comparative studies.

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**ADDITIONAL KEYWORDS:**—allometry – climate – clutch size – comparative methods – fecundity – host plant – phenology – polyphagy.

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## INTRODUCTION

As holometabolous insects, butterflies (superfamilies Papilionoidea and Hesperioidea) do not grow further once they reach adulthood. Oviposition may follow different temporal patterns (Boggs, 1986), but occurs as a single event in a female's lifetime. With few exceptions such as the genus *Heliconius* (Boggs *et al.*, 1981), nectar and protein-poor fluids constitute the basic adult diet. Even when materials transferred by the male during copulation may contribute to egg production (as described from some polyandric species: Boggs & Gilbert, 1979; Wiklund *et al.*, 1993), a large proportion of the material invested into eggs must derive primarily from the reserves gathered during the larval stage (Wickman & Karlsson, 1989; Karlsson & Wickman, 1990). These reserves are thus fixed at the moment of adult eclosion, and must be converted into eggs that are tightly packed in the female's abdomen. All these circumstances suggest a strong physical interdependence between female body size, the amount of material available for egg yolk, and the number of eggs produced. Evolutionary change in one of the traits should cause relatively rapid reciprocal adjustment of the others. This makes these organisms valuable tools for the study of the relationship between body size, and egg size and number within an adaptationist program.

The two extremes of the butterfly 'size cycle' (adult and egg size) vary considerably (e.g. Labine, 1968; Hawkins & Lawton, 1995; García-Barros & Munguira, 1997). Evolutionary relationships with environmental variables have been the subject of study in recent years. Most studies have focused on intraspecific relations between key life history traits, or between these and environmental variables. In contrast, comparative research on butterfly size at the interspecific level has been carried out for little more than a decade. The processes involved in the evolution of size within and among species may share similar backgrounds but, as pointed out by Schmidt-Nielsen (1984), constraints can be overcome with novel designs, which may involve more or less profound allometric changes. Such evolutionary shifts are more likely to be found at taxonomic levels higher than the species boundaries.

The results of prior comparative interspecific studies conducted to determine possible ecological and evolutionary correlates of egg and adult body size of butterflies are summarized in Table 1. Egg size is generally strongly related to body size (although not in all taxa) and proximate factors that influence survival or performance of immature stages (e.g. hibernation in the egg stage, physical characteristics of the larval foodplants). In the case of satyrine nymphalids, there is also a correlation

TABLE 1. Summary of the evidence for interspecific relationships between size (egg and adult) and proposed explanatory variables for butterflies (Papilionoidea and Hesperioidea). Size estimates: L, linear; V, volume; W, weight. Direction of the relationship (e.g., correlation): +, positive; -, negative; n.s., not significant. References: 1, Wiklund & Karlsson, 1984; 2, Nakasujii, 1987; 3, Wiklund, Karlsson & Forsberg, 1987; 4, Reavey, 1992; 5, Barlow, 1994; 6, Garcia-Barros, 1994; 7, Hawkins & Lawton, 1995; 8, Garcia-Barros & Munguira, 1997. Notes: (a) probably positive relationship, but non-linear; (b) based on a *posteriori* interpretation of outliers from regression; (c) relationship significant when species means used, implying that it is probably due to taxonomic effects

Life stage	Size estimate	Taxa	Geographic area	Variable/trait	Number of species	Direction of relationship	Type of data	Reference
Egg	W	Satyrinae	NW Europe	Female weight	10	+	Individual weights	1
Egg	W	Satyrinae	NW Europe	Female weight	14	+	Species means	3
Egg	W	Satyrinae	W Europe	Female weight	42	+ / n.s. (a)	Contrasts	6
Egg	W	Pieridae	NW Europe	Female weight	11	n.s.	Species means	3
Egg	V	Hesperinae	Japan	Adult wing length	18	+	Species means	2
Egg	L	Butterflies	Holarctic	Female wing length	253	+	Contrasts	8
Egg	V	Hesperinae	Japan	Host plant leaf toughness	19	+	Species means	2
Egg	W	Satyrinae	NW Europe	Host plant leaf toughness	10	n.s. (b)	Individual weights	1
Egg	L	Lycacnidae, Hesperidae	Britain, N America	Host plant growth form	7-24	+	Species means, within family	4
Egg	L	Nymphalidae	Britain, N America	Host plant growth form	20	n.s.	Species means, within family	4
Egg	L	Butterflies	Holarctic	Host plant growth form	253	n.s.	Contrasts	8
Egg	L	Butterflies	Holarctic	Monocotyledon larval foodplant	248	n.s. (c)	Contrasts	8
Egg	L, V	Lycacnidae, Nymphalidae	Britain, N America	Larval feeding specificity	7-23	+ / - / n.s.	Species means, within family	4
Egg	W	Satyrinae	NW Europe	Increased fecundity	14	- (b)	Species means	3
Egg	L, V	Lycacnidae	Britain, N America	Egg overwintering	15-30	+ / n.s.	Species means, within family	4
Egg	L	Butterflies	Holarctic	Egg overwintering	253	n.s.	Contrasts	8
Egg	V	Lycacnidae, Nymphalidae	Britain, N America	Egg location	36	n.s.	Species means, within family	4
Egg	W	Satyrinae	W Europe	Long female pre-oviposition	40	-	Contrasts	6
Egg	W	Satyrinae	W Europe	Latitude	42	+	Contrasts	6
Egg	W	Satyrinae	W Europe	Adult sexual size dimorphism	39	n.s.	Contrasts	6
Egg	W	Satyrinae	W Europe	Egg not fixed to substrate	42	n.s.	Contrasts	6
Egg	L	Butterflies	Holarctic	Uni- vs multivoltinism	244	n.s. (c)	Contrasts	8
Adult	L	Butterflies	Australia, Afrotropics	Latitude	3000	-	Species means, within areas	5
Adult	W	Satyrinae	W Europe	Latitude	42	n.s.	Contrasts	6
Adult	L	Butterflies	Africa, Australia, Europe, N. America	Latitude	>3000	+ / - / n.s.	Species means, within areas	7
Adult	L	Butterflies	Holarctic	Host plant growth form	238	+	Contrasts	8
Adult	L	Butterflies	Holarctic	Monocotyledon larval foodplant	248	n.s. (c)	Contrasts	8
Adult	L	Butterflies	Holarctic	Uni- vs multivoltinism	244	n.s.	Contrasts	8
Adult	L	Butterflies	Holarctic	Egg overwintering	229	n.s.	Contrasts	8
Adult	L	Butterflies	Holarctic	Egg development time	151	n.s.	Contrasts	8
Adult	L	Butterflies	Holarctic	Adult sexual size dimorphism	39	n.s.	Contrasts	6
Adult	W	Satyrinae	W Europe	Long female pre-oviposition	40	n.s.	Contrasts	6
Adult	W	Satyrinae	W Europe	Egg not fixed to substrate	42	n.s.	Contrasts	6

between latitude and egg size, which has been explained by adverse weather constraining increases in fecundity that could otherwise be achieved by reducing egg size (Wiklund *et al.*, 1987; García-Barros, 1994). There is some evidence of an inverse relationship between adult body size and latitude (the converse of Bergmann's Rule: Barlow, 1994), which is consistent with results from other Lepidoptera (Wasserman & Mitter, 1978). However, Hawkins & Lawton (1995) found that the results are not consistent among different geographical regions. In temperate species, body size may be related to the structure of the host plant.

It is obvious from Table 1 that most of the relationships have been assessed from small sets of species exhibiting a strong geographical bias, using different methods and size estimates (e.g. length, volume, weight), often with no control for the taxonomic effects of 'phylogenetic inertia' (Felsenstein, 1985). In spite of this, considerable published information on butterfly life histories is available and can be used in comparative studies if a degree of measurement error in the data is admitted.

This study aimed to identify general patterns in the relationships between egg size and adult body size, and overall relationships between size and environmental and life history variables in butterflies. The objective was to identify general trends that could be of use in further research in this, and related, insect groups, rather than to test specific hypotheses. To do this, a number of variables was selected according to factors that have been claimed to be significant in the evolution of insect size, or more specifically, butterfly size. These were reassessed using a comparative method that took effects of shared ancestry into account. The variables considered were constrained by the limitations of data collection and the recording procedures employed, which required some degree of simplification in order to cover as many species as possible.

#### DATA SOURCES

An effort was made to consider as taxonomically and geographically varied a selection of species as possible. The availability of sources was the main limiting factor. For inclusion in the study, it had to be possible to estimate egg size in a species. This proved feasible for 1183 species, data on which were compiled from 301 published references, and a further 40 species reported in unpublished sources. Related life history and geographical data (described below) were commonly extracted from life history reports containing descriptions of eggs, but were complemented by information from additional literature wherever possible. For the sake of brevity, not all data or references are presented here, although a summary of the egg and adult size estimates at the genus level appears in Appendix 1. A more detailed account is presented elsewhere (García-Barros, 2000). Some of the published studies are remarkable due to the large number of egg descriptions included (about 80% of the descriptions of species were obtained from a mere 25 articles or books). The relevant literature concerning the Holarctic is cited in García-Barros & Munguira (1997). Complementing this, and with information from other faunal regions, are the publications of Van Someren & Van Someren (1926), Van Son (1955, 1963, 1979), Beebe *et al.* (1960), Clark & Dickson (1971), Pennington (1978), Brown (1981), Kitching (1985), Nakasuji (1987), Henning (1989), Häuser *et al.* (1993), Brown & Freitas (1994), Pringle *et al.* (1994), Hesselbarth *et al.* (1995), Igarashi & Fukuda

(1997), and Teshirogi (1997). Important complementary sources (e.g. those providing additional information on adult size, geographic distribution, foodplants and other life history details) include Hayward (1964–1967), Smart (1975), Corbet & Pendlebury (1992), D'Abbrera (1981–1995), Common & Waterhouse (1981), Ackery & Vane-Wright (1984), Collins & Morris (1985), Scott (1986), De La Maza (1987), De Vries (1987, 1997), Kielland (1990), Fiedler (1991), Larsen (1996), Bink (1992), Pringle *et al.* (1994), Smith *et al.* (1994), Neild (1996), Tennent (1996), Tolman & Lewington (1997), and Tuzov *et al.* (1997).

#### VARIABLES

The variables were chosen primarily to test some of the relationships summarized in Table 1. Besides adult and egg size, these had to represent larval host plant specificity and structure, butterfly phenology, development time and latitude. Latitude has often been invoked as a potential correlate of insect size. This is because of the correlation between geographic latitude and some parameters of climate with a strong potential weight on life-history evolution, such as temperature, or the length of the growth season (see Nylin & Svård, 1991). Even for a reputedly well known insect group such as the butterflies, geographic distributions cannot be drawn with much accuracy at a world-wide level. Recent approaches to the relationship between butterfly size and climate had thus to be based on relatively broad estimates of latitude (Barlow, 1994; Hawkins & Lawton, 1995). Based on the same faunistic information, temperature and water availability can be estimated with a degree of accuracy comparable to that of latitude. Since these variables determine the period available for growth (e.g. Schultz, 1995), using them has the advantage of providing more explicit tests for the evolutionary relevance of climate. With this purpose, estimates of mean temperature and aridity were included. Since butterflies may lay their eggs singly or in batches, a further variable (clutch size) was considered that took possible life history correlates of egg clustering into account.

Sixteen variables were tested. Variables 1–10 and 16 were continuous, and variables 11–15 were categorical. Absence of information, and unreliable or conflicting data were coded as missing. The comparative method used (described below) is especially well-suited to the study of quantitative continuous traits such as size. Due to the limits imposed by the nature of the data, two of the traits were coded in two different ways and tested separately (variables 3 and 4, and 7 and 8). Two qualitative variables (14 and 15) were designed to test special cases of three others (7–9). These procedures indicated whether there was any subjectivity in the scales used, and gave a perspective on the precise meaning of correlations based on approximate measurements. Except where otherwise stated, median values were calculated for quantitative variables when two or more sources of data were found.

##### 1. *Egg size*

Egg size (mm) was estimated as the cubic root of the volume of a regular, prolate, ellipsoid according to the formula:

$$\text{egg size} = (0.5236 \times d^2 \times h)^{1/3},$$

where  $d$  = egg diameter, and  $h$  = egg length. The regular ellipsoid is a shape that

has frequently been used to estimate insect egg volumes (e.g. Price, 1974; Nakasuji, 1987; Blackburn, 1991b), and allows reasonable estimates of the volume of eggs with round profiles to be made. The error is larger for other egg shapes but this is ameliorated by the cube root transformation. This had the additional advantage of producing a linear estimate based on the two egg parameters (length and width) most frequently used in descriptions of butterfly eggs. Scale figures of the eggs were used to estimate egg dimensions where possible when no explicit measurements were available. There were a few instances in which egg diameter alone was recorded but where the shape was described as 'spherical', or 'subspherical'. In these cases, length and width were assumed to be equal when this was deemed justified from descriptions of the most closely related species.

## 2. *Adult size*

Adult size was estimated as the median of male and female forewing lengths, in order to overcome problems caused by unknown patterns of variation in sexual dimorphism for size. Wing lengths were measured from the point of insertion in the body to the wing apex. Detailed statistics of butterfly wing lengths are infrequent in the literature, so most estimates were based on ranges, or measured from plates representing life-sized individuals. Sources with the closest geographical association with the egg and life history reports were given preference (including unpublished data provided by authors of the life history reports, or collection data, where available). The plates in the volumes by D'Abrera (1980–1995) were used by default.

## 3 & 4. *Polyphagy*

The information on the number and identity of larval hosts used by butterfly species is likely to be biased with respect to taxa and geographic areas. In an attempt to reduce such heterogeneity in the data, genera rather than species of foodplants were considered, even though this probably gives results of lower resolution. The degree of polyphagy was coded in two different ways: the number of foodplant genera recorded for each butterfly species (3), and a taxonomy-based index (4) similar to those adopted by Fiedler (1991) and Loder *et al.* (1998), with five categories: (1) one plant genus; (2) one plant family; (3) one plant order; (4) one plant subclass; (5) feeding on plants from more than one subclass (plant taxonomy according to Mabberley, 1997). The two indices of polyphagy were correlated across species ( $r = 0.53$ ,  $P < 0.0001$ ,  $n = 1065$ ).

## 5. *Mean temperature*

The mean temperatures of the species' geographic distributions were estimated by superposition of approximate distribution maps (derived from the pertinent literature) on broad-scale temperature maps (Blüthgen, 1966, was used as primary reference). Five broad temperature 'bands' were set on the basis of annual 5°C isotherms:  $\leq 5^\circ\text{C}$ , 6–10°C, 11–15°C, 16–20°C, and  $\geq 21^\circ\text{C}$ . The midpoints of these ranges (i.e. 3, 8, 13, 18, 23°C) were used as mean temperatures for the species occurring in the respective temperature zones. The median between the two extreme values were assigned to species spread throughout two or more of the bands. Further subdivision of the temperature ranges could have been attempted with some degree of confidence for areas such as Europe, North America and—to some extent—Australia (following e.g. Common & Waterhouse, 1981, Scott, 1986, or



Tolman, 1997), but this proved impractical because of the difficulties of determining with accuracy the ranges of most tropical species. This may cause a loss of resolution in the results, especially in the upper temperature range. Species restricted to narrow mountain ranges were carefully considered, since local climatic conditions cannot be derived from broad-scale maps. When detailed geographic information was accessible from additional sources, the data were corrected accordingly. If this was not the case, but at least the elevation at which the species occurs was known, estimates were corrected on the basis of a decrease of 5°C per 1000 m elevation (mean surface temperatures are known to decrease by 0.5 to 0.7°C per 100 m elevation: Margalef, 1980). Whenever a reasonable doubt arose, this variable was coded as missing.

#### 6. *Aridity*

This variable was intended to categorize the amount of water stress that an environment is likely to experience during the period when temperatures are adequate for growth and reproduction. Four classes were designated, based on a simplification of the climate types of Köppen-Geiger-Pohl (Strahler & Strahler, 1987; de Blij, 1995): (1) no dry season; (2) dry season of at least 1 month, but high total water influx; (3) semiarid, or temperate with a dry summer; (4) arid (desert and semidesert). The species were scored according to the value (1–4) that characterized their geographic distribution, or as the median between the extreme values (when two or more aridity zones were intercepted by the species range). The classes 1 to 4 respectively correspond to Köppen climate subtypes ( $A_f + D + C_f + E$ ), ( $A_w + B_s$ ), ( $C_s + C_w$ ), and ( $B_w$ ). There was a small but significant correlation between species values for temperature and aridity ( $r=0.06$ ,  $P=0.027$ , 1163 species). Treating this variable as a continuous character was practical because of the features of the comparative method applied in this work (described below). The transition 1–2–3–4 is to a reasonable extent justified in terms of water stress, in spite of the fact that the character is actually measured in a qualitative way.

#### 7 & 8. *Seasonal patterns of butterflies*

Seasonal patterns of activity were classified in two ways. First, the degree of voltinism (7), an index that summarizes the number of generations per year: 0.5, biennial; 1, strictly monovoltine; 2, two broods per year; 3, three or more broods, but no adult activity during one part of the year; 4, three or more generations, adults present and active all year round. The second measure of seasonal pattern (8) was that of adult time window, which is the proportion of months per year when adults are reported to be on the wing.

#### 9. *Duration of egg stage*

This variable represents the number of days spent in the egg stage. Species in which the eggs of successive generations may hibernate or develop directly were coded as missing. Interpretation of any results where this variable is involved should be cautious because the conditions in which the length of egg development was measured varied widely from one species to another. When egg diapause is present, the time spent in this developmental stage is only loosely equivalent to the length of embryonic development. The mean egg development time is 22.2 days (SD = 54.4, 765 species), with modal duration between 4 and 10 days. Egg diapause is

not exceptional among butterflies and occurs in about 6% of the species sampled, which are concentrated in few taxa such as some genera within the tribes Theclini and Eumaeini (Lycaenidae), or Parnassiini (Papilionidae). Because the Phylogenetically Independent Contrasts method applied uses values calculated at the nodes of the taxonomy, the possible bias caused by the presence of egg diapause will not be strong. Anyway, one further variable (variable 14) was added specifically to test the relationship between size and egg hibernation or aestivation.

#### *10. Duration of larval development*

This variable represents the number of days spent as a larva. In cases where larval development varied within very broad limits (e.g. when some larvae hibernate while others develop directly), the shortest duration was used. Larval development typically lasts for 15–40 days in most butterflies, but can be considerably longer (for the species prospected, mean = 94.9, SD = 119.4,  $n = 665$ ; for the subset of species whose larvae develop directly, mean = 38.4, SD = 23.8,  $n = 526$ ). The time spent as a larva is actually a composite variable that results from the presence or absence of larval diapause, the duration of the adverse period, and growth rate. For species that present obligatory larval hibernation or aestivation, this variable overestimates the real growth period (since the shortest value was adopted where larval development is variable, the problem is restricted to data from species that show only one generation per year, or less). While, as for the former variable, some caution is required for interpretation, these problems should be controlled by incorporating the variables intended to describe climate, phenology, and voltinism (variables 5–8 and 14–15).

#### *11. Foodplant structure*

Three categories were considered, based on a gradient of structural complexity and spatial predictability: (1) trees (woody, trunk well-developed); (2) intermediate (bushes, woody vines, semi-woody monocotyledons); (3) herbs. Classification of the plants into the three types depended primarily on the descriptions found in the life history reports, but otherwise Hutchinson (1964–1967) was used as a general reference.

#### *12. Monocotyledonous or dicotyledonous larval foodplant*

Species whose larvae feed on dicots or monocots were coded 0 and 1, respectively. Larvae known to use both kinds of plants as hosts, or to feed on other kinds of materials such as lichens, ferns, or other insects, were coded as missing.

#### *13. Eggs laid in clusters*

Three patterns were designated, based on the number of eggs laid by the female in an oviposition event: (1) eggs laid singly; (2) small batches of up to 20 eggs, never laid singly; (3) large egg batches laid.

#### *14. Hibernation or aestivation in the egg stage*

This represents an extreme case of variable 9, and applies to instances where the egg remains inactive for long periods of time ( $\geq 2$  months). It was coded dichotomously (0, absent; 1, present).



### 15. *Strict monovoltinism*

Strictly monovoltine species produce one brood per year, representing a single generation. Monovoltinism is generally confined to temperate, markedly seasonal climates, and can usually be easily identified from published information. It provides an explicit test for the relationship between size and one extreme in the range of phenological patterns exhibited by butterflies. The variable was dichotomous (one versus more than one generation per year). Species showing variation (e.g. latitudinal shifts between one and more generations per year) had to be coded as missing because, at the level of resolution adopted, they share the two possible states of the character analysed. For the purposes of this study, a few biennial species such as some subarctic or alpine satyrine Nymphalids (*Oeneis*, *Erebia*), or Australian Hesperiiidae from arid zones (*Antipodia*, e.g. Atkins, 1984) were classified as monovoltine.

### 16. *Potential fecundity*

Although the tradeoff between egg size and egg number is explicitly or implicitly considered in most comparative approaches, there is no evidence for its existence in butterflies at the interspecific level. Fecundity data are available for a limited number of species. These are usually in the form of laboratory counts that are made under very varied conditions (different temperature or photoperiod regimes, seminatural conditions). Data of this kind were abstracted for those species whose egg sizes were known. This allowed relationships between egg size, body size, and egg number to be tested. The small sample sizes prevented correlations between fecundity and the remaining variables being sought. The data are summarized in Table 2.

## COMPARATIVE METHOD

The method of Phylogenetically Independent Contrasts was used to obtain results independent of shared ancestry (Harvey & Pagel, 1991; Harvey & Keymer, 1991; Brooks & McLennan, 1991; Starck, 1998). The data matrix was analysed using the CAIC program (Purvis & Rambaut, 1994) to obtain standardized contrasts (differences) at the taxonomic nodes (see below). Details of the method can be found in Harvey & Purvis (1991), Martins & Garland (1991), Garland *et al.* (1992) and Purvis & Rambaut (1995). Branch lengths were all set to a value of 2, an option justified under the assumption of punctuated evolution, although in fact this decision relied entirely on two practical criteria: the absence of estimates of evolutionary distances for the data set, and the facilitation of repeatability of the analyses in future reassessments.

The combined characteristics of the data matrix and the CAIC program gave rise to four problems that required the sets of contrasts to be replicated in subsequent analyses (>30 runs of the program were necessary). First, CAIC cannot deal with more than one categorical variable at a time, and thus different matrices of contrasts had to be obtained to assess the relationships between each non-continuous variable and the quantitative variables. Second, the value and sign of a contrast depend on the test variable used, and so a different set of contrasts had to be calculated for each test variable. Third, the number of missing values in the original data varied greatly, between 0%, for egg and adult sizes, to almost 60%, for the duration of

TABLE 2. Potential fecundity (*FEC*), and estimates of egg size (*ES*, mm) and adult size (*AS*, mm). Estimates of fecundity were taken from the following sources: 1, Richards (1949); 2, Magnun (1958); 3, Teotia & Nand (1966); 4, Höeg-Guldberg & Jarvis (1970); 5, Young (1972); 6, Martín Cano (1976); 7, Dunlap-Pianka *et al.* (1977); 8, Nakasuji (1978); 9, Wiklund & Persson (1983); 10, Karlsson & Wiklund (1984); 11, García-Barros (1987); 12, Shapiro (1987); 13, Wickman & Karlsson (1987); 14, Wiklund & Karlsson (1987); 15, Svård & Wiklund (1988); 16, García-Barros (1989); 17, Karlsson & Wickman (1990); 18, Bink (1992 and other references therein); 19, Thomas, quoted by Dennis (1993a); 20, Litsinger *et al.* (1994); 21, Braby & Jones (1995); 22, Brakefield & Kesbeke (1995); 23, García-Barros, unpublished (data from at least 5 females). With few exceptions, the egg and adult sizes (see methods) may come from sources other than data on the mean number of eggs laid. The taxonomic arrangement for this subset of species, in parenthetical notation, is: (1, ((2, (3, 4), (((5, 6), (7, 8)), 9), (10, 11, 12, 13)), ((14, 15), (16, (17, 18))), (((19, 20), (21, 22)), (23, (24, 25))), 26, (27, 28), (((29, (30, 31, 32), 33), ((34, 35, 36, 37), 38)), (39, 40, (41, (42, ((43, 44), (45, 46))))), 47), (48, (49, ((50, 51), 52))))))

# Species	<i>FEC</i>	<i>ES</i>	<i>AS</i>	Source
01 <i>Pelopidas mathias</i>	63.0	0.69	17.5	3;20
02 <i>Perhybris lypera</i>	378.5	0.46	35.3	5
03 <i>Phulia nymphula</i>	35.1	0.37	17.0	12
04 <i>P. rosea</i>	38.5	0.41	15.0	12
05 <i>Pieris brassicae</i>	1100.0	0.56	29.8	18
06 <i>P. rapae</i>	430.0	0.51	24.5	1;18
07 <i>P. occidentalis</i>	298.8	0.37	23.7	12
08 <i>P. virginiensis</i>	91.8	0.47	24.4	12
09 <i>P. protodice</i>	311.7	0.37	23.4	12
10 <i>Tatochila mercedis</i>	260.8	0.34	26.9	12
11 <i>T. microdice</i>	197.1	0.46	26.9	12
12 <i>T. steridice</i>	159.0	0.41	28.0	12
13 <i>T. vanvolxemii</i>	374.6	0.52	29.9	12
14 <i>Papilio machaon</i>	357.0	0.88	40.0	18
15 <i>Papilio anchisiades</i>	342.4	0.92	52.5	5
16 <i>Battus polydamus</i>	312.5	0.87	47.9	5
17 <i>Parides arcas</i>	253.4	0.89	38.9	5
18 <i>P. childrenae</i>	211.7	0.89	48.5	5
19 <i>Dryas julia</i>	270.5	0.88	43.5	7
20 <i>Heliconius charitonius</i>	700.0	0.74	40.1	7
21 <i>Argynnis paphia</i>	450.0	0.73	32.9	2
22 <i>Pandoriana pandora</i>	1500.0	0.43	34.0	23
23 <i>Anartia fatima</i>	520.8	0.43	28.5	5
24 <i>Siproeta epaphus</i>	323.7	0.85	44.6	5
25 <i>S. stelenes</i>	268.4	0.87	46.5	5
26 <i>Euphydryas aurinia</i>	430.0	0.59	21.5	18
27 <i>Limenitis camilla</i>	180.0	0.73	28.0	18
28 <i>L. populi</i>	140.0	1.01	40.0	18
29 <i>Lopinga achine</i>	107.0	0.90	26.5	14;18
30 <i>Lasiommata maera</i>	230.0	0.82	25.0	14;18
31 <i>L. megera</i>	182.0	0.72	22.4	10
32 <i>L. petropolitana</i>	78.0	0.74	21.4	14;18
33 <i>Pararge aegeria</i>	153.0	0.71	21.9	9;17
34 <i>Mycalopsis perseus</i>	117.9	0.79	23.7	21
35 <i>M. sirius</i>	118.8	0.84	24.8	21
36 <i>M. terminus</i>	126.1	0.82	24.8	21
37 <i>M. gotama</i>	130.0	0.82	25.5	8
38 <i>Bicyclus anynana</i>	321.1	0.80	21.1	22
39 <i>Coenonympha pamphilus</i>	210.5	0.58	16.6	13;23
40 <i>Maniola jurtina</i>	362.0	0.44	25.8	18
41 <i>Kanetisa circe</i>	666.0	0.69	37.1	23
42 <i>Chazara briseis</i>	340.0	0.69	31.6	23
43 <i>Hipparchia alcyone</i>	369.0	0.84	30.2	11
44 <i>H. semele</i>	597.0	0.63	26.8	14;16;18
45 <i>H. fidia</i>	217.0	1.02	29.7	11
46 <i>H. statilinus</i>	598.0	0.66	26.9	16
47 <i>Danaus plexippus</i>	663.0	0.80	45.8	15
48 <i>Thecla betulae</i>	158.0	0.56	16.3	19
49 <i>Lampides boeticus</i>	200.0	0.34	16.5	6;18
50 <i>Aricia agestis</i>	235.0	0.34	12.9	4
51 <i>Polyommatus icarus</i>	180.0	0.37	15.2	6;18
52 <i>Maculinea arion</i>	378.0	0.37	19.9	19

the larval stage. CAIC proceeds in a list-wise fashion, so that the greater the number of variables processed simultaneously, the lower the number of contrasts obtained. In order to optimize the potential explanatory power of each variable, three series of contrasts based on three combinations of variables were calculated: 496 contrasts (including variables 1–6), 456 contrasts (variables 1–11), and 310 contrasts (variables 1–13). The contrasts originating from the three series were not comparable: even for the same node, a contrast may be derived from different subsets of subtaxa joining at that node. Finally, categorical variables cannot be processed together, unless all but one of them are treated as continuous. Such relationships were not tested to avoid spurious results. These methodological problems constrained the possibilities of applying complex multivariate statistical methods.

#### STATISTICAL ANALYSIS

Variables 1–10 and 16 were logarithmically transformed before calculating the contrasts (except for variable 6, which was arcsin-transformed). The relationships between sets of independent contrasts from these variables were assessed by regression forced through the origin (Gittleman & Luh, 1994; Purvis & Rambaut, 1995). Step-wise multiple regressions were carried out on six non comparable sets of contrasts. These were obtained from three runs of CAIC, one for each of the three combinations of variables (1–6, 1–11, and 1–13, as detailed above) with egg size set as the independent one, and three further runs using adult size as the independent variable. To control for the effect of adult size in regressions of egg size contrasts on other variables, the residuals from the regression of both traits on adult size were used.

When categorical variables are involved, these are set as the independent (test) variable, and contrasts are calculated only at the nodes where shifts in the test variable occur. All contrasts for the test variable are positive integers (+1 for a binary variable), while those for the dependent variables may take any positive or negative value. The appropriate test for a significant relationship between the qualitative and quantitative (dependent) variables requires determining whether or not the shifts in the former predominantly correspond to positive or negative contrasts of the test variable. In other words, the mean value of the contrasts of the dependent variable should be significantly larger, or smaller, than 0. The relationships between categorical variables 11–15 and the continuous ones were thus assessed with one-tailed *t*-tests (Purvis & Rambaut, 1994).

Because of the potential interdependence among several of the variables selected, some control for co-linear effects in correlations was desirable. For the numerical variables, the matrix of partial correlations was calculated as a final step. The smallest set of contrasts had to be used for that purpose, since this was the only way to obtain fully comparable contrasts for the 13 variables. Unfortunately, no combined test (similar to multifactor ANOVA) could be applied to the qualitative variables. As described above, these had to be processed in different runs of the program CAIC. The shifts between states of the different variables were located at different nodes of the taxonomy. As a result, very few of the contrasts obtained in the analyses of qualitative factors were comparable.

## BUTTERFLY TAXONOMY

It was not possible to obtain a fully resolved, objective phylogeny of the species used in this study. A tree was derived from available phylogenetic studies and traditional taxonomy, applying the following four criteria. Firstly, published phylogenetic approaches for taxa were given priority over intuitive taxonomies. Secondly, as many species data points as possible were included. This probably resulted in a loss of phylogenetic resolution when a species in the data set was not included in an existing phylogenetic study. Thirdly, in the case of conflicting phylogenetic approaches, a strict consensus was adopted. Consensus trees do not represent phylogenetic hypotheses, but the possible error introduced was assumed to be low, given the high number of polytomies. Finally, informal groups such as those of genera within a tribe or subtribe, or groups of species within a subgenus, were adopted only for taxa that yielded unresolved polytomies of more than 10 subtaxa. The degree of resolution of the derived taxonomic tree was approximately 40%. At most, 20% of the nodes were derived from phylogenetic research, but this figure is probably inflated because some of the taxa used as operative taxonomic units in phylogenetic studies may ultimately prove not to be monophyletic.

The highest structural levels (down to subfamily) follow the majority rule consensus tree of De Jong *et al.* (1996). Within subfamilies, the arrangement was based on Bridges (1994) for the Hesperidae, Miller (1987, 1988), Saigusa *et al.* (1982), and Collins & Morris (1985, and other sources therein) for Papilionidae, and Fiedler (1991) for Lycaenidae. Riodininae were ordered following a provisional consensus presented by DeVries (1997). Nymphalid subfamilies were arranged after Harvey (1991) but, where pertinent, cladograms from Brown (1981), Ackery & Vane-Wright (1984), Kitching (1985), Pierre (1987), Vane-Wright *et al.* (1992), Brown *et al.* (1994) and Brower (1997), were adopted. Additional branching patterns concerning genera, or species within genera of several families, were incorporated from Geiger (1986), Friedlander (1987), Henning (1989), Mensi *et al.* (1990), García-Barros (1991), Sperling (1993), and Lattes *et al.* (1995).

## RESULTS

*General description of the data*

While the subsequent account is based on independent contrasts, a few points of descriptive interest may be drawn from the species means. Taxonomic and geographic biases certainly occurred in the selection of species. For instance, data from the family Lycaenidae (25% of the data set) were scarcer than expected, and the neotropical fauna (22% of species in the study) was obviously under-represented (cf. Heppner, 1991). The data collected may be valid for general purposes, however. For example, about 64% of the species inhabit subtropical or tropical areas. There was a ten-fold variation in both adult wing length (8–100 mm), and egg size estimates (0.23–2.74 mm), encompassing a 1500-fold range of volumes. Both estimates of size were approximately log-normally distributed (Figs 1, 2). On the basis of the raw

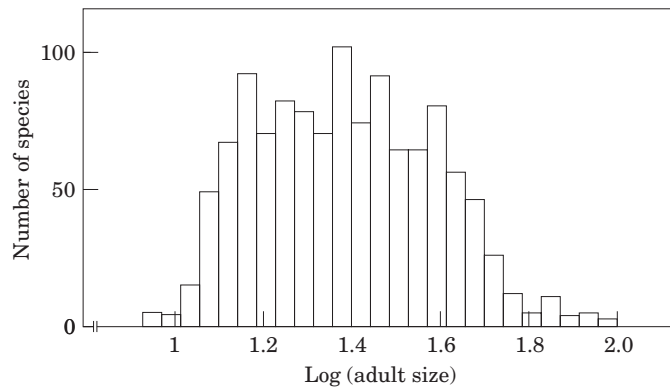


Figure 1. Frequency distribution of adult size estimates (wing lengths in mm, transformed to decimal logarithms).

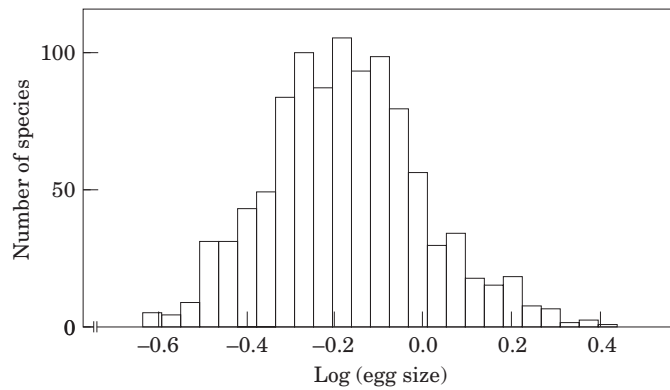


Figure 2. Frequency distribution of egg size estimates (cubic root of estimated egg volume, transformed to decimal logarithms).

values for species (transformed to decimal logarithms), egg size was significantly correlated with adult size ( $r=0.71$ ,  $P<0.0001$ ,  $n=1183$ ), and the least squares regression line relating them was  $\log(\text{egg size}) = -1.04 + 0.622 \times \log(\text{adult size})$  (Fig. 3).

#### *Relationship between potential fecundity, egg size, and adult size*

Based on the 39 contrasts derived from the data given in Table 2, fecundity was positively correlated with adult size ( $r=0.41$ ,  $P=0.008$ ), and not significantly with egg size ( $r=-0.28$ ,  $P=0.08$ ). Multiple regression of the contrasts of fecundity on those of egg and adult size accounted for a larger proportion of the variance than adult size alone ( $R^2=0.425$ ,  $F=14.52$ ,  $P<0.0001$ ). The equation was:  $\text{fecundity} = -2.02 (\text{egg size}) + 0.22 (\text{adult size})$ , with  $F$  values for egg and adult size of 16.75 ( $df=1$ ;  $P=0.0002$ ) and 10.76 ( $df=1$ ,  $P=0.0024$ ), respectively. Relative egg size (egg size/adult size) was negatively correlated with fecundity ( $r=-0.62$ ,  $P<0.0001$ ;

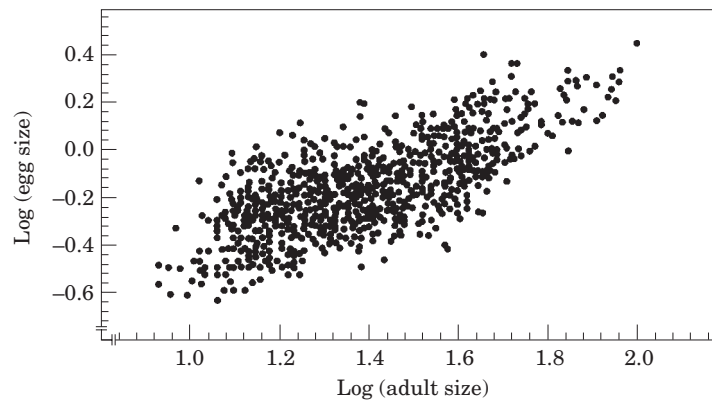


Figure 3. Plot of butterfly egg size against adult body size estimates: species values, logarithmically transformed (see text for statistics).

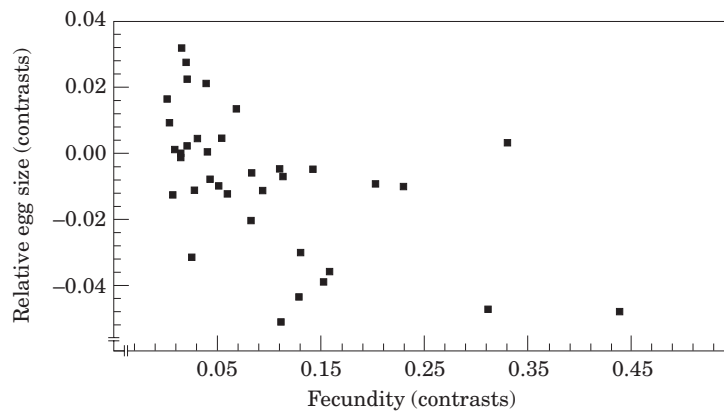


Figure 4. Relationship between independent contrasts of potential fecundity (number of eggs) and relative egg size (egg size/adult size).

Fig. 4). Similar results were obtained from regressing the residuals of the regressions of fecundity on adult size, and of egg size on adult size ( $r = -0.57$ ,  $P < 0.0001$ ).

#### *Relationship between egg and adult body sizes*

The correlation between egg and adult size contrasts was positive,  $r = 0.40$ ,  $P < 0.0001$ , 519 contrasts; regression equation: egg size = 0.437 (adult size). The 95% confidence interval for the slope was 0.389–0.582. Contrasts were much more dispersed than the original size values (cf. Fig. 5).



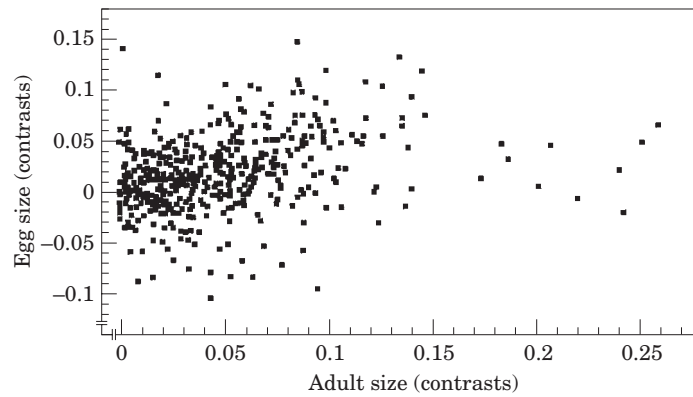


Figure 5. Plot of independent contrasts of egg size against adult size (see text for statistics).

TABLE 3. Relationships between adult butterfly size, egg size, and climate or life history variables. Relative egg size = residuals from the regression of egg size on adult size. The values are Pearson  $r$  (for pairs of continuous variables), or one-tailed  $t$  values when the independent variable is categorical;  $n$ , sample size (number of independent contrasts)

	1. Adult size	2. Egg size	Relative egg size
3. Polyphagy (plant genera) ( $n=456$ )	$r=0.047$ $P=0.312$	$r=0.105$ $P=0.025$	$r=0.057$ $P=0.224$
4. Polyphagy (index) ( $n=496$ )	$r=0.015$ $P=0.747$	$r=0.001$ $P=0.984$	$r=0.008$ $P=0.864$
5. Temperature ( $n=496$ )	$r=0.138$ $P=0.002$	$r=0.006$ $P=0.889$	$r=0.071$ $P=0.109$
6. Aridity ( $n=496$ )	$r=-0.159$ $P=0.0004$	$r=0.045$ $P=0.315$	$r=0.024$ $P=0.586$
7. Voltinism ( $n=456$ )	$r=0.087$ $P=0.063$	$r=0.009$ $P=0.854$	$r=0.006$ $P=0.904$
8. Adult time window ( $n=456$ )	$r=0.162$ $P=0.0005$	$r=0.005$ $P=0.919$	$r=0.042$ $P=0.373$
9. Egg development ( $n=310$ )	$r=0.083$ $P=0.139$	$r=0.123$ $P=0.031$	$r=0.033$ $P=0.557$
10. Larval development ( $n=310$ )	$r=0.164$ $P=0.004$	$r=0.204$ $P=0.0003$	$r=0.152$ $P=0.007$
11. Foodplant structure ( $n=126$ )	$T=2.935$ $P=0.002$	$T=0.437$ $P=0.331$	$T=-1.668$ $P=0.049$
12. Monocot/dicot plant ( $n=11$ )	$T=0.236$ $P=0.409$	$T=1.300$ $P=0.111$	$T=1.433$ $P=0.089$
13. Egg clustering ( $n=69$ )	$T=1.951$ $P=0.028$	$T=-1.180$ $P=0.121$	$T=-2.236$ $P=0.014$
14. Long egg stage ( $n=17$ )	$T=-0.620$ $P=0.272$	$T=1.201$ $P=0.124$	$T=1.675$ $P=0.057$
15. Monovoltinism ( $n=77$ )	$T=0.802$ $P=0.213$	$T=0.016$ $P=0.493$	$T=-0.629$ $P=0.266$

*Relationship between egg and adult sizes, and life-history or environmental variables*

Positive correlations between egg size and the number of foodplant genera, and the duration of the egg and larval stages were discovered (Table 3). Statistically significant relationships were also found between adult size and the two climate

TABLE 4. Results of stepwise multiple regression of quantitative variables on egg size and adult size. Three analyses were carried out for each size variable in order to explore the explanatory power of the sets of contrasts obtained from three separate runs of the CAIC program. Numbers displayed are partial correlations. Only variables that were selected for the final model are shown. The coefficients of determination for the full regressions ( $R^2$ ) are given on the lower line. Bold numbers indicate the analysis where the maximum number of contrasts for each pair of variables could be analysed. Levels of significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* =  $P < 0.001$ . —, not tested. n.i., not included in model

Independent variables	Dependent variable: ADULT SIZE		
	Analysis/number of contrasts		
	Vars. 1–6 ( $n = 496$ )	Vars. 1–8 ( $n = 456$ )	Vars. 1–10 ( $n = 310$ )
1. Egg size	0.42***	0.44***	0.51***
5. Temperature	0.14***	0.16***	0.12*
6. Aridity	0.16***	0.15***	0.13**
8. Adult time window	—	0.16**	n.i.
7. Voltinism	—	0.09*	n.i.
Regression, $R^2$	0.223***	0.244***	0.288***

Independent variables	Dependent variable: EGG SIZE		
	Analysis/number of contrasts		
	Vars. 1–6 ( $n = 496$ )	Vars. 1–8 ( $n = 456$ )	Vars. 1–10 ( $n = 310$ )
2. Adult size	0.42***	0.47***	0.51***
3. Nr. Foodplant genera	—	0.10*	0.15**
10. Larval development, days	—	—	0.20**
Regression, $R^2$	0.178***	0.229***	0.292***

variables, adult time window, duration of larval stage, as well as with foodplant structure and the habit of laying eggs in clutches. Aridity was the single variable that showed a significant negative correlate with butterfly size.

Controlling for the effect of adult size (using the residuals from regressions of all other variables on adult size) revealed a positive, significant relationship between egg size and the duration of the larval stage, and negative relationships between egg size and both foodplant structure and egg clustering (Table 3). The correlations between egg and adult size and the remaining variables remained almost unchanged after taking into account the possible effects of temperature and aridity (results not shown).

The results of stepwise multiple regressions for the two size variables are given in Table 4. Variables other than adult size (for egg size) or egg size (for adult size) displayed relatively small additional explanatory power. The variables selected in the final model illustrate the different nature of the set of variables related to egg and adult size.

#### *Correlations between life history variables other than size*

A number of relationships between the test variables (climate and life history features other than size) were discovered (Table 5). Some of the significant results were expected, such as the positive correlations between the pattern of voltinism (or adult time window) and temperature, the negative correlation between the duration of the immature (egg, larva) stages and temperature (or factors related to climate,

TABLE 5. Relationships between variables 4-11, and 13 (independent contrasts). The figures are correlation coefficients ( $r$ ) or one-tailed  $t$ -tests, as in Table 2.  $n$ , number of pairs of contrasts available for the two variables; n.s., not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; \*\*\*\*,  $P < 0.0001$

	4. Polyphagy (index)	5. Temperature	6. Aridity	7. Voltinism	8. Adult time window	9. Egg development	10. Larval development	11. Foodplant structure	13. Eggs laid in clusters
3. Polyphagy (plant genera)	$r = 0.758^{****}$ $n = 457$	$r = 0.028$ (n.s.) $n = 457$	$r = 0.095^*$ $n = 456$	$r = 0.080$ (n.s.) $n = 457$	$r = 0.123^{**}$ $n = 457$	$r = -0.010$ (n.s.) $n = 314$	$r = -0.147^{**}$ $n = 314$	$T = 0.206$ (n.s.) $n = 121$	$T = -0.970$ (n.s.) $n = 69$
4. Polyphagy (index)	$r = 0.036$ (n.s.) $n = 499$	$r = 0.023$ (n.s.) $n = 496$	$r = 0.041$ (n.s.) $n = 457$	$r = 0.044$ (n.s.) $n = 457$	$r = 0.044$ (n.s.) $n = 457$	$r = 0.100$ (n.s.) $n = 321$	$r = -0.141^*$ $n = 321$	$T = -0.216$ (n.s.) $n = 123$	$T = -1.505$ (n.s.) $n = 69$
5. Temperature		$r = 0.253^{****}$ $n = 514$	$r = 0.409^{****}$ $n = 457$	$r = 0.446^{****}$ $n = 457$	$r = 0.446^{****}$ $n = 457$	$r = -0.276^{***}$ $n = 324$	$r = -0.363^{***}$ $n = 324$	$T = 3.578^{***}$ $n = 123$	$T = 0.079$ (n.s.) $n = 69$
6. Aridity		$r = 0.202^{***}$ $n = 456$	$r = 0.202^{***}$ $n = 456$	$r = 0.230^{***}$ $n = 456$	$r = 0.230^{***}$ $n = 456$	$r = -0.071$ (n.s.) $n = 324$	$r = -0.170^{**}$ $n = 324$	$T = 1.566$ (n.s.) $n = 123$	$T = -0.438$ (n.s.) $n = 69$
7. Voltinism			$r = 0.875^{****}$ $n = 478$	$r = 0.875^{****}$ $n = 478$	$r = 0.875^{****}$ $n = 478$	$r = -0.416^{****}$ $n = 322$	$r = -0.637^{****}$ $n = 322$	$T = 1.982^*$ $n = 123$	$T = -0.976$ (n.s.) $n = 69$
8. Adult time window						$r = -0.328^{****}$ $n = 322$	$r = -0.534^{****}$ $n = 322$	$T = 2.377^{**}$ $n = 123$	$T = -0.618$ (n.s.) $n = 69$
9. Egg development							$r = 0.293^{****}$ $n = 324$	$T = 1.548$ (n.s.) $n = 110$	$T = 2.642^{**}$ $n = 42$
10. Larval development								$T = 0.630$ (n.s.) $n = 110$	$T = 0.604$ (n.s.) $n = 42$

such as voltinism). Others were unexpected, for instance, foodplant structure becomes progressively more complex (herb to shrub to tree) along the temperature gradient. Finally, trophic specialization showed interesting correlations with the duration of the larval stage, and with the adult time window (more polyphagous species tend to have more rapid larval development, and perhaps are more polyphagous where the adult flight period is longer), but these relationships were diluted when the partial correlations were calculated (Table 6).

#### DISCUSSION

The correlations based on independent contrasts were generally characterized by low values. It is not possible to discern the effects of incorrect phylogenetic hypotheses, errors due to the lack of reliable estimates of evolutionary distances, or those attributable to inaccurate measurement. On similar grounds, intraspecific variation, as well as errors attributable to combining specific data taken from unrelated sources, are disregarded in this kind of approach. The potential explanatory power of some variables may have been underestimated. For example, the variables intended to measure temperature and aridity were coded in a single linear way, thereby making it impossible to consider combinations of states that might have yielded more specific conclusions upon more detailed examination. Alternative ways of coding climate types, together with a fully qualitative treatment, may provide further insights that have not been tested in the present approach. In spite of these problems, a number of conclusions of general interest may be drawn from these results.

#### *Egg size, adult size, number of eggs and allometry*

A compromise between egg size and egg number is frequently assumed in evolutionary work where fecundity, or related traits, are involved (e.g. Smith & Fretwell, 1974). If this tradeoff is important then it should be evident from interspecific comparisons. Nevertheless, documented examples in insects are scarce (Price, 1974; Llewelyn & Brown, 1985). Blackburn (1991b) recently provided the first evidence for this kind of compromise across species, using a comparative framework that controlled for taxonomic effects.

The current results suggest that evolutionary changes favouring increased egg size act as a constraint on fecundity and vice versa. Furthermore, there is a significant positive relation between adult size and fecundity. Within species, similar relationships have often been reported in butterflies (Blau, 1981; Karlsson & Wickman, 1990; Banno, 1990; Braby & Jones, 1995), other Lepidoptera (Smith, 1986; Tammaru *et al.*, 1996) and species of other insect orders (Masaki, 1967; Blanckenhorn, 1994), although the trend in these latter is not universal (Klingenberg & Spence, 1997, and references therein). The pattern exhibited by Papilionoidea and Hesperioidea contrasts with that of parasitic Hymenoptera, in which adult size and fecundity are unrelated (Blackburn, 1991a). On this basis, butterfly fecundity may be considered as being directly related to the relative sizes of the egg and the adult insect. It may otherwise simply be a function of adult body size since, as discussed below, egg size is related to adult size by negative allometry. This requires that the reserves available



for egg production scale allometrically to body size, with a slope at least as steep as that relating egg size to adult body size. Unfortunately, potential fecundity, egg size, and adult size could be estimated only in a small number of species. Whether the pattern is a general trend in these insects requires that fecundity and egg size be investigated in a substantial number of butterfly species.

The overall allometric trend relating egg size to adult body size in butterflies is confirmed on a worldwide basis. Of the variables studied, these two exhibit the highest degree of interdependence. The slope of the line relating egg and adult size (0.43) falls well below 1.0 (negative allometry), and is very similar to that derived from a selection of temperate butterflies (0.45, using similar assumptions of branch lengths; García-Barros & Munguira, 1997). Although both approaches appear to be consistent, it is difficult to predict the meaning of the allometric pattern in terms of body weight. The ratio of body weight to forewing length is likely to vary considerably in butterflies. Miller (1977, 1997) has suggested that such variation may have a taxonomic component in other Lepidoptera, since conservatism in the body design of some taxa is intuitively obvious. However, this pattern of variation is probably superimposed on another resulting from selection on life history characters, such as flight ability or mate locating behaviour (Marden & Chai, 1991; Wickman, 1992). Comparable weight and size heterogeneity may affect the egg stage, and hence the estimated value of the allometric slope should be regarded with caution.

Non-directional methods, such as regression of independent contrasts, identify correlations, not patterns of causation (Harvey & Purvis, 1991; Nylin & Wedell, 1994). In allometric studies, eggs are generally viewed as parts of the adult female organism. This is strictly true from an ontogenetic point of view, but eggs may also be regarded as individuals in their own right. Thus, it is correct to claim that the evolution of adult butterfly size is partially determined by an allometric trend relating adult size to egg size evolution. The size of newly hatched larvae should generally be correlated with egg size (Reavey, 1992), and thus evolutionary shifts in egg size may, if adult size is kept constant, modify larval development time or the number of larval instars (as suggested by Chew & Robbins, 1984, and Wickman *et al.*, 1990). Selection for egg size may be expensive in terms of other life history parameters because, as a consequence of the allometry between egg and adult size, changes in the former should correspond to proportionally large shifts in adult butterfly size. This may explain the significant correlation between egg size and larval development time, that holds even when adult size and climate are factored out: the distance between newly hatched and full grown larvae increases, on average, as egg and body size do.

#### *Butterfly size, climate and phenology*

Animal body size has often been related to latitude (e.g. Lawton, 1991). Although size and latitude are correlated in European ants (Cushman *et al.*, 1993), the converse of Bergmann's rule (body size increasing as latitude decreases) seems to apply in several insect taxa (May, 1978; Hawkins, 1995), including African and Australian butterflies (Barlow, 1994). However, Hawkins & Lawton (1995) found inconsistencies in the patterns of size distribution of butterflies from different faunal regions. They argued that the observed patterns could be the product of historical patterns of speciation. Latitude is believed to be relevant to life history evolution because of its



correlation with important environmental variables that are related to climate (season length, temperature, the amplitude and predictability of changes; see Nylin & Svård, 1991). From this perspective, the results of the current study are complementary to those of Barlow (1994) and Hawkins & Lawton (1995). Even if the sample of species examined is comparatively small, it contains geographically, taxonomically and ecologically varied butterfly species, and taxonomic effects have ruled out as far as the limits of current information allow. They show that mean temperature, a correlate of latitude, is generally related to body size. The effect of 'aridity' gives rise to a novel perspective based on factors such as water availability which (directly or indirectly) limits adult nectaring, foodplant growth, quality and abundance, and the importance of a dry season (which relates phenology with seasonality) (Wolda, 1988). These represent potentially important constraints on insect size (Dennis, 1993b), and their effects on similar organisms, as well as new tests based in more refined estimates, may be of interest.

Patterns in butterfly phenology revealed the expected relationships with climate (more broods per year, and a longer adult time window), and these seem to be paralleled by that between phenology and adult size. However, the absence of a significant relationship between adult size and strict monovoltinism suggests that the patterns are not simple. The correlation between size and larval development time (as stated above, probably a collateral effect of the negative egg to body size allometry), provides an explanation for the relationship between large adult sizes and warm climate. Climate may act upon the amount of growth that can be achieved in one season, rather than on size itself. As adult size increases, so does the difference between newly born and full grown larval weights, which means higher comparative costs (in terms of development time and associated risks) for larger species, in cool temperature areas (as argued by Barlow, 1994). Large body size would still be compensated by enhanced potential fecundity, and thereby the dilemma: larger eggs, or higher fecundity? should be more likely to result in deviations from the common trends where the environment constrains realized fecundity, or makes prolonged growth ecologically or physiologically expensive (cf. Wiklund *et al.*, 1987; García-Barros, 1994).

#### *Size, trophic specificity and host plant characteristics*

A trend towards higher polyphagy in larger Lepidoptera has been documented for several taxa from temperate regions (Wasserman & Mitter, 1978; Niemelä *et al.*, 1981; Reavey, 1993; Inkinen, 1994; Lindström *et al.*, 1994), including at least one family of Papilionoidea (Scriber, 1973). Based on 750 British moths, Loder *et al.* (1998) found the pattern to be consistent after taxonomic effects were controlled for. According to the present results, such pattern does not hold for butterflies (Papilionoidea and Hesperioidea) considered as a whole. It should be pointed out that none of the explanations proposed to account for the relationship between host specificity and lepidopteran body size enjoys solid support from the data (Loder *et al.*, 1998), and that most of the evidence for such relationships comes from a few lepidopteran families in cool temperate areas. The question arises as to whether the pattern would still be evident over a broader geographic scale. If it were not, this would probably help to delimit the relationship. As stated in the methods section, the present estimates of polyphagy were manipulated to compensate for unbalanced

information from different regions (strictly monophagous species were not recorded as such). Since strict monophagy is the best expression of trophic specialization, reconsideration of the reciprocal effects of size and polyphagy on selected, thoroughly studied taxa may prove necessary to obtain clearer results.

The relation between size and the larval habit of feeding on monocotyledonous plants is not supported by the data. The hypothesis that species whose larvae feed on monocots develop large eggs and first instar larvae is attractive to lepidopterists, since few butterfly taxa use these plants as larval food. The relationship found is in the predicted direction, although statistically non-significant, and based on a small number of contrasts. Comparative methods such as those adopted in the present study are effective when homoplasy (e.g. convergent adaptation) is relatively frequent. Rare evolutionary events remain difficult to test statistically, irrespective of their consequences in terms of innovation or speciation (Nylin & Wedell, 1994). Additional data from other Lepidoptera have to be added in order to test if the relationship holds under a broader taxonomic basis (as suggested by Gaston & Reavey, 1989).

Incidentally, no trace of a significant relation between climate and trophic specificity was obtained. This agrees with the conclusions of Fiedler (1998) based on a comparison between West Palaearctic and South Asian butterflies. Current evidence thus contradicts the contention that tropical butterflies are more specialized than those from temperate areas, which is to be taken into account in relation to the hypothesized explanation of high diversity of phytophagous insects in the tropics as a result of feeding specificity. Recent work (Janz & Nylin, 1998) supports the idea that comparatively lower specificity may characterize tree-feeding butterfly taxa, compared to herb-feeding ones. The present results indicate an association between large body size and large, or more complex, foodplants. If butterflies from tropical areas use woody plants as larval food more often than temperate species do, a lower foodplant specificity characterizing tropical butterflies should be predicted. No evidence for this was obtained in this study, however, but a proper test using information from plant taxonomic and structural diversity would be necessary to contrast the results.

Among the correlations relating foodplant specificity to other traits, two negative associations were interesting in terms of life-history strategies. First, the one between the number of foodplant genera and egg size (more polyphagous butterflies lay smaller eggs, opposite to that estimated from samples of temperate Lepidoptera: Gaston & Reavey, 1989). And, second, the association between specificity and larval development time (specialists require longer times than generalists to reach the final size). Taken together, they suggest an association of fast-opportunistic versus slow-specialist traits: small eggs (small size, high fecundity?), rapid growth and polyphagy, against large eggs (large size, low fecundity?), long development and sthenophagy. Attractive as this may be, the first of the two relationships did not show up when the polyphagy index was used, and the second disappeared when partial correlations were calculated.

#### *Implications of egg clustering*

Laying eggs in batches or clusters instead of singly may have important consequences for the number of eggs laid and larval survival. The results indicate general trends in this group of Lepidoptera whereby egg clustering is associated

with large adult size, small egg size, and (the opposite of that proposed by Stamp, 1980) short egg development time. This implies that fecundity is probably comparatively high in species that lay groups of eggs (Courtney, 1984). This makes sense in terms of the energy saved by spatial concentration of reproductive effort. With a few exceptions, butterflies that lay masses of eggs have gregarious larvae, or at least larvae that feed communally during the first instars (reviewed by Fitzgerald, 1993). Hence, small egg size and rapid egg development may also have implications for sib-competition, and an increased risk of food depletion related to host plant distribution and abundance (Le Masurier, 1993). It is therefore interesting that values of adult size, and egg size relative to adult body size, tend to be highest in the most complex foodplants. The consideration of host plant complexity in this study leaves room for speculation, and further work is required to identify which of the several plant characters involved (e.g. physical structure, size, predictability, etc.) is of prevailing importance.

#### CONCLUSION

While the methods adopted precluded a complete analysis of all the interrelationships among the variables, some general patterns could nevertheless be drawn for the papilionoid and hesperiid butterflies. Basically, and perhaps oversimplifying, the evolution of butterfly size may be understood in terms of economy and investment of the energy that members of a species will predictably be able to process, involving: (1) the amount of resources available per unit time, where relevant resources take the shape of food (foodplant characteristics, perhaps size or biomass per unit area), and climate (temperature and water, the latter probably with an indirect effect on size through foodplant ecology); (2) the way in which the energy invested in reproduction is shaped as egg size, egg number (fecundity, partially resulting from the negative interspecific allometry between egg size to adult size), and egg concentration in space and time (clustering).

Size is usually accepted as being a highly complex trait because of its many proximate, long term, ecological, and evolutionary implications. The same assumption may be made of any relationship concerning climate. Obviously, the degree of complication rises exponentially with the potential interrelations between these variables. Their effects on the plant hosts are also of interest. These problems are apparent in this study, although the results do serve to draw general conclusions regarding the main relationships involved.

Comparative biology is faced with a host of problems, including the diversity of comparative methodologies (e.g. Starck, 1998), the amount and quality of the data to be analysed, and the errors arising from poor knowledge of the phylogenies and evolutionary distances. Criticism of comparative interspecific analyses based on incomplete phylogenies or taxonomies may be well-founded (Wenzel & Carpenter, 1994), but it is clear that these problems will frequently affect reviews based on large taxa. As a kind of compensation, broad taxonomic approaches can help to delimit apparent evolutionary relationships thus benefiting subsequent research by identifying the kind of data needed, more accurately delimiting the processes implied, and indicating the taxa in which such processes may be important.

## ACKNOWLEDGEMENTS

I thank M.L. Munguira, D. Jutzeler, S.J. Johnson, P.J. Merrett and F.C. Urich for providing specimens, or measurements of adult butterflies from collections or rearing experiments. For varied reasons that include help and advice in locating and collecting literature data, botanical literature and computing facilities, I am also indebted to J. Fernández-Haeger, A. Vives, P.R. Ackery, R. de Jong, T. Racheli, J.C. Moreno, I. de Castro, A.F. Atkins, and J. Martín Cano. Part of the work was funded by project PB94-0173 (MEC).

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## APPENDIX 1

Hierarchically averaged values of egg size (ES, in mm), and adult wing length (WL, in mm), for the genera of butterflies in the data matrix. nr = genus number, NSP = number of species included in the genus.

nr	GENUS	NSP	ES	WL	nr	GENUS	NSP	ES	WL
1	<i>Coeliades</i>	2	0.645	27.7	55	<i>Celaenorrhinus</i>	1	0.654	20.0
2	<i>Allora</i>	1	0.758	22.5	56	<i>Eagris</i>	1	0.697	14.3
3	<i>Acleros</i>	1	0.686	15.0	57	<i>Eretis</i>	1	0.554	14.0
4	<i>Kedestes</i>	3	0.876	13.6	58	<i>Netrobalane</i>	1	0.638	18.5
5	<i>Cymaenes</i>	1	0.639	13.5	59	<i>Anastrus</i>	1	0.646	21.0
6	<i>Lerema</i>	1	0.983	18.0	60	<i>Erynnis</i>	4	0.571	16.9
7	<i>Aeromachus</i>	1	0.479	12.5	61	<i>Alenia</i>	1	0.448	11.5
8	<i>Metisella</i>	2	0.566	13.6	62	<i>Carcharodus</i>	1	0.584	14.0
9	<i>Thoressa</i>	1	0.776	15.5	63	<i>Gomalia</i>	1	0.629	13.5
10	<i>Tsitana</i>	1	0.808	15.5	64	<i>Heliopetes</i>	1	0.594	17.5
11	<i>Calpodus</i>	1	0.876	25.0	65	<i>Hesperopsis</i>	1	0.798	13.0
12	<i>Nyctelius</i>	1	0.946	18.0	66	<i>Pyrgus</i>	4	0.454	12.9
13	<i>Panoquina</i>	2	0.816	19.8	67	<i>Spialia</i>	7	0.545	11.8
14	<i>Parasmodes</i>	1	0.956	14.5	68	<i>Syrichthus</i>	1	0.730	14.5
15	<i>Borbo</i>	5	0.634	16.2	69	<i>Sarangesa</i>	2	0.568	16.4
16	<i>Gegenes</i>	1	0.686	14.5	70	<i>Tagiades</i>	1	0.629	23.5
17	<i>Parnara</i>	3	0.551	15.6	71	<i>Aguna</i>	1	0.669	16.0
18	<i>Pelopidas</i>	4	0.748	16.6	72	<i>Cabares</i>	1	0.638	18.0
19	<i>Polytremis</i>	1	0.793	18.5	73	<i>Codatractus</i>	1	0.669	23.5
20	<i>Isoteinon</i>	1	0.711	18.0	74	<i>Polygonus</i>	1	0.697	23.0
21	<i>Amblyscirtes</i>	1	0.654	12.3	75	<i>Typhedanus</i>	1	0.646	21.0
22	<i>Lerodea</i>	1	0.679	13.0	76	<i>Urbanus</i>	2	0.675	20.9
23	<i>Hidari</i>	1	1.169	27.8	77	<i>Archon</i>	1	0.638	28.3
24	<i>Lotongus</i>	1	1.541	24.5	78	<i>Hypermnestra</i>	1	0.621	26.9
25	<i>Unkana</i>	1	1.491	31.3	79	<i>Pamassius</i>	24	0.852	31.3
26	<i>Artitropa</i>	1	1.368	24.0	80	<i>Sericinus</i>	1	0.584	37.0
27	<i>Moltena</i>	1	1.566	24.0	81	<i>Allancastris</i>	1	0.554	28.0
28	<i>Zophopetes</i>	1	1.066	21.0	82	<i>Zerynthia</i>	2	0.601	26.7
29	<i>Ocybadistes</i>	1	0.531	10.7	83	<i>Bhutanitis</i>	1	1.016	59.0
30	<i>Potanthus</i>	1	0.679	15.0	84	<i>Luehdorfia</i>	3	0.803	32.1
31	<i>Choranthus</i>	1	0.531	14.5	85	<i>Eurytides</i>	3	0.782	41.6
32	<i>Hesperia</i>	2	0.887	17.0	86	<i>Iphiclides</i>	2	1.165	40.3
33	<i>Ochlodes</i>	2	0.615	14.5	87	<i>Graphium</i>	9	0.825	43.0
34	<i>Poanes</i>	1	0.707	15.0	88	<i>Pharmacophagus</i>	1	1.664	68.5
35	<i>Polites</i>	4	0.597	13.2	89	<i>Battus</i>	1	0.870	48.0
36	<i>Pompeius</i>	1	0.621	13.3	90	<i>Troides</i>	9	1.928	90.7
37	<i>Wallengrenia</i>	2	0.600	14.2	91	<i>Parides</i>	9	1.290	52.1
38	<i>Ancyloxypha</i>	1	0.519	11.5	92	<i>Pachliopta</i>	1	1.096	48.0
39	<i>Oarisma</i>	1	0.531	12.6	93	<i>Cressida</i>	1	1.032	50.5
40	<i>Thymelicus</i>	5	0.584	13.6	94	<i>Papilio</i>	24	1.050	53.6
41	<i>Carterocephalus</i>	2	0.511	13.1	95	<i>Dismorphia</i>	3	0.726	31.2
42	<i>Leptalina</i>	1	0.603	15.5	96	<i>Leptidea</i>	1	0.531	20.2
43	<i>Anisynta</i>	1	0.531	14.0	97	<i>Colotis</i>	9	0.582	23.1
44	<i>Hesperilla</i>	5	0.888	15.4	98	<i>Eronia</i>	1	0.654	29.2
45	<i>Mesodina</i>	1	1.280	17.7	99	<i>Hebomia</i>	1	1.013	50.0
46	<i>Neohesperilla</i>	4	0.682	12.4	100	<i>Nepheronia</i>	2	1.003	34.0
47	<i>Pasma</i>	1	0.730	19.2	101	<i>Paveronia</i>	1	1.126	36.0
48	<i>Toxidia</i>	1	0.646	17.2	102	<i>Anthocharis</i>	2	0.466	24.1
49	<i>Trapezites</i>	9	0.841	16.2	103	<i>Euchloe</i>	6	0.491	21.4
50	<i>Antipodia</i>	2	1.034	16.6	104	<i>Pinacopteryx</i>	1	0.448	29.3
51	<i>Croitana</i>	2	0.857	12.2	105	<i>Aporia</i>	1	0.479	32.3
52	<i>Herimosa</i>	1	0.824	13.5	106	<i>Appias</i>	1	0.506	28.7
53	<i>Proeidosia</i>	1	0.908	14.0	107	<i>Belenois</i>	5	0.522	29.1
54	<i>Abantis</i>	1	0.697	21.5	108	<i>Cepora</i>	1	0.430	29.5

continued

APPENDIX 1—*continued*

nr	GENUS	NSP	ES	WL	nr	GENUS	NSP	ES	WL
109	<i>Delias</i>	1	0.594	41.5	166	<i>Tylopaedia</i>	1	0.748	22.0
110	<i>Dixeia</i>	2	0.477	23.4	167	<i>Lycæna</i>	11	0.442	15.0
111	<i>Ixias</i>	1	0.574	33.5	168	<i>Heliophorus</i>	1	0.391	16.0
112	<i>Leptophobia</i>	1	0.742	27.0	169	<i>Arhopala</i>	4	0.474	17.1
113	<i>Mylothris</i>	3	0.636	29.8	170	<i>Acrodipsas</i>	1	0.519	13.9
114	<i>Perrhybris</i>	1	1.000	35.3	171	<i>Paralucia</i>	3	0.521	12.8
115	<i>Phulia</i>	2	0.390	16.1	172	<i>Thecla</i>	2	0.451	17.5
116	<i>Pieris</i>	11	0.487	23.7	173	<i>Cordelia</i>	1	0.479	15.5
117	<i>Prioneris</i>	1	0.661	46.0	174	<i>Laeosopsis</i>	1	0.646	22.5
118	<i>Tatochila</i>	4	0.433	25.5	175	<i>Ussuriana</i>	2	0.527	22.7
119	<i>Leptosia</i>	1	0.506	22.0	176	<i>Shirozua</i>	1	0.754	22.0
120	<i>Anteos</i>	1	0.542	44.0	177	<i>Artopetes</i>	1	0.638	23.0
121	<i>Catopsilia</i>	3	0.547	35.2	178	<i>Coreana</i>	1	0.519	19.5
122	<i>Colias</i>	6	0.483	24.3	179	<i>Chrysozephyrus</i>	5	0.593	20.3
123	<i>Eurema</i>	6	0.447	20.2	180	<i>Habrodais</i>	1	0.724	16.8
124	<i>Gonepteryx</i>	2	0.482	32.2	181	<i>Neozephyrus</i>	2	0.519	16.1
125	<i>Nathalis</i>	1	0.271	14.3	182	<i>Sibatanozephyrus</i>	2	0.647	16.6
126	<i>Phoebis</i>	1	0.430	32.5	183	<i>Iratsume</i>	1	0.506	18.8
127	<i>Gandaca</i>	1	0.519	24.0	184	<i>Japonica</i>	3	0.575	20.2
128	<i>Abisara</i>	1	0.391	23.8	185	<i>Favonius</i>	7	0.550	18.9
129	<i>Hamearis</i>	1	0.603	15.2	186	<i>Araragi</i>	1	0.479	15.3
130	<i>Euselasia</i>	2	0.378	14.2	187	<i>Wagimo</i>	1	0.564	15.5
131	<i>Napaea</i>	2	0.437	15.5	188	<i>Antigius</i>	2	0.585	16.8
132	<i>Mesosemia</i>	1	0.412	20.0	189	<i>Ogyris</i>	1	0.506	18.0
133	<i>Calephelis</i>	4	0.375	11.8	190	<i>Myrina</i>	2	0.645	18.2
134	<i>Caria</i>	1	0.368	11.0	191	<i>Eooxylides</i>	1	0.684	16.0
135	<i>Lasia</i>	1	0.391	16.0	192	<i>Iolais</i>	7	0.541	16.9
136	<i>Metacharis</i>	1	0.310	17.5	193	<i>Hypolycaena</i>	1	0.368	16.5
137	<i>Panara</i>	1	0.310	19.0	194	<i>Leptomyrina</i>	3	0.432	13.4
138	<i>Apodemia</i>	4	0.574	13.9	195	<i>Capys</i>	2	0.865	19.4
139	<i>Emesis</i>	5	0.572	16.7	196	<i>Deudorix</i>	4	0.594	19.6
140	<i>Audre</i>	2	0.507	18.6	197	<i>Artipe</i>	1	0.704	17.5
141	<i>Lemonias</i>	2	0.500	18.1	198	<i>Rapala</i>	1	0.464	15.8
142	<i>Stichelia</i>	1	0.506	12.0	199	<i>Callophrys</i>	5	0.438	13.9
143	<i>Xenandra</i>	1	0.412	19.5	200	<i>Evenus</i>	1	0.564	25.0
144	<i>Charis</i>	1	0.430	13.0	201	<i>Satyrrium</i>	6	0.553	15.6
145	<i>Synargis</i>	1	0.493	21.5	202	<i>Eumæus</i>	3	0.689	25.2
146	<i>Baliochila</i>	1	0.310	16.0	203	<i>Candalides</i>	2	0.495	14.6
147	<i>Durbania</i>	1	0.531	14.9	204	<i>Anthene</i>	8	0.392	13.4
148	<i>Durbaniopsis</i>	1	0.554	16.8	205	<i>Cupidopsis</i>	2	0.413	16.6
149	<i>Alaena</i>	2	0.540	13.1	206	<i>Pseudonacaduba</i>	1	0.271	13.8
150	<i>Pentila</i>	1	0.430	17.7	207	<i>Nacaduba</i>	1	0.342	12.0
151	<i>Lachnocnema</i>	2	0.329	13.1	208	<i>Actizera</i>	2	0.310	9.8
152	<i>Thestor</i>	8	0.439	17.0	209	<i>Cacyreus</i>	5	0.344	12.7
153	<i>Taraka</i>	1	0.368	14.5	210	<i>Harpendyreus</i>	1	0.531	14.7
154	<i>Cuwetis</i>	1	0.661	22.8	211	<i>Lampides</i>	1	0.342	16.5
155	<i>Aloeides</i>	9	0.597	16.1	212	<i>Jamides</i>	2	0.386	18.3
156	<i>Aphnaeus</i>	1	0.724	18.3	213	<i>Leptotes</i>	3	0.319	12.9
157	<i>Argyrocupha</i>	1	0.848	15.2	214	<i>Tarucus</i>	2	0.410	13.1
158	<i>Axiocerses</i>	1	0.594	15.9	215	<i>Tuxentius</i>	2	0.338	11.8
159	<i>ChrySORITIS</i>	1	0.554	13.4	216	<i>Zintha</i>	1	0.430	13.0
160	<i>Crudaria</i>	1	0.531	15.6	217	<i>Zizeeria</i>	2	0.329	12.1
161	<i>Oxychaeta</i>	1	0.554	16.3	218	<i>Zizina</i>	2	0.360	11.6
162	<i>Phasis</i>	2	0.903	19.2	219	<i>Zizula</i>	1	0.215	9.9
163	<i>Poecilmitis</i>	11	0.598	13.2	220	<i>Brephidium</i>	2	0.259	8.7
164	<i>Spindasis</i>	3	0.534	15.4	221	<i>Everes</i>	8	0.324	11.7
165	<i>Trimenia</i>	2	0.88	18.5	222	<i>Azanus</i>	4	0.270	12.4

*continued*

APPENDIX 1—*continued*

nr	GENUS	NSP	ES	WL	nr	GENUS	NSP	ES	WL
223	<i>Eiochrysops</i>	2	0.329	10.6	280	<i>Siproeta</i>	2	0.825	45.5
224	<i>Celastrina</i>	2	0.359	14.1	281	<i>Catacroptera</i>	1	0.804	29.7
225	<i>Actyolepis</i>	1	0.342	15.0	282	<i>Protogonimorpha</i>	1	0.857	43.8
226	<i>Megisba</i>	1	0.310	12.5	283	<i>Hypolimnas</i>	3	0.536	42.4
227	<i>Udara</i>	1	0.368	16.0	284	<i>Euphydryas</i>	4	0.559	24.2
228	<i>Glaucopsyche</i>	12	0.397	17.5	285	<i>Chlosyne</i>	2	0.431	20.3
229	<i>Pseudophilotes</i>	4	0.339	11.9	286	<i>Melitaea</i>	5	0.471	20.3
230	<i>Euphilotes</i>	2	0.588	11.3	287	<i>Mellicta</i>	3	0.460	18.5
231	<i>Philotiella</i>	1	0.342	8.5	288	<i>Thessalia</i>	1	0.697	19.7
232	<i>Sinia</i>	1	0.430	20.0	289	<i>Eresia</i>	1	0.554	25.0
233	<i>Scoliantides</i>	1	0.430	12.5	290	<i>Phyciodes</i>	2	0.436	17.5
234	<i>Euchrysops</i>	5	0.398	16.3	291	<i>Atlantea</i>	1	0.638	31.0
235	<i>Lepidochrysops</i>	10	0.401	16.9	292	<i>Colobura</i>	1	0.711	36.0
236	<i>Orachrysops</i>	1	0.391	17.9	293	<i>Historis</i>	2	1.056	52.2
237	<i>Oboronia</i>	2	0.335	15.9	294	<i>Smyrna</i>	1	0.684	40.0
238	<i>Polyommatus</i>	10	0.383	14.9	295	<i>Sea</i>	1	0.638	32.0
239	<i>Chilades</i>	1	0.310	9.5	296	<i>Eunica</i>	1	0.594	30.2
240	<i>Plebeius</i>	11	0.428	13.2	297	<i>Sallya</i>	3	0.457	24.6
241	<i>Hemiargus</i>	1	0.215	11.5	298	<i>Ariadne</i>	1	0.493	32.9
242	<i>Niphanda</i>	1	0.412	20.5	299	<i>Eurytela</i>	2	0.644	27.1
243	<i>Libythea</i>	2	0.438	30.7	300	<i>Byblia</i>	2	0.509	24.9
244	<i>Libytheana</i>	1	0.391	22.8	301	<i>Hamadryas</i>	1	0.866	36.0
245	<i>Philaetria</i>	3	0.993	49.3	302	<i>Adelpha</i>	3	0.684	26.2
246	<i>Podotricha</i>	1	0.730	38.0	303	<i>Cymothoe</i>	1	0.669	27.0
247	<i>Dryadula</i>	1	1.019	40.5	304	<i>Limenitis</i>	5	0.769	33.4
248	<i>Agraulis</i>	1	0.742	37.6	305	<i>Pseudacraea</i>	2	1.366	39.2
249	<i>Dione</i>	3	0.470	37.6	306	<i>Pantoporia</i>	2	0.894	27.1
250	<i>Dryas</i>	1	0.870	43.5	307	<i>Neptis</i>	3	0.733	26.2
251	<i>Eueides</i>	9	0.657	33.1	308	<i>Bebearia</i>	1	0.936	32.7
252	<i>Neruda</i>	3	0.651	38.7	309	<i>Dophla</i>	1	2.256	54.0
253	<i>Laparus</i>	1	0.711	40.0	310	<i>Euthalia</i>	1	1.394	40.5
254	<i>Heliconius</i>	35	0.487	41.1	311	<i>Lexias</i>	1	1.394	46.5
255	<i>Argynnis</i>	1	0.724	33.0	312	<i>Mahaldia</i>	1	1.421	45.0
256	<i>Argyreus</i>	1	0.612	39.0	313	<i>Tanaecia</i>	1	1.373	33.0
257	<i>Brenthis</i>	4	0.703	23.0	314	<i>Hamanumida</i>	1	1.154	31.6
258	<i>Fabriciana</i>	3	0.671	26.7	315	<i>Marpesia</i>	1	0.506	40.0
259	<i>Issoria</i>	1	0.493	21.0	316	<i>Cyrestis</i>	1	0.724	28.5
260	<i>Mesoacidalia</i>	1	0.717	29.0	317	<i>Charaxes</i>	50	1.222	41.3
261	<i>Pandoriana</i>	1	0.430	34.0	318	<i>Prothoe</i>	1	1.264	50.5
262	<i>Speyeria</i>	7	0.636	34.2	319	<i>Agrias</i>	2	1.939	44.7
263	<i>Boloria</i>	6	0.544	19.3	320	<i>Archaeoprepona</i>	1	1.993	52.4
264	<i>Euptoieta</i>	1	0.574	30.5	321	<i>Noreppa</i>	1	1.476	51.5
265	<i>Phalanta</i>	2	0.569	26.8	322	<i>Prepona</i>	1	1.714	48.4
266	<i>Acraea</i>	18	0.509	26.9	323	<i>Fountainea</i>	1	0.804	29.5
267	<i>Pardopsis</i>	1	0.594	16.8	324	<i>Consul</i>	1	0.804	36.9
268	<i>Aglais</i>	1	0.584	23.8	325	<i>Euxanthe</i>	3	1.482	49.1
269	<i>Araschnia</i>	1	0.996	18.0	326	<i>Palla</i>	1	0.857	42.8
270	<i>Cynthia</i>	1	0.531	29.4	327	<i>Apatura</i>	1	0.887	37.5
271	<i>Inachis</i>	1	0.479	28.6	328	<i>Asterocampa</i>	5	0.707	27.1
272	<i>Nymphalis</i>	3	0.497	28.2	329	<i>Sephis</i>	1	0.996	39.0
273	<i>Polygonia</i>	5	0.616	26.3	330	<i>Morpho</i>	5	1.532	73.1
274	<i>Vanessa</i>	1	0.493	30.0	331	<i>Antirrhaea</i>	1	1.599	47.0
275	<i>Anitamartia</i>	2	0.656	25.2	332	<i>Amathusia</i>	1	1.188	55.0
276	<i>Amosia</i>	1	1.016	43.5	333	<i>Faunis</i>	2	1.103	37.7
277	<i>Anartia</i>	4	0.490	24.6	334	<i>Taenaris</i>	3	1.189	47.2
278	<i>Junonia</i>	6	0.506	26.3	335	<i>Thauria</i>	1	1.715	58.0
279	<i>Precis</i>	6	0.575	29.2	336	<i>Zeuxidia</i>	3	1.615	62.7

*continued*

APPENDIX 1—*continued*

nr	GENUS	NSP	ES	WL	nr	GENUS	NSP	ES	WL
337	<i>Pierella</i>	1	0.804	44.0	393	<i>Tarsocera</i>	1	0.777	26.0
338	<i>Melanitis</i>	2	1.025	40.4	394	<i>Anetia</i>	2	0.907	45.7
339	<i>Gnophodes</i>	1	0.936	36.5	395	<i>Idea</i>	2	1.259	67.0
340	<i>Kirinia</i>	1	0.564	31.3	396	<i>Euploea</i>	4	0.890	43.1
341	<i>Lasiommata</i>	3	0.769	23.0	397	<i>Amauris</i>	4	1.056	39.4
342	<i>Lethe</i>	7	0.857	30.8	398	<i>Ideopsis</i>	1	1.068	41.0
343	<i>Lopinga</i>	1	0.896	26.5	399	<i>Parantica</i>	3	0.875	38.0
344	<i>Neorina</i>	1	1.525	57.0	400	<i>Tirumala</i>	4	0.806	44.8
345	<i>Pararge</i>	3	0.800	23.9	401	<i>Danaus</i>	7	0.808	41.9
346	<i>Satyroides</i>	2	0.805	26.7	402	<i>Athesis</i>	1	0.924	38.0
347	<i>Aeroptes</i>	1	0.912	46.0	403	<i>Patricia</i>	1	0.809	35.0
348	<i>Paralethe</i>	1	0.804	38.0	404	<i>Tithonea</i>	2	0.732	39.9
349	<i>Zethenia</i>	1	1.214	42.5	405	<i>Aeria</i>	2	0.668	23.7
350	<i>Elymnias</i>	4	1.232	40.9	406	<i>Melinaea</i>	2	0.870	43.5
351	<i>Bicyclus</i>	2	0.817	23.2	407	<i>Athyrtis</i>	1	0.793	44.5
352	<i>Mycalasis</i>	6	2.107	27.3	408	<i>Eutresis</i>	1	0.866	44.0
353	<i>Orsotriaena</i>	1	0.804	23.0	409	<i>Paititia</i>	1	1.022	34.5
354	<i>Henotesia</i>	1	0.777	21.5	410	<i>Placidula</i>	1	0.629	38.5
355	<i>Ragadia</i>	1	0.654	23.3	411	<i>Methona</i>	1	0.950	47.5
356	<i>Acrophtalmia</i>	1	0.412	18.8	412	<i>Thyridia</i>	1	0.564	41.5
357	<i>Hypocista</i>	2	0.558	18.4	413	<i>Scada</i>	1	0.669	24.5
358	<i>Tisiphone</i>	1	1.121	36.0	414	<i>Sais</i>	1	0.612	29.5
359	<i>Ipthima</i>	4	0.755	23.0	415	<i>Mechanitis</i>	1	0.704	37.5
360	<i>Coenyra</i>	2	0.745	18.4	416	<i>Callithomia</i>	1	0.638	32.0
361	<i>Melampias</i>	2	0.763	19.6	417	<i>Talamancana</i>	1	0.711	35.0
362	<i>Strabena</i>	1	0.887	19.0	418	<i>Velamysta</i>	1	0.717	32.0
363	<i>Physcaeneura</i>	1	0.896	19.0	419	<i>Ithomia</i>	2	0.598	28.4
364	<i>Cassionympha</i>	1	0.819	19.0	420	<i>Miraleria</i>	1	0.621	28.5
365	<i>Neita</i>	2	0.879	22.2	421	<i>Napeogenes</i>	1	0.782	29.5
366	<i>Pseudonympha</i>	5	0.797	20.1	422	<i>Hyaliris</i>	2	0.797	30.4
367	<i>Stygionympha</i>	3	0.877	20.6	423	<i>Rhodussa</i>	1	0.564	26.5
368	<i>Megisto</i>	1	0.676	20.2	424	<i>Hypothyris</i>	4	0.618	28.9
369	<i>Neonympha</i>	1	0.883	18.1	425	<i>Epityches</i>	1	0.542	28.5
370	<i>Taygetis</i>	1	1.047	35.0	426	<i>Oleria</i>	3	0.708	24.5
371	<i>Coenonympha</i>	14	0.577	18.5	427	<i>Hyposcada</i>	2	0.924	31.2
372	<i>Aphantopus</i>	1	0.638	21.2	428	<i>Ollantaya</i>	1	0.936	32.5
373	<i>Ceryonis</i>	2	0.811	25.4	429	<i>Hyalenna</i>	1	0.603	28.0
374	<i>Hyponphele</i>	3	0.498	20.9	430	<i>Dircenna</i>	2	0.521	35.7
375	<i>Maniola</i>	2	0.432	24.2	431	<i>Pteronymia</i>	4	0.673	24.6
376	<i>Pyronia</i>	3	0.553	19.7	432	<i>Episcada</i>	2	0.511	23.4
377	<i>Proterebia</i>	1	1.013	22.8	433	<i>Prittivitzia</i>	1	0.479	23.5
378	<i>Erebia</i>	25	0.583	22.0	434	<i>Ceraticscada</i>	1	0.564	23.5
379	<i>Calisto</i>	6	0.689	17.5	435	<i>Dygoris</i>	1	0.542	35.5
380	<i>Oeneis</i>	3	0.879	26.2	436	<i>Godyris</i>	2	0.688	37.6
381	<i>Arethusana</i>	1	0.669	24.0	437	<i>Hypoleria</i>	2	0.571	24.2
382	<i>Kanetisa</i>	1	0.691	37.1	438	<i>Hypomenitis</i>	1	0.654	28.0
383	<i>Minois</i>	1	0.861	32.7	439	<i>Greta</i>	4	0.639	28.1
384	<i>Berberia</i>	2	1.397	48.3	440	<i>Pseudoscada</i>	2	0.612	24.4
385	<i>Satyrus</i>	4	0.983	27.4	441	<i>Mcclungia</i>	1	0.603	24.5
386	<i>Chazara</i>	2	0.713	32.7	442	<i>Heterosais</i>	1	0.574	30.0
387	<i>Pseudochazara</i>	5	0.890	26.9	443	<i>Brassolis</i>	1	1.169	49.0
388	<i>Hipparchia</i>	15	0.780	27.5	444	<i>Caligo</i>	3	1.592	79.3
389	<i>Melanargia</i>	12	0.762	28.5	445	<i>Dynastor</i>	2	1.970	52.9
390	<i>Dira</i>	4	0.810	32.3	446	<i>Eryphanis</i>	3	1.692	57.2
391	<i>Dingana</i>	2	0.792	26.1	447	<i>Opoptera</i>	1	1.116	38.0
392	<i>Torynesis</i>	1	0.965	26.5	448	<i>Opsiphanes</i>	3	1.461	45.5



## APPENDIX 2.

Taxonomic/phylogenetic arrangement of the genera in Appendix 1, in parenthetical notation.  
Numbers (1–448) correspond to those in the first column of Appendix 1.

((1, 2), (((3), (4), (5, 6), (7, 8, 9, 10), (11, 12, 13), (14), (15, 16, 17, 18, 19), (20), (21, 22), (23, 24, 25), (26, 27, 28), (29, 30), ((31, 32, 33, 34, 35, 36, 37), (38, 39, 40)), (41, 42)), (43, 44, 45, 46, 47, 48, 49, (50, 51, 52, 53))), ((54, 55, 56, 57, 58), (59, 60), (61, 62, 63, 64, 65, 66, 67, 68), (69, 70), (71, 72, 73, 74, 75, 76))), (((77, 78, 79), (80, 81, 82, 83, 84)), ((85(86, 87)), ((88(89(90, 91, 92, 93))),94))), ((95, 96), ((97, 98, 99, 100, 101), (102, 103, 104), (105, 106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119)), (120, 121, 122, 123, 124, 125, 126, 127))), (((128, 129), (130), ((131, 132), (133, 134, 135, 136, 137), (138, 139), (140, 141), (142, 143), (144), (145))), (((146, 147, 148), (149, 150)), ((151, 152, 153)), (154)), ((155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166), (167, 168), ((169), (170, 171), (172, 173, 174, 175, 176, 177, 178), (179, 180, 181, 182, 183, 184, 185), (186, 187, 188), (189)), ((190), (191), (192), (193, 194), (195, 196, 197, 198), (199, 200, 201, 202)), ((203), (204), ((205), (206), (207), (208), (209, 210, 211, 212), (213), (214, 215), (216), (217, 218), (219), (220), (221), (222), (223), (224, 225, 226, 227), (228, 229, 230, 231, 232, 233), (234, 235, 236, 237), (238, 239, 240, 241)), (242))), ((243, 244), (((245), ((246(247(248, 249))), (250(251(252(253, 254))))))), (255, 256, 257, 258, 259, 260, 261, 262), (263), (264), (265)), (266), (267)), ((268, 269, 270, 271, 272, 273, 274, 275), (276, 277, 278, 279, 280, 281, 282, 283), ((284), (285, 286, 287, 288), (289, 290), (291))), ((292, 293, 294), ((295, 296, 297), (298, 299, 300, (301)), ((302, 303, 304, 305), (306, 307), (308, 309, 310, 311, 312, 313, 314), (315, 316)), ((317), (318), (319, 320, 321, 322), (323, 324), (325), (326)), (327, 328, 329), ((330, 331), (332, 333, 334, 335, 336)), ((337), (338, 339), ((340, 341, 342, 343, 344, 345, 346, 347, 348), 349), (350), (351, 352, 353, 354)), (355, 356), ((357, 358), (359, 360, 361, 362, 363, 364, 365, 366, 367), (368, 369, 370), (371), (372, 373, 374, 375, 376), (377, 378), (379), ((380), ((381, 382, 383), (384, 385), (386, 387, 388))), (389), (390, 391, 392, 393))), (((394), (395, 396), ((397), (398, 399), (400, 401))), ((402, 403), (404(405(406(407(408, 409))), ((410, 411), (412(413(414, 415))), ((416), (417), (418), (((419, 420), 421), (422(423, 424)))425), (426, 427, 428)), (((429, 430)431), ((432, 433, 434), (435, 436, 437, 438, 439, 440, 441, 442)))))), (443, 444, 445, 446, 447, 448))));