

## Comparative data on the adult biology, ecology and behaviour of species belonging to the genera *Hipparchia*, *Chazara* and *Kanetisa* in central Spain (Nymphalidae: Satyrinae)

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**Summary.** The potential longevity, fecundity, mating frequencies, behaviour, and seasonal reproductive biology were studied in several satyrine butterflies belonging to the genera *Hipparchia*, *Chazara* and *Kanetisa*, in an area located in central Spain. All the species studied appear to be potentially long-lived, and a relatively long period of pre-oviposition is shown to occur in *C. briseis* and *K. circe*. Potential fecundity varies between 250 and 800 eggs depending on the species (with maxima exceeding 1300 eggs in *K. circe*). The results are discussed in terms of the possible ecological relationships between adult ecological traits and the species abundance, and the possibility of a marked geographic variation between species, that might be of interest in relation to specific management and conservation.

**Zusammenfassung.** Für mehrere Vertreter der Gattungen *Hipparchia*, *Chazara* und *Kanetisa* (Satyrinae) wurden in einem Gebiet in Zentralspanien potentielle Lebensdauer, potentielle Fekundität, Paarungshäufigkeiten im Freiland und saisonaler Verlauf der Reproduktionstätigkeit untersucht. Alle untersuchten Arten sind potentiell langlebig, eine relativ lange Präovipositionsperiode tritt bei *C. briseis* und *K. circe* auf. Die potentielle Fekundität variiert je nach Art zwischen 250 und 800 Eiern (mit einem Maximum von über 1300 Eiern bei *K. circe*). Die Befunde werden diskutiert im Hinblick auf mögliche Zusammenhänge zwischen ökologischen Charakteristika der Imagines und der Abundanz der einzelnen Arten, sowie unter dem Gesichtspunkt, daß ausgeprägte geographische Variabilität in den ökologischen Eigenschaften auch für spezifische Management- und Naturschutzplanungen bedeutsam sein kann.

**Résumé.** Le potentiel de longévité, la fécondité, la fréquence d'accouplement, le comportement et la reproduction saisonnière ont été étudiés chez plusieurs espèces appartenant aux genres *Hipparchia*, *Chazara* et *Kanetisa* (Satyrinae), dans une région localisée au centre de l'Espagne. Toutes les espèces étudiées paraissent avoir potentiellement une longue vie, *C. briseis* et *K. circe* montrant une période de préoviposition relativement longue. La fécondité potentielle varie entre 250 et 800 œufs selon l'espèce (avec un maximum de plus de 1300 œufs pour *K. circe*). Les résultats sont discutés en termes de relations écologiques possibles entre les exigences écologiques des adultes et l'abondance des

espèces, et la possibilité de variations géographiques marquées entre espèces, ce qui peut être intéressant à relier à des mesures spécifiques d'aménagement et de protection.

Key words: Lepidoptera, Nymphalidae, Satyrinae, fecundity, life history, longevity, mating frequency, seasonality, Spain.

## Introduction

Some adult life history traits such as potential longevity and fecundity may have a relevant bearing on other ecological features of practical interest, like the ability for dispersal, the capability for colonisation, or the potential for population growth (e.g. Young, 1972; Spitzer *et al.*, 1984; Bink & Siepel, 1986). In spite of the fact that the members of the superfamily Papilionoidea have been thoroughly studied in the Western Palaearctic, detailed data on their reproductive biology are largely confined to a relatively small number of target species.

This work intends to present some basic features of the adult reproductive biology of *Hipparchia alcyone* ([Denis & Schiffermüller], 1775), *H. statilinus* (Hufnagel, 1766), *H. fidia* (Linnaeus, 1767), *Kanetisa circe* (Fabricius, 1775) and *Chazara briseis* (Linnaeus, 1764), with comparative data on *H. semele* (Linnaeus, 1758) in central Spain. The main adult life history traits involved are potential longevity, female potential fecundity, temporal distribution of oviposition in the wild, mating frequencies as estimated by spermatophore counts, and a general description of the activity of the insects in the field. The results are largely based on data collected more than ten years ago for a comparative study on Spanish *Hipparchia* (García-Barros, 1988a), to which new field and rearing data were added.

All the species involved are strictly univoltine across their range, and hibernate as small larvae (usually 1st or 2nd instar larvae, depending on species and locality — Bink, 1992a and references below). Life history data from *H. statilinus* and *H. fidia* in central Iberia can be found elsewhere (García-Barros, 1989a, 1989b; see also Jutzeler, 1993; Jutzeler *et al.*, 1998). Available information on local larval host plants of the species involved is summarised by Munguira *et al.* (1997). The female reproductive biology of *H. semele* in the study area has been dealt with in detail elsewhere (García-Barros, 1988b, 1989a, 1992), and thus only some un-

published details on the behaviour of this species are included here. This grayling is characteristic with a long flight period much alike that of *K. circe* and *C. briseis* described below; the females undergo delayed ovarian maturation throughout the driest part of the summer, and are plugged during copulation so that female monogamy is obligatory. The adults of *K. circe* and *C. briseis* occur all along the summer in the study area, from the beginning of July until September (early males can be seen in June, or even late May at especially warm locations). *H. alcyone* has a shorter flight period (July to late August or early September). The adults of *H. fidia* and *H. statilinus* are the latest to emerge (mid July, with fresh females still appearing 1 to 15 August) and remain on the wing until mid or late September. Except for *H. alcyone*, some adults may stay alive as late as early October when early autumn is sunny and dry.

## Methods

Data from captive insects were derived from small numbers of adults obtained from larvae, either reared in the laboratory or collected in the study area described below. Once mated, the females were kept in individual voliaries and the eggs laid were counted daily (as described in García-Barros, 1988b). Potential fecundity was calculated as the sum of all the eggs laid by one female (realised fecundity) plus all chorionated eggs contained in the abdomen of a dead insect, counted after dissection. The males were maintained in small groups (4–10 individuals) in larger cages (1 m<sup>3</sup>). The rearing cages were placed outdoors in a grassy outer yard at the Universidad Autónoma (Madrid) in a sunny exposure, in a way such that a shadowy shelter was available within the voliare allowing the insects to avoid overheating. Environmental conditions were not controlled or measured. Weather was usually fine to hot during the season when adults were available (July and August), so that oviposition normally proceeded in a more or less continuous manner during a female's life period.

Field work was carried out at 15 sites within a 40 × 30 km area surrounding the artificial lake of Entrepeñas, in the province of Guadalajara (central Spain), at elevations between 700 and 900 m. Preliminary field work was directed to obtain estimates of the

species' abundance and site specificity. First, the study area was divided in 48 squares of  $5 \times 5$  km. An area with reasonably well preserved vegetation (usually consisting of succession stages of *Quercus ballota* or *Q. faginea* woodlands) was selected within each square, and assessed four times (once per 15 days during July and August 1984) for the presence of each species. Second, 15 sites that proved particularly suitable for at least one of the species studied, were selected for regular sampling. Transect surveys ( $500 \times 5$  m) were carried out at these locations every ten days during two seasons (June to October, 1985–1986), using a procedure basically similar to that popularised by Pollard *et al.* (1975), but with explicit reference to a known area extension. The data from the main flight period (July and August) were then used to calculate the average number of butterflies per area unit.

Further field observations were conducted in order (1) to determine the reproductive condition of wild females, (2) to estimate the change in wing wear condition along a season, and (3) to quantify the patterns of activity displayed by the two sexes of each species. Field observations on *C. briseis* were restricted to step 1 since, although spread across the study area, this hermit was comparatively scarce in most of the sites prospected (see Table 1).

Table 1. Species abundance in the study area, as derived from counts of adult insects and presence/absence data: Mean number of adults per hectare (mean and standard deviation in 15 sites), percentage of sites where the species was collected (15 sites – 100%), and percentage of 5 km squares (48 squares – 100%) in the study area where each species was observed. For comparative purposes, data from taxonomically allied species (*Satyrus* series) that occur in the area are given. These are, in addition to the species dealt with in this study: *Hipparchia semele* (L., 1758), *Arethusana arethusa* ([D. & Schiff.], 1775), and *Satyrus actaea* (Esp., 1780).

Species	Mean population density		Area coverage	
	Mean	s.d.	% sites	% $5 \times 5$ km squares
<i>H. alcyone</i>	28.9	42.0	73.3	41.7
<i>H. semele</i>	19.3	19.8	93.3	35.4
<i>H. fidia</i>	15.7	23.9	40.0	43.8
<i>H. statilinus</i>	29.3	24.1	100.0	97.9
<i>C. briseis</i>	2.5	3.2	60.0	37.5
<i>K. circe</i>	14.7	10.9	100.0	72.9
<i>A. arethusa</i>	1.5	3.6	20.0	6.3
<i>S. actaea</i>	2.7	8.3	20.0	8.3

(1) *The reproductive status* of adult females was estimated from subsamples of female insects (up to 10 individuals per site and date) that were transported to the laboratory in a portable fridge within 6 hours after collection, and then dissected or frozen for further dissection. The specimens were checked for the presence of mature eggs within the common oviduct (indicating that the female was ovipositing). The diameter of the largest eggs within the ovaries was measured to the nearest 0.03 mm. The total number of eggs and number of spermatophores within the mating pouch (*bursa copulatrix*) were counted (e.g. Burns, 1968). These results are based on samples taken during two subsequent years. Care was taken to obtain samples of comparable size at least once every ten days each year, to avoid misinterpretations caused by between-year variation.

(2) *Wing wear state*. The transect surveys described above were repeated over the full flight season (June to October). In each transect, all the butterflies were collected to assess their wing state according to the scale 1–4 (where 1 — young to 4 — old).

(3) *Adult activity*. The activity displayed by the adults was recorded along the transect surveys (for obvious reasons this had to be done before assessment of wing states). Apparently resting individuals that were suspected to have been disturbed by the researcher were observed for one to five minutes, and then classified as resting unless other activity was displayed in that period. This proved necessary to prevent inflated records of “resting” individuals that might actually represent cryptic behaviour as a response to the observer’s activities. All surveys were conducted between 11.00 and 17.00 hours, in sunny weather and under ambient temperature above 25°C.

## Results

*Butterfly counts and species frequencies*. The estimates obtained are shown in Table 1. The number of adults counted per hectare reached 50, but varied widely depending on the species and location. On average, none of the species studied could be defined as very abundant, with average estimated densities reaching 30 adults/hectare at most.

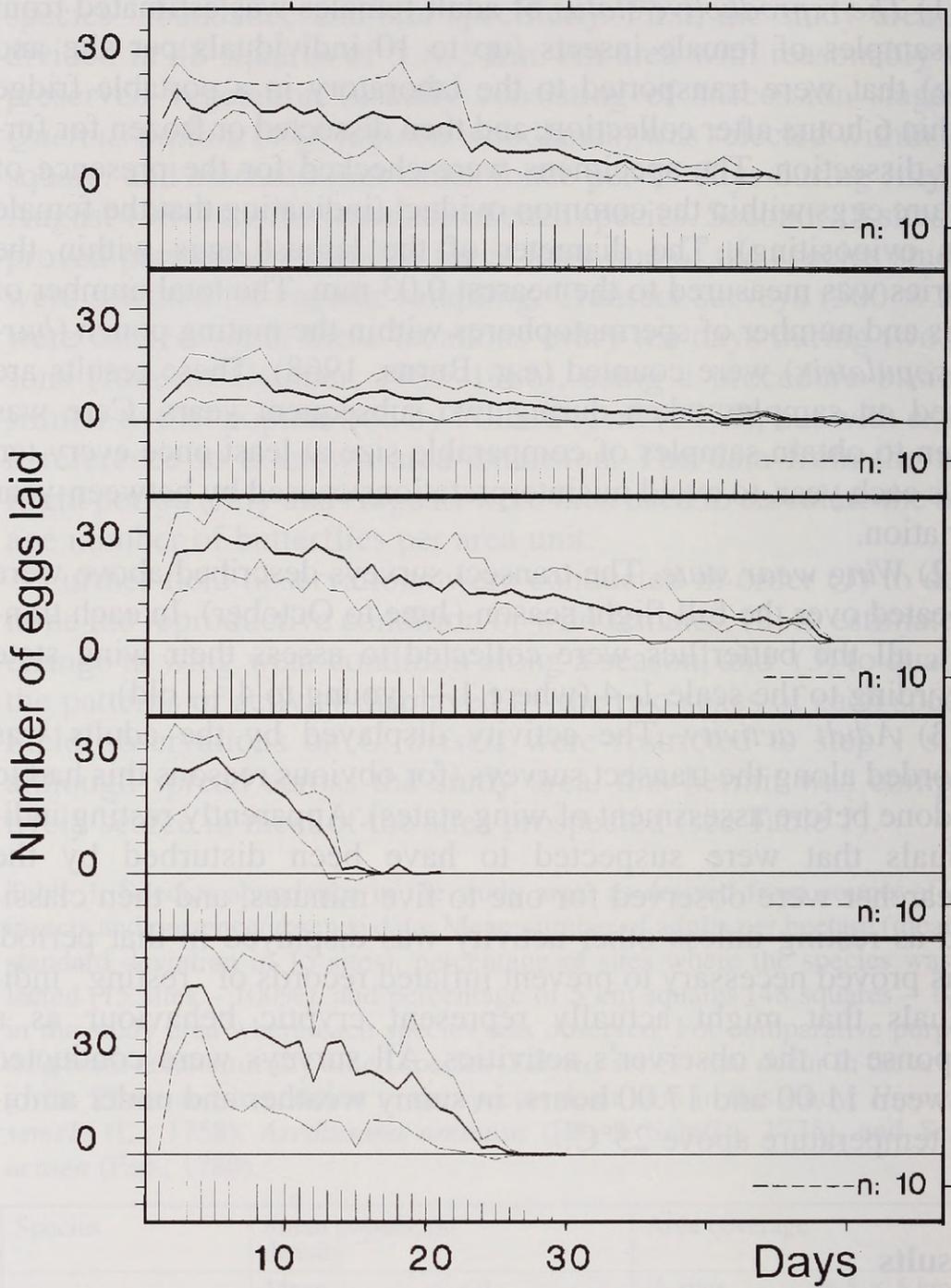


Fig. 1. Average patterns of daily egg production by captive females of (upper to lower): *H. alcyone*, *H. fidia*, *H. statilinus*, *C. briseis* and *K. circe*. Thick line in each graph indicates daily means, and thin lines the value of standard deviation above and below the mean. Sample sizes (number of females alive on date d) are given by the bars in the lower part of the plots (scale in lower right angle). In all instances, date 1 is the first day of oviposition.

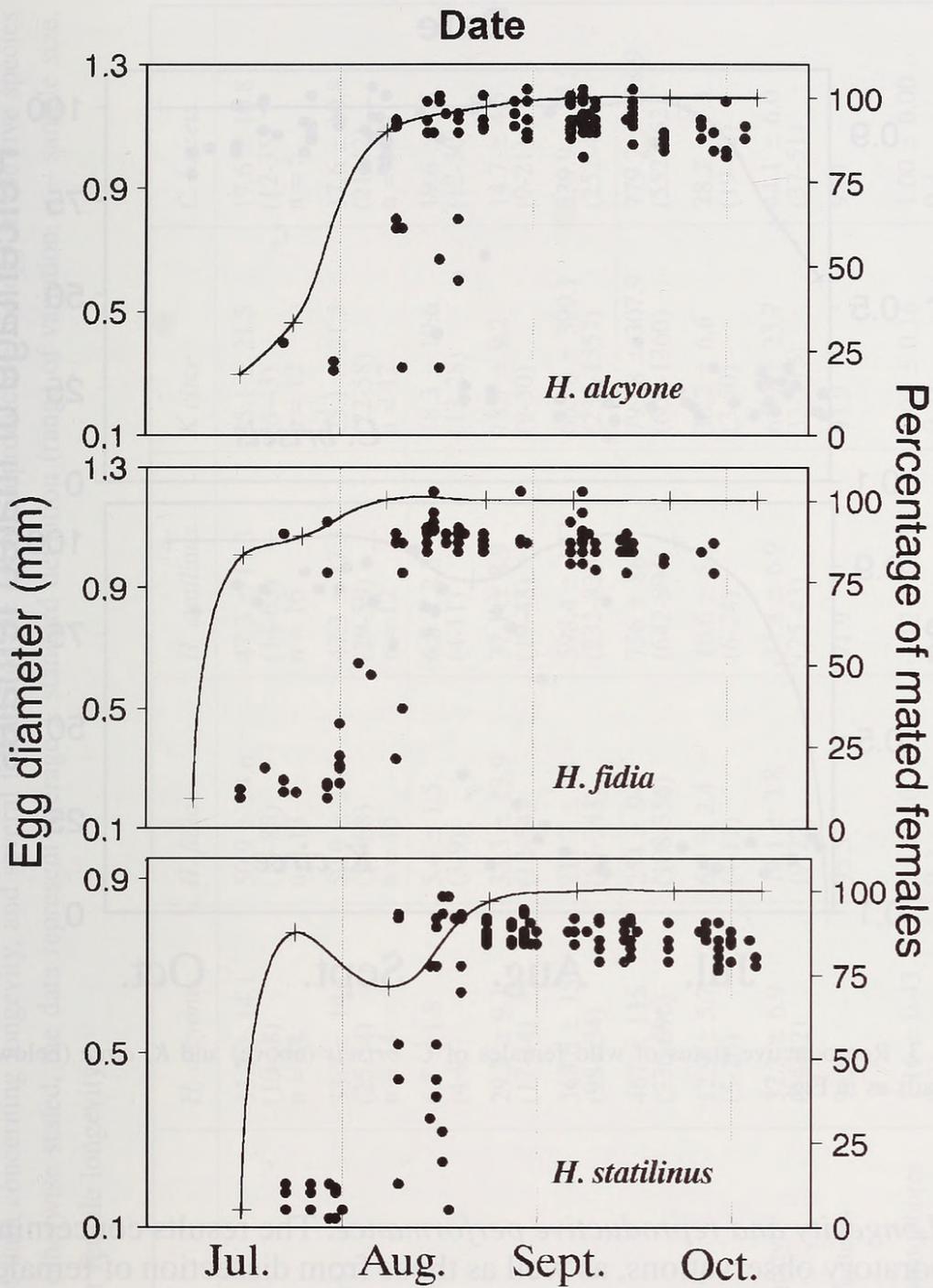


Fig. 2. Reproductive status of wild females of *H. alcyone* (upper), *H. fidia* (centre) and *H. statilinus* (lower). Dots represent the diameter of the widest eggs contained in the abdomen (in mm, left scale in all plots). The crosses indicate the percentage of mated females plotted on 15-days intervals (right scale; the continuous line is simply a smoothed line connecting the successive percentages). The number of individuals dissected per date is not proportional to the actual abundance of the species on that date.

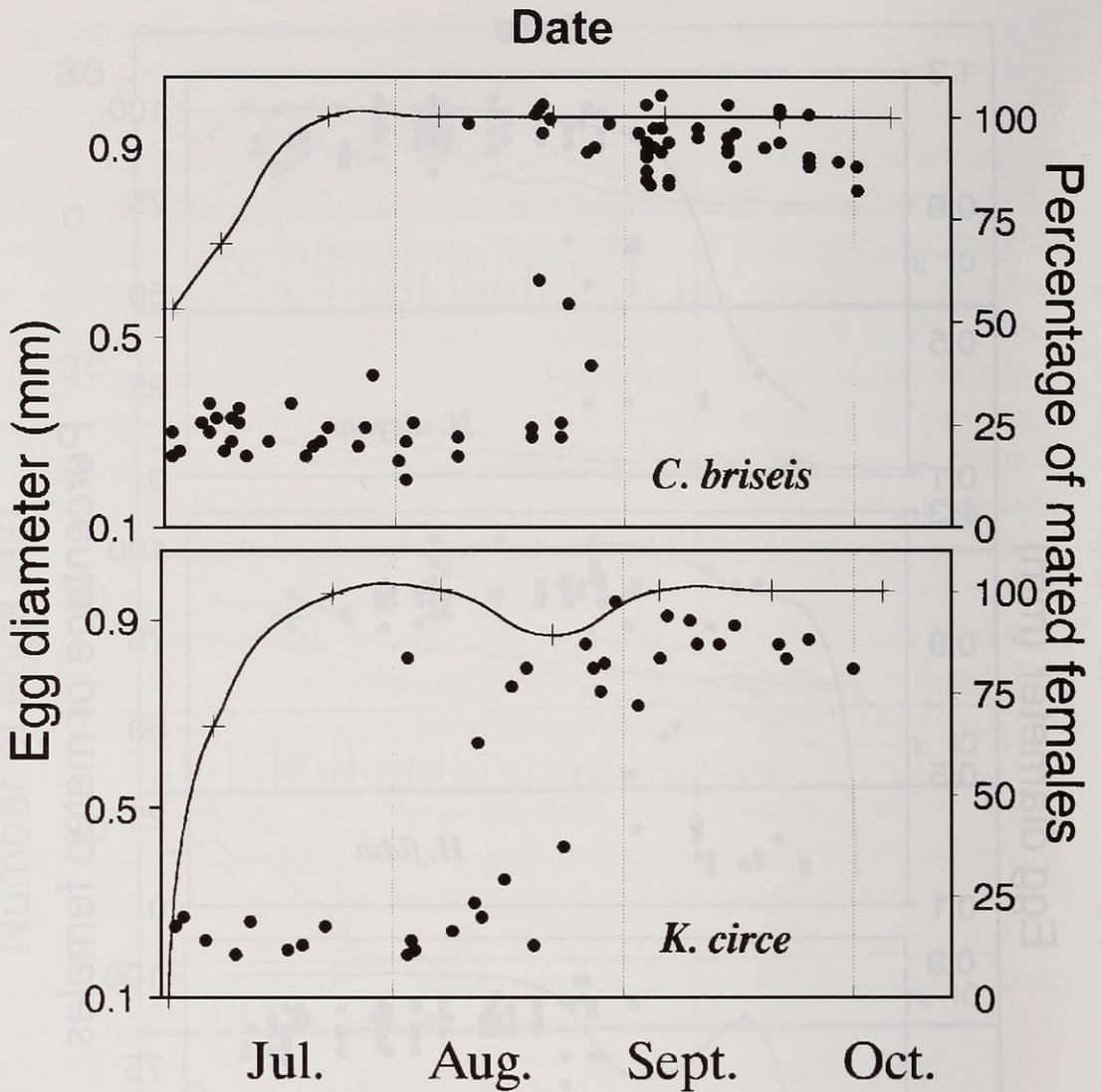


Fig. 3. Reproductive status of wild females of *C. briseis* (above) and *K. circe* (below). Details as in Fig. 2.

*Longevity and reproductive performance.* The results concerning laboratory observations, as well as those from dissection of females from the wild, are summarised in Table 2. The temporal patterns of oviposition of captive females are shown in Fig. 1, and the reproductive status of wild females is represented in Figs 2 and 3. It was evident that the females of all the species required no less than four days to reach ovarian maturation. The dissection of small series of adult females of *H. alcyone* and *H. fidia* aged 1 to 10 days

Table 2. Summary of data concerning longevity, and several features of the female reproductive biology in the five species under study. Unless otherwise stated, the data represent average  $\pm$  standard deviation (range of variation,  $n$  – sample size, <sup>1</sup> – sample size as for female longevity).

	<i>H. alcyone</i>	<i>H. fidia</i>	<i>H. statilinus</i>	<i>K circe</i>	<i>C. briseis</i>
Male longevity (days)	33.7 $\pm$ 14.1 (10-58) n = 34	50.9 $\pm$ 24.6 (10-88) n = 13	47.3 $\pm$ 17.3 (14-63) n = 16	25.1 $\pm$ 21.5 (6-43) n = 12	17.6 $\pm$ 10.8 (12-35) n = 5
Female longevity (days)	33.7 $\pm$ 14.1 (25-54) n = 14	50.9 $\pm$ 24.6 (17-68) n = 15	47.3 $\pm$ 17.3 (29-59) n = 12	25.1 $\pm$ 21.5 (22-58) n = 12	17.6 $\pm$ 10.8 (21-42) n = 10
Preoviposition (days) <sup>(1)</sup>	6.7 $\pm$ 1.8 (4-9)	5.4 $\pm$ 1.5 (3-9)	6.8 $\pm$ 2.3 (4-11)	18.3 $\pm$ 10.6 (13-28)	19.6 $\pm$ 5.5 (12-30)
Oviposition (days) <sup>(1)</sup>	29.2 $\pm$ 9.1 (17-44)	33.3 $\pm$ 13.9 (12-54)	37.1 $\pm$ 8.9 (19-48)	18.1 $\pm$ 9.2 (9-30)	14.7 $\pm$ 4.5 (9-21)
Realised fecundity <sup>(1)</sup>	368.6 $\pm$ 157 (98-634)	217.7 $\pm$ 98 (85-343)	598.4 $\pm$ 187 (232-820)	665.8 $\pm$ 399.1 (235-1357)	339.9 $\pm$ 73.5 (252-473)
Potential fecundity <sup>(1)</sup>	467 $\pm$ 115 (336-696)	254 $\pm$ 94 (108-356)	756 $\pm$ 86 (642-894)	799.8 $\pm$ 307.9 (600-1360)	779.7 $\pm$ 138.9 (552-962)
Mean daily fecundity <sup>(1)</sup>	12.9 $\pm$ 5.7 (5-26)	6.7 $\pm$ 2.4 (4-11)	16.6 $\pm$ 5.1 (6-24)	36.2 $\pm$ 6.6 (3-50)	28.2 $\pm$ 7.3 (19-42)
Maximum daily fecundity <sup>(1)</sup>	32.3 $\pm$ 6.9 (24-42)	14.1 $\pm$ 3.8 (9-22)	33.8 $\pm$ 6.9 (25-43)	65.9 $\pm$ 23.7 33-115)	44.1 $\pm$ 6.0 (37-51)
Percentage of mated females (field samples)	96.6	95.5	91.9	93.9	92.1
Mean number of spermatophores in mated females (field)	1.16 $\pm$ 0.43 0-3 n = 84	1.14 $\pm$ 0.38 0-3 n = 84	1.12 $\pm$ 0.33 0-2 n = 102	1.03 $\pm$ 0.16 0-2 n = 78	1.00 $\pm$ 0.00 0-1 n = 37

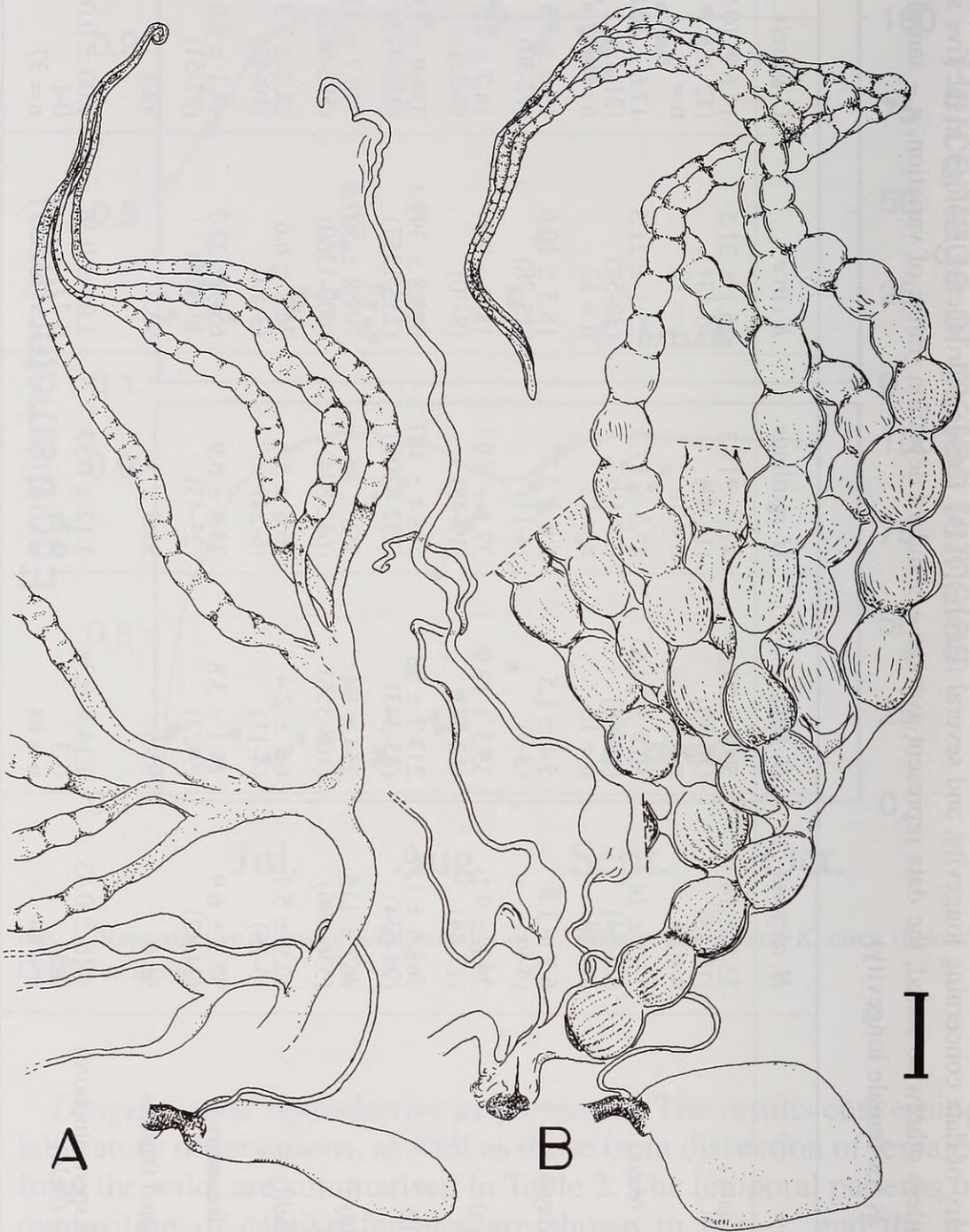


Fig. 4. Comparison between the female reproductive tracts of two *H. alcyone* females of different age: A – 24 hours after emergence, and B – a 10 days old female on its first day of oviposition. A part of the ovarioles omitted for clarity (reference bar – 1 mm).

confirmed that the absence of oviposition during early adult life was due to the fact that females were reproductively immature upon emergence (Fig. 4), and was not an artefact caused by rearing procedures.

*Wing state distribution and seasonal variation.* Since wing state was correlated to observation date (as expected, see Fig. 5), an analysis of the variance with observation date (date 1 — June 1) as the covariate was used to compare male and female average wing wear controlling for the effect of capture date. The effect of the covariate (date) was always significant ( $F > 594$  in all instances,  $P < 0.0001$ , 1.d.f.). Between-sex differences were significant for the four species tested (in all instances  $P < 0.001$ , 1.d.f.): *H. alcyone* ( $F = 857.8$ ), *H. fidia* ( $F = 63.33$ ), *H. statilinus* ( $F = 902.4$ ), and *K. circe* ( $F = 70.0$ ). In summary, the degree of wing wear differs between sexes within each species, if dates are kept constant.

In order to detect between-sex differences in the seasonal progression of wing status, the slopes of the regression lines of male and female individuals within each species were subsequently compared. The interaction between the variables “sex” and “date” was examined in an analysis of the variance of “wing state”, where “sex” was set as the classification factor and “date” as a covariate (GLM procedure). Evidence for heterogeneity of the slopes arose for *H. statilinus* ( $F = 9.39$ ;  $P = 0.002$ , d.f. = 1) and *K. circe* ( $F = 4.43$ ;  $P = 0.037$ , d.f. = 1), but not for *H. alcyone* ( $F = 0.23$ ;  $P = 0.628$ , d.f. = 1) or *H. fidia* ( $F = 1.56$ ;  $P = 0.213$ , d.f. = 1) (see Fig. 5).

*Fecundity, species abundance, and site specificity.* The estimates of fecundity obtained in the laboratory were compared with the data in Table 1 for *Hipparchia* spp., *C. briseis* and *K. circe*. Fecundity was not correlated with the species mean densities, although it was related to the dispersion across the study area (measured as the number of study sites where a species was recorded, see Table 1 (Fig. 6). No other obvious relationships were obtained (results not given in detail). Such comparisons are probably meaningless because of the small number of species included. In any case, it is interesting to note that there is some degree of correspondence between range size and potential fecundity across the study sites.

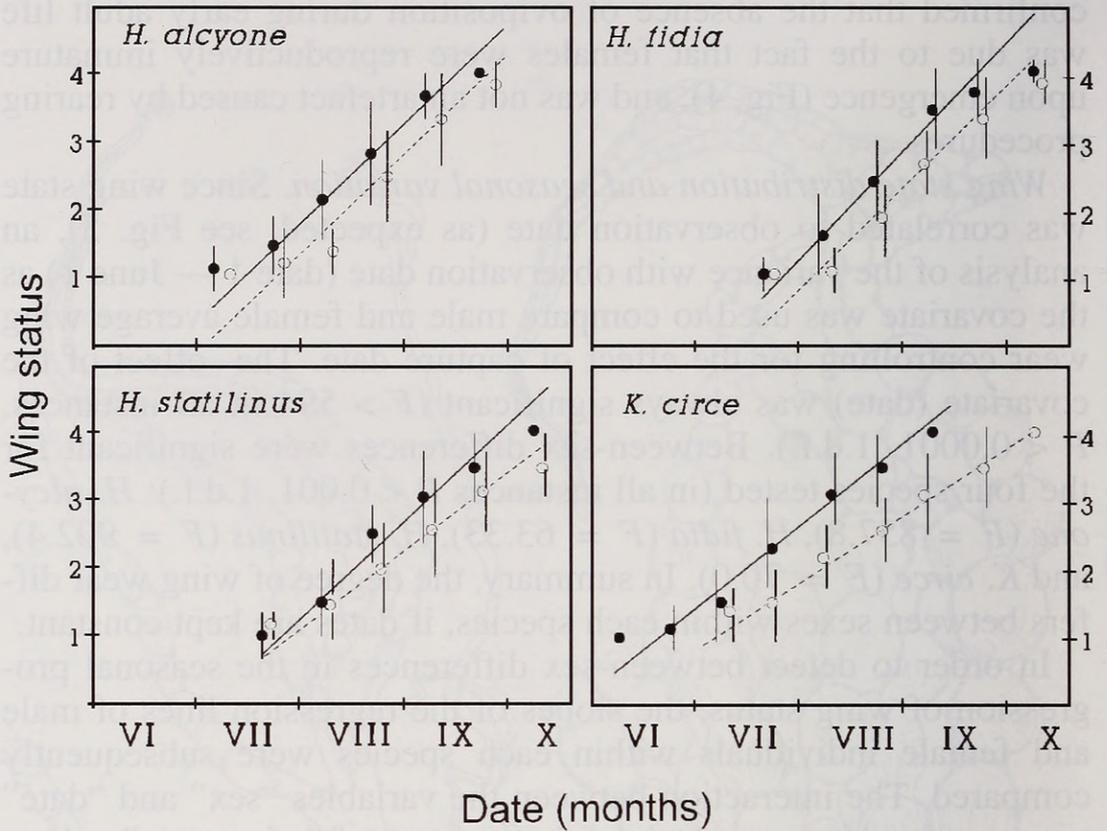


Fig. 5. Relationship between wing state and date in males (solid line, filled dots) and females (dashed lines, circles) of *H. alcyone*, *H. fidia*, *H. statilinus* and *K. circe*. The dots represent average values for each 15-days period (vertical bars –  $2 \times$  s.d.). Regression lines for males and females in each species are ( $WS$  – wing state,  $D$  – date where 1 – June 1): *H. alcyone* —  $WS_{\text{males}} = -8.52 + 0.049(D)$ ,  $WS_{\text{females}} = -9.43 + 0.050(D)$ ; *H. fidia* —  $WS_{\text{males}} = -10.0 + 0.053(D)$ ,  $WS_{\text{females}} = -9.37 + 0.048(D)$ ; *H. statilinus* —  $WS_{\text{males}} = -8.90 + 0.048(D)$ ,  $WS_{\text{females}} = -7.12 + 0.039(D)$ ; *K. circe* —  $WS_{\text{males}} = -7.25 + 0.041(D)$ ,  $WS_{\text{females}} = -6.24 + 0.03(D)$ . Correlations ( $r$ ) are above 0.76 and significant ( $P < 0.0001$ ) in all instances. Sample sizes are those given in Table 3.

*Activity and behavioural notes.* The summary of adult activities provides a general description that may well fit to intuitive descriptions of the behaviour of the species involved. The males of *Chazara* and *Hipparchia* spp. displayed typical perching behaviour, often fighting for territories. The males of *K. circe* showed a mixed strategy, where patrolling for females (often close to emergence sites in grassy areas) was combined with perching activity. Overall, the group of species under study can be described

as conservative in relation to flight activity. As a general rule, less than 20% of the observations concern what could be described as erratic flight, while a large proportion of records consisted of apparently inactive, or thermoregulating butterflies. Although males and females show sharply different behaviour patterns, the sexes appear not to be very far apart when behaviour is classified into four main categories (as in Table 3). In short, males and females devote broadly similar periods of time to activities related to reproduction, feeding, and displacement. However, these activity schedules involve a significantly higher investment in flight for the male sex, as shown in Table 4. Finally, shifts in activity patterns are obvious for the female sex in all species, while male activity appears to be more constant over the season (*K. circe* males may be an exception: see Table 5).

Incidentally, some differences between the kind of substrates used as perching sites by the males of *Hipparchia* spp. was detected (Table 6). The males of *H. alcyone* and *H. semele* perched more often on tree trunks or low branches, while those of *H. fidia* and *H. statilinus* preferred rocks, stones or decaying wood pieces upon the ground surface. This dichotomy is to some extent parallel to that in the adult wing colour patterns (upperside brown with light band, or uniformly greyish). Although interesting, this may simply reflect the preference of the former two species for woody places in the study area.

As noted for *H. statilinus*, *H. fidia* and *H. semele* (García-Barros, 1989a, 1989b and references therein), the eggs of *C. briseis* and *H. alcyone* were laid singly, most frequently on dry grass stems or other decaying plant material on the ground and more rarely attached to the base of grass tufts. *K. circe* females drop their eggs while settling close to the ground (e.g. Geiger, 1987, and personal observations). This was frequently observed during September. Ovipositing females concentrated at wood margins, road verges, and especially at relatively moist sites around small water courses. The females of this satyrine were observed all along the summer, but they were scarcer and more concentrated in wooded areas during the driest period (mostly August). The adults of this species have a complex biology that probably implies relatively important movements between different areas. Captive females of *K. circe*

have been reported to stridulate, probably as a part of their behaviour to reject courting males (García-Barros, 1986), but no further data on this behaviour were obtained in the field.

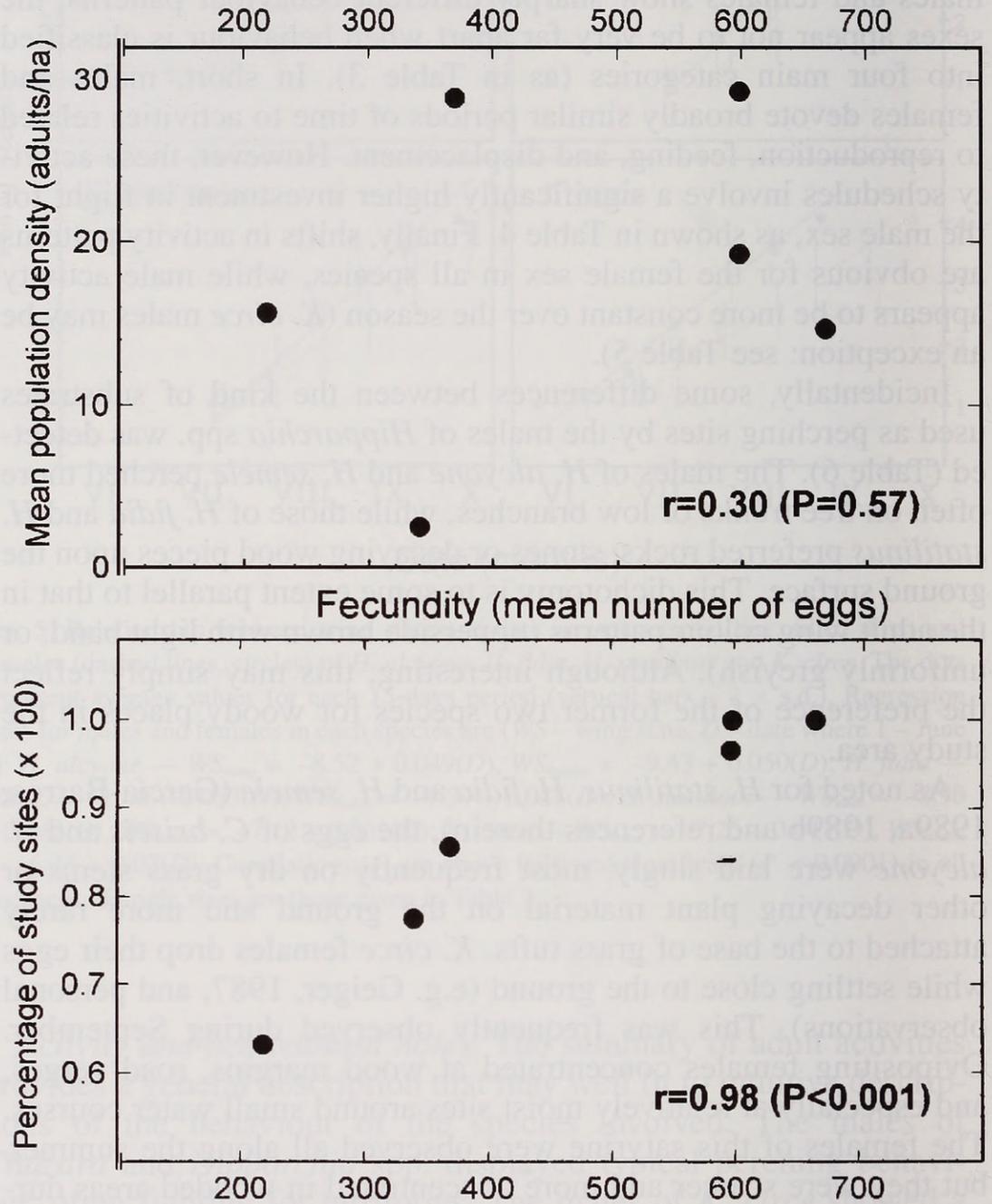


Fig. 6. Interspecific relations between average fecundity and the relative abundance and range size of the species in the study area. Data from Table 1 (data on egg production by *H. semele* from García-Barros, 1988b, 1992).

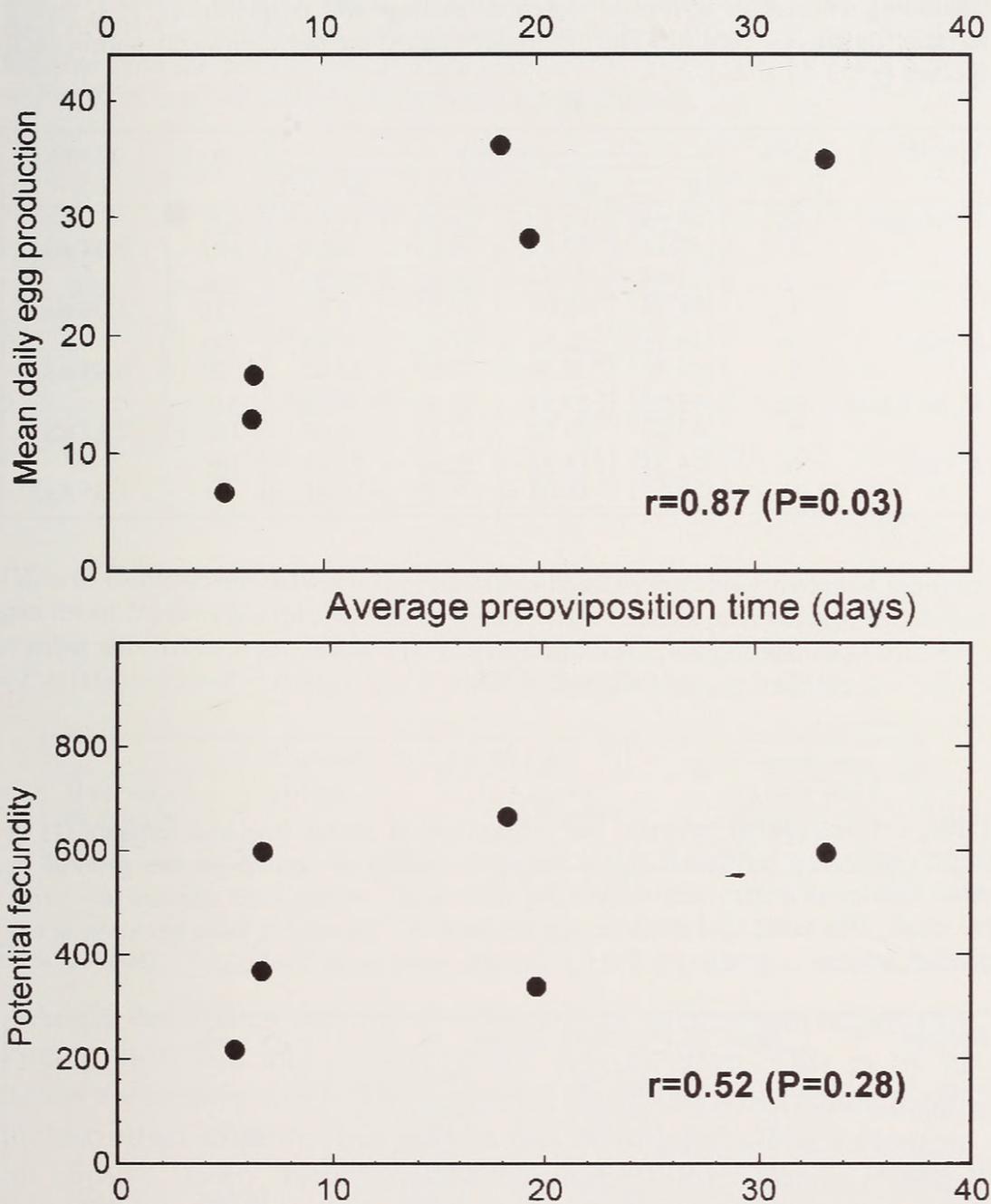


Fig. 7. Interspecific relationships between the average time required to lay the first egg (preoviposition), and both potential fecundity (number of eggs) and mean daily egg production in laboratory reared females. Based on the data from the species included in the study plus *Hipparchia semele* (from García-Barros, 1988b, 1992).

Table 3. Frequency distribution of main activity types in males (m) and females (f) within each species, expressed as a percentage of the total number of records ( $n$  – sample size). *B* – resting or basking, *R* – reproduction and related activities (including courtship, territorial defence, mating and oviposition), *F* – flying (erratic flight), *N* – feeding. The differences tested are between sexes within each species ( $\chi^2$ , 3 d.f.).

Species	Sex	Activity				n	$\chi^2$ m/h
		B	R	F	N		
<i>H. alcyone</i>	m	49.26	19.70	19.70	11.33	203	2.94 n.s.
	f	55.14	22.43	15.89	6.54	107	
<i>H. semele</i>	m	48.73	20.76	18.22	12.29	236	5.00 n.s.
	f	58.78	16.03	18.32	6.87	131	
<i>H. fidia</i>	m	49.71	22.54	17.92	9.83	173	0.83 n.s.
	f	53.33	17.78	18.89	10.00	90	
<i>H. statilinus</i>	m	45.23	27.39	19.50	7.88	241	2.17 n.s.
	f	47.27	31.52	15.15	6.06	165	
<i>K. circe</i>	m	35.24	13.33	28.57	22.86	105	7.05 n.s.
	f	50.62	16.05	18.52	14.81	81	

Table 4. Comparison between the proportion of males (m) and females (f) in flight (including territorial fights between males) or settled on the ground or other substrates (either active, basking or resting), within each species ( $n$  – sample size). The value and statistic significance of Chi-square tests between sexes of each species is given ( $\chi^2$ , 1 d.f.). Sample sizes as in Table 3.

Species	Sex	Activity classes		$\chi^2$ m/h	
		Flying	Settled		
<i>H. alcyone</i>	m	39.41	60.59	18.03	p < 0.001
	f	15.89	84.11		
<i>H. semele</i>	m	38.98	61.02	16.64	p < 0.001
	f	18.32	81.68		
<i>H. fidia</i>	m	40.46	59.54	12.45	p < 0.001
	f	18.89	81.11		
<i>H. statilinus</i>	m	46.89	53.11	43.97	p < 0.001
	f	15.15	84.85		
<i>K. circe</i>	m	64.76	35.24	4.15	p < 0.05
	f	77.78	22.22		

Table 5. Evidences for seasonal shifts in activity types along the season for adults of *Hipparchia* spp. and *K. circe*. The variable "date" was tested by means of one-way analyses of variance using "activity type" as classification factor (independent ANOVAs for each sex and species). The value of the *F* statistic is given together with the level of significance (3 d.f.; \*\*\* –  $P < 0.001$ , \*\* –  $P < 0.01$ , \* –  $P < 0.05$ , n.s. –  $P > 0.05$ ). Sample sizes as in Table 3.

Species	Sex	F
<i>H. alcyone</i>	m	0.92 (n.s.)
	f	4.42 (**)
<i>H. semele</i>	m	2.03 (n.s.)
	f	6.61 (***)
<i>H. fidia</i>	m	1.50 (n.s.)
	f	3.00 (*)
<i>H. statilinus</i>	m	1.51 (n.s.)
	f	5.02 (**)
<i>K. circe</i>	m	3.81 (*)
	f	6.28 (***)

Table 6. Comparison between the substrates used by perching males of the four species of *Hipparchia* (proportion of males on tree trunks or branches, vs. stones or other substrates at ground level):  $\chi^2$  value and level of significance (1 d.f.: \*\*\* –  $P < 0.001$ , \*\* –  $P < 0.01$ , n.s. –  $P > 0.10$ ). Sample sizes as in Table 3.

	<i>H. semele</i>	<i>H. fidia</i>	<i>H. statilinus</i>
<i>H. alcyone</i>	1.016 <sup>n.s.</sup>	67.12***	112.603***
<i>H. semele</i>		57.930***	10.496**
<i>H. fidia</i>			3.093 <sup>n.s.</sup>

## Discussion

Adult butterflies are often regarded as ephemeral organisms, with a short life and relatively fast reproduction. This is by no means a general pattern. The temporal distribution of female reproductive effort of butterflies may in fact be ordered along a continuum (Boggs, 1986; Tammaru & Haukioja, 1996). Female *Hipparchia*, *Chazara* and *Kanetisa* have a potentially long adult life span (in terms of an insect), and at least a few days are required before the eggs mature and are ready to be laid. Ovarian maturation is delayed for no less than two weeks in *K. circe* and *C. briseis* (as in *H. semele*: García-Barros, 1988b). Whether or not long delayed ovarian maturation is a geographically variable trait within species

is central to the interpretation of the observed patterns in terms of intraspecific variation (i.e., at a population or regional level, e.g. García-Barros, 1992 for *H. semele*), or interspecific variation. For instance, the flight period of *C. briseis* in the southern and northern boundaries of its distribution range is apparently uniform (basically, July to September: Seufert & Grosser, 1996), but no evidence for any kind of aestivating behaviour has been recorded from non-Mediterranean populations. According to available evidence, delayed oviposition in this and closely related species with wide geographic distribution has to be interpreted in terms of adaptation to local climate conditions that imply a dry summer period when adequate food plants (grasses) are not suitable as larval food. The species considered show remarkable coincidence in their period of oviposition in the wild, irrespective of their pattern of adult emergence. It could be argued that species where the females undergo a long pre-reproductive life would have comparatively less chances to reach fecundity comparable to those of related species with a more or less immediate oviposition, unless pre-reproductive female mortality was compensated for. This may have important consequences related to adult mortality schedules, and it is thus interesting that there is some coincidence between long pre-reproductive female life and high daily egg production rates among the species studied here which, however, does not result in a correlation between long preoviposition and high potential fecundity (Fig. 7).

Female fecundity varies widely across species, and may reach remarkably high figures in *K. circe* (up to 1300 eggs). The present estimates are well above those presented by Bink (1992a) for the same species (for instance, 140 versus 598 in *H. statilinus*, 250 versus 666 in *K. circe*, 100 vs. 369 in *H. alcyone*). These differences could probably be attributed to the more favourable temperatures experienced by the insects at Madrid (in comparison with The Netherlands), or to geographic variation in the life history traits involved (sharp differences in fecundity and female pre-reproductive life span have been found after comparison of geographically distant populations of *H. semele* — Bink, 1992a; García-Barros, 1992; see also Wiklund & Karlsson, 1988). However, there is the possibility that some of the data on butterfly fecundity by Bink (1992a) have to be critically reviewed on the light of new evidence.

While counts of ripe eggs contained in the abdomen of female butterflies have occasionally been proposed as estimates of potential fecundity (e.g. Ehrlich & Ehrlich, 1978), such procedure is obviously inaccurate in species where egg maturation proceeds along the female's life. Most females in this study died without having laid even all the mature eggs contained in their abdomens. Such counts might, however, represent reasonable approximations to daily egg production under favourable conditions (e.g. compare Table 2 and Fig. 4 for *H. alcyone*). Follicle counts (as used by Braby & New, 1988) may produce less conservative estimates, but still the contents of an individual ovariole can represent a continuum between ca. 0.05 mm and a mature egg (up to 1 mm, depending on species). The results of dissection of wild females show that, while female monogamy is the rule, repeated copulation does sometimes occur (unlike *H. semele* from southern Europe, where multiple mating is usually prevented by a sphragis secreted by the male: García-Barros, 1989a). *C. briseis* females appear to be strictly monogamous, but this might be due to small sample size.

Male and female activity patterns differ not as much in the time spent in activities intended to get food resources or reproductive success, but in the effort required: males invest more energy in flight-related activities. Interestingly, there is evidence for seasonal shifts in activity in the female sex, probably highlighting the importance of seasonal distribution of female activity. This might result from the seasonally uneven distribution of adult food resources, that may be crucial to complete ovarian maturation (cf. Wheeler, 1996). The results show that the females mate relatively soon after emergence (alternatively, the catchability of virgin females is very low). Young mated females probably remain moderately active until the onset of oviposition. The observed pattern would lead to predict different patterns of wing state change along the summer in the female sex. The fact that this is corroborated in only two species (*H. statilinus* and *K. circe*) is difficult to explain, but little else can be said until more accurate methods are applied. Seasonal variation in male behaviour has been found in other satyrines (Wickman & Wiklund, 1983; Wickman, 1992; Van Dyck & Matthysen, 1998), and seasonal changes in behaviour and habitat selection have been reported for satyrines from tropical or

subtropical areas where rainfall is strongly seasonal (e.g. Braby, 1995). What is of interest is that West-Palaeartic satyrine nymphalids are predominantly univoltine (that is, they complete one generation per year), and that this pattern applies as well to the Mediterranean species or populations. Hence, seasonal variation in activity patterns in *Hipparchia*, *Kanetisa* or *Chazara* represents environmental variation that is faced by the individual adults (not by the different individuals belonging to successive generations).

The amount of time spent settling on the ground by the adults of both sexes must be partly attributable to thermoregulating behaviour (since overheating must be a serious risk for several hours a day during the central part of the summer), as well as to the dominating perching strategy used by the males to locate mates.

In summary, that insects such as butterflies have varied and complex life styles is not a surprise. A more detailed knowledge of some key biological traits may help in our understanding of the species responses to environmental changes. As suggested by Bink (1992b), some ecological characters of the adults might prove of predictive value in relation to changes in abundance. More estimates of such traits are required, however, to get an adequate contrast of their reliability and of their possible geographic variation (which in turn constitutes an evidence of genetic diversity). To the extent that such variation occurs, the extrapolation of local results (e.g. for purposes of population management for conservation) may prove inadequate.

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