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NATURAL SELECTION AND MATERNAL EFFECTS IN LIFE HISTORY TRAITS OF *BREVICORYNE BRASSICAE* (HOMOPTERA: APHIDIDAE) ON TWO SYMPATRIC CLOSELY RELATED HOSTS

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ABSTRACT

In this study we used 2 reciprocal transference experiments to estimate the mode and magnitude of selection on life history traits of the aphid *Brevicoryne brassicae* L. on 2 sympatric host plants, *Brassica campestris* L. and *Brassica oleraceae* L. In the first experiment, we recorded success in establishment, age at first reproduction, duration of reproduction, number of nymphs laid, reproductive rate, and rate of increase (r_i) on each host. In the second experiment, the offspring of females collected on *Br. campestris* or *Br. oleraceae* were reared on hosts through 3 generations. Age at first reproduction, duration of reproduction, fecundity, and rate of increase (r_i) were measured during the third generation in order to determine presence of maternal effects. Within each recipient host, we estimated selection gradients by performing a multiple linear regression of relative number of nymphs in relation to age at first reproduction and duration of reproduction. Results of the first experiment indicate that successful establishment was higher on the source host on which the mother was collected. A significant effect associated with the recipient host was detected for most life history traits. Positive directional selection on duration of reproduction was detected on both hosts whereas selection on the age at first reproduction was detected only in *Br. oleraceae*. In the second experiment we did not find evidence of maternal effects since the recipient host exerted a significant effect on fecundity. Again, the selection on duration of reproduction was detected on both hosts. Despite these results suggesting incipient ecological specialization in *B. brassicae*, we recognize factors that may prevent the evolution of host plant specialization.

Key Words: host-specialization, local adaptation, phenotypic plasticity, life-history traits

RESUMEN

Usamos dos experimentos de transferencia recíproca para estimar el modo y magnitud de la selección en caracteres de historia de vida de *Brevicoryne brassicae* L. en dos especies huésped simpátricas, *Brassica campestris* L. y *Brassica oleraceae* L. En el primer experimento registramos el éxito en el establecimiento, edad a primera reproducción, duración de la reproducción, número de ninfas producidas, tasa reproductiva y tasa de incremento (r_i) en cada planta huésped. En el segundo experimento diseñado para medir los efectos maternos, la descendencia de las hembras colectadas en *Br. campestris* o *Br. oleraceae* fueron desarrolladas durante dos generaciones en la misma especie de planta en la que fueron colectadas y en la tercera generación se hizo la transferencia recíproca y se midió la edad a la primera reproducción, duración de la reproducción, fecundidad y tasa de incremento (r_i). Se estimó la selección natural en cada huésped para la duración y la edad a la primera reproducción mediante regresión lineal múltiple. El número de ninfas depositadas por cada madre se empleó como el estimador del éxito reproductivo. En el primer experimento, el éxito en el establecimiento fue superior en la especie huésped donde la madre fue colectada. Hubo un efecto significativo del huésped receptor para la mayoría de las características de historia de vida. Se detectó selección direccional positiva en la duración de la reproducción en ambas especies huésped, mientras que sólo en *Br. oleraceae* se detectó selección en la edad a la primera reproducción. No hubo evidencia de efectos maternos; sólo el huésped receptor tuvo un efecto significativo en la fecundidad. Hubo selección direccional en la duración de la reproducción. Aunque los

resultados sugieren especialización ecológica incipiente en *B. brassicae*, se discuten los factores que pueden limitar la evolución de la especialización de huéspedes.

Translation by the authors.

Host plants may constitute environments with distinct selection pressures for phytophagous insects, resulting in host race formation or host specialization (Diehl & Bush 1984; Farrell 1998; Bush 1994). However, a phenotypic adaptive change in phytophagous insects may be expected whenever phenotypic variations in traits related to host use are heritable and linked to fitness, and when phenotypic plasticity is negligible (Via & Lande 1985; Scheiner 1993).

In many organisms, environmental effects may be transmitted through generations via mechanisms other than transmission of nuclear genes (Rossiter 1987; Mosseau & Dingle 1991; Hunt & Simmons 2000; Agrawal 2001; McAdam et al. 2002). For example, if a phytophagous insect is reared on a given host species, its offspring is "acclimated" to that host, possibly via induction of enzymatic activity in the offspring (Fox et al. 1995; Hunter 2002). This type of inheritance, known as maternal effects, may be relevant for phytophagous insects if more than 1 potential host plant species occur together within a habitat. Maternal effects may influence the evolutionary trajectories of host specialization by preventing selection (Fox & Savalli 2000; Rossiter 1991; McAdam et al. 2002) and may be adaptively important in heterogeneous environments.

Throughout its geographic distribution, the cabbage aphid, *Brevicoryne brassicae* L. (Homoptera: Aphididae) uses different Brassicaceae plant species and displays variability in performance among host plants (Costello & Altieri 1995). *Brevicoryne brassicae* uses 2 related host plant species that occur sympatrically in Chiapas, Mexico (the weed *Brassica campestris* L. and the cultivated *Br. oleraceae* L.). In Chiapas, *B. brassicae* reproduces parthenogenetically and lives from Oct through Mar (L. Ruiz-Montoya, personal observation). Because *B. brassicae* feeds upon both hosts, its performance on 1 host could be affected if the mother lived on the other host during the previous generation (i.e., maternal effects).

This study assessed whether *B. brassicae* exhibits differential performance on *Br. campestris* and *Br. oleraceae*, whether selection on life history traits is similar in both hosts, and whether the offspring's phenotype is influenced by the mother's environment. Using a reciprocal transference experimental design, we performed 2 experiments in order to estimate (1) direction and magnitude of phenotypic selection on age at first reproduction and duration of reproduction of *B. brassicae* on each host plant, and (2) the extent of maternal effects on offspring's age at first reproduction, duration of reproduction, and fecundity.

MATERIALS AND METHODS

Brevicoryne Biology in the Zone Study

Brevicoryne brassicae is an oligophagous herbivore which uses Brassicaceae species throughout its worldwide distribution (Blackman & Eastop 2000). In our study site, *B. brassicae* feeds upon *Br. campestris* and *Br. oleraceae* and has a parthenogenetic life cycle with winged and wingless morphs. The host plant species, *Br. campestris* and *Br. oleraceae*, were introduced to Mexico approximately 200 years ago (Rollins 1993). *Br. oleraceae* (green cabbage) has been cultivated annually in the Chiapas Highlands for at least 5 decades (Montoya-Gomez 1998). The weed *Br. campestris* (Syn. *Brassica rapa*, turnip) is an annual herbaceous plant that grows in abandoned fields and on the borders of cultivated *Br. oleraceae* fields. As annuals, both host plant species complete their life cycle in 3 to 4 months. Up to 3 generations of the aphid have been recorded in the field during a given growing season.

Brevicoryne Performance and Natural Selection without Considering Maternal Effects

Adult wingless aphids from the locality of Balun Canan (16°38' 19" N latitude; 92°32' 43" W longitude; 2240m) in the state of Chiapas, Mexico were randomly collected from 30 individual plants of each host species during Mar of 1999. Both host plants were found in the same 4-ha field, and distance among plants ranged from 30–300 m. *Brevicoryne campestris* plants were growing adjacent to the cultivated *Br. oleraceae* fields. In a reciprocal transplant experiment, aphids collected in the field from each host plant species (hereafter referred to as source host), were placed singly on individual plants of each host (hereafter referred to as recipient host). Females collected on *Br. campestris* were transferred to individual plants of *Br. campestris* ($n = 18$) or *Br. oleraceae* ($n = 25$), whereas aphids derived from *Br. oleraceae* were placed on *Br. oleraceae* ($n = 22$) or *Br. campestris* ($n = 21$). Individual plants were randomly assigned to greenhouse benches and individually covered with a rearing chamber made with a fine mesh to exclude other aphids and natural enemies (Blackman 1974). Plants were kept at ambient temperature and photoperiod ($13 \pm 4^\circ\text{C}$ and 12 h daylight).

Each female collected in the field was allowed to lay a single nymph (1st generation). The life of each nymph was followed until death, recording

whether or not it was successfully established (i.e., was able to reproduce), age at first reproduction (days), total number of nymphs laid during its life (2nd generation), duration of reproduction (days), and reproductive rate (number of nymphs laid per day). A rate of increase for each individual aphid (r_i) was calculated based on the aphid's schedule of survivorship and fecundity:

$$1 = \sum_{x=0} r_i^{-(x+1)} B_{xi}$$

where x_i is age-class (days in this study), and B_{xi} is number of nymphs produced in that age-class (Lenski & Service 1982).

Establishment of a nymph on a given host was recorded as successful (1) if the nymph was able to reproduce, and unsuccessful (0) if it failed to reproduce. Because this response variable is binary, we analyzed the data using logistic regression (Quinn & Keough 2002). The model tests whether $\beta_0 = 0$. The whole model is $g(x) = \beta_0$ (intercept) + β_1 (source host) + β_2 (recipient host) + β_3 (source host × recipient host), where $g(x)$ is the natural log of the odds of establishment relative to non-establishment. The model was tested by the log-likelihood test, $G^2 = -2[(\log\text{-likelihood reduced model}) - (\log\text{-likelihood full model})]$ (i.e., the deviance). Reduction in deviance attributed to the inclusion of predictor variables in the full model was tested for significance by a Chi-squared test. To test individual coefficients, we used likelihood ratio tests by partitioning the deviance (Quinn & Keough 2002). Analyses were performed with the JMPTM statistical package (v. 5.1.01.2, SAS Institute 2003). In addition, the difference in the proportion of established versus non-established aphids within each recipient host was tested by the odds ratio analysis. The departure from zero was assessed by a G -test (Sokal & Rohlf 1995). The confidence interval was calculated for binomial proportions,

$$p \pm 1.96 \sqrt{pq/n}$$

where p is the proportion of individuals established, $q = 1 - p$ is the proportion of non-established individuals, and n is the total of individuals assayed in each recipient host (Snedecor & Cochran 1989).

For established females, age at first reproduction, duration of reproduction, total number of nymphs, reproductive rate, and rate of individual increase (r_i) were analyzed by means of two-factor ANOVA, with source and recipient host and interaction as factors (Sokal & Rohlf 1995). A significant source × recipient host interaction would indicate that the aphids' performance changes between the two environments (i.e., hosts). A signifi-

cant effect of the source host may be indicative of genetic differences (or maternal effects) between the two aphid populations, whereas a significant recipient host effect may indicate differences in the general quality of host plants. Variables were log transformed (except r_i) before performing the ANOVAs in order to approximate residuals to a normal distribution.

Phenotypic selection analyses were performed to determine whether different host species impose differential selection on aphids' life history traits. The effect of both age at first reproduction and duration of reproduction on individual fitness was analyzed by means of multiple linear regressions within each recipient host (Lande & Arnold 1983). Regression analyses were performed with the standardized variables (i.e., mean = 0, standard deviation = 1), and thus selection gradients are interpretable in terms of standard deviations (Lande & Arnold 1983). Covariance analysis was used to assess differences, if any, in the regression coefficients (slopes) between environments (host plants). Relative female fitness (w_i) was estimated as the total number of nymphs laid divided by the mean number of nymphs in the population \bar{w} . Analyses were performed with the JMPTM statistical package (v. 5.1.01.2, SAS Institute 2003).

Performance and Natural Selection in the Presence of Maternal Effects

In the greenhouse, females randomly collected from each host in the field were allowed to produce nymphs on the same species during three generations (acclimation period in the source host; Fig. 1). In each generation, nymphs were placed on a new single plant of the corresponding host species. Nymphs from the third generation were randomly selected and placed on individual plants of *Br. oleraceae* or *Br. campestris* (recipient host). One nymph was placed on an individual plant as previously described. For each individual aphid, we then recorded age at first reproduction, duration of reproduction, and number of offspring deposited until death. Using these data, we computed individual rate of increase (r_i). Sample sizes of each source-recipient host combination were, as follows: *Br. campestris* to *Br. campestris*, 40; *Br. campestris* to *Br. oleraceae*, 34; *Br. oleraceae* to *Br. campestris*, 29; and *Br. oleraceae* to *Br. oleraceae*, 34. In order to assess the effect of source and recipient host on life history traits, a two-factor ANOVA was performed for each measured trait. A significant effect of the source host would indicate environmental effects upon life history traits, including maternal effects. On the contrary, a recipient effect would indicate that the host plant distinctly affects aphids' performance.

Finally, selection on life history traits (duration of reproduction and age at first reproduction) was estimated for aphids derived from different

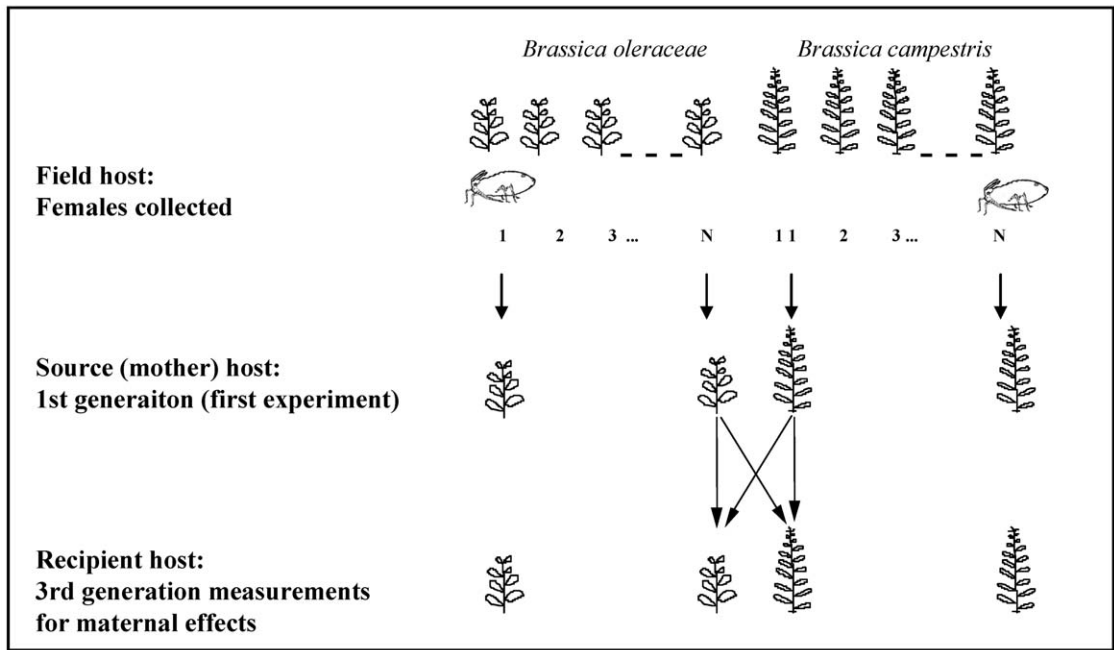


Fig. 1. Schematic diagram of the reciprocal transfer experiment to estimate performance, natural selection, and maternal (source) host effects on life history traits of *Brevicoryne brassicae* growing on recipient hosts *Brassica oleraceae* and *Brassica campestris*.

source hosts and developed on different recipient hosts, following the methodology stated above. Magnitude of selection between hosts was compared by means of an ANCOVA.

RESULTS

Performance and Natural Selection without Maternal Effects

The logistic regression model of establishment as a function of source, recipient host, and interaction was statistically significant (-Log likelihood = 5.096, $df = 3$, $\chi^2 = 10.192$, $P = 0.017$, $R^2 = 0.089$). Only the interaction source host _ recipient host was significant (Table 1). Establishment

was higher when source host was similar to recipient host (Fig. 2a). The *G*-tests indicated significant differences in establishment between source hosts when the recipient host was *Brassica oleraceae*, while no difference was detected within *Br. campestris* (Fig. 2a).

Analyses of variance performed to assess the effect of the source and recipient host and interaction on life history characters indicated a significant effect of the recipient host on age at first reproduction, total number of nymphs, reproductive rate, and individual rate of increase (r_1), whereas no significant effect was detected on duration of reproduction (Table 2). Source host had an effect on individual fitness (i.e., number of nymphs), and source host \times recipient host interaction did

TABLE 1. LOGISTIC REGRESSION OF ESTABLISHMENT/NON ESTABLISHMENT OF *BREVICORYNE BRASSICAE* ON 2 HOST PLANTS (EXPERIMENT WITHOUT CONSIDERING MATERNAL EFFECTS). THE MODEL TESTS WHETHER $\beta_i = 0$. THE WHOLE MODEL IS $G(X) = \beta_0$ (INTERCEPT) + β_1 (SOURCE HOST) + β_2 (RECIPIENT HOST) + β_3 (SOURCE HOST β_2 RECIPIENT HOST), WHERE $G(X)$ IS THE NATURAL LOG OF THE ODDS OF ESTABLISHMENT RELATIVE TO NON ESTABLISHMENT. SAMPLE SIZE $N = 86$.

Parameter	Estimate	df	χ^2 (Likelihood ratio test)	P
β_0 (intercept)	-0.618	1	6.170	0.013
β_1 (Source host)	-0.016	1	0.004	0.948
β_2 (Recipient host)	0.330	1	1.821	0.177
β_3 (source host \times recipient host)	-0.677	1	8.096	0.004

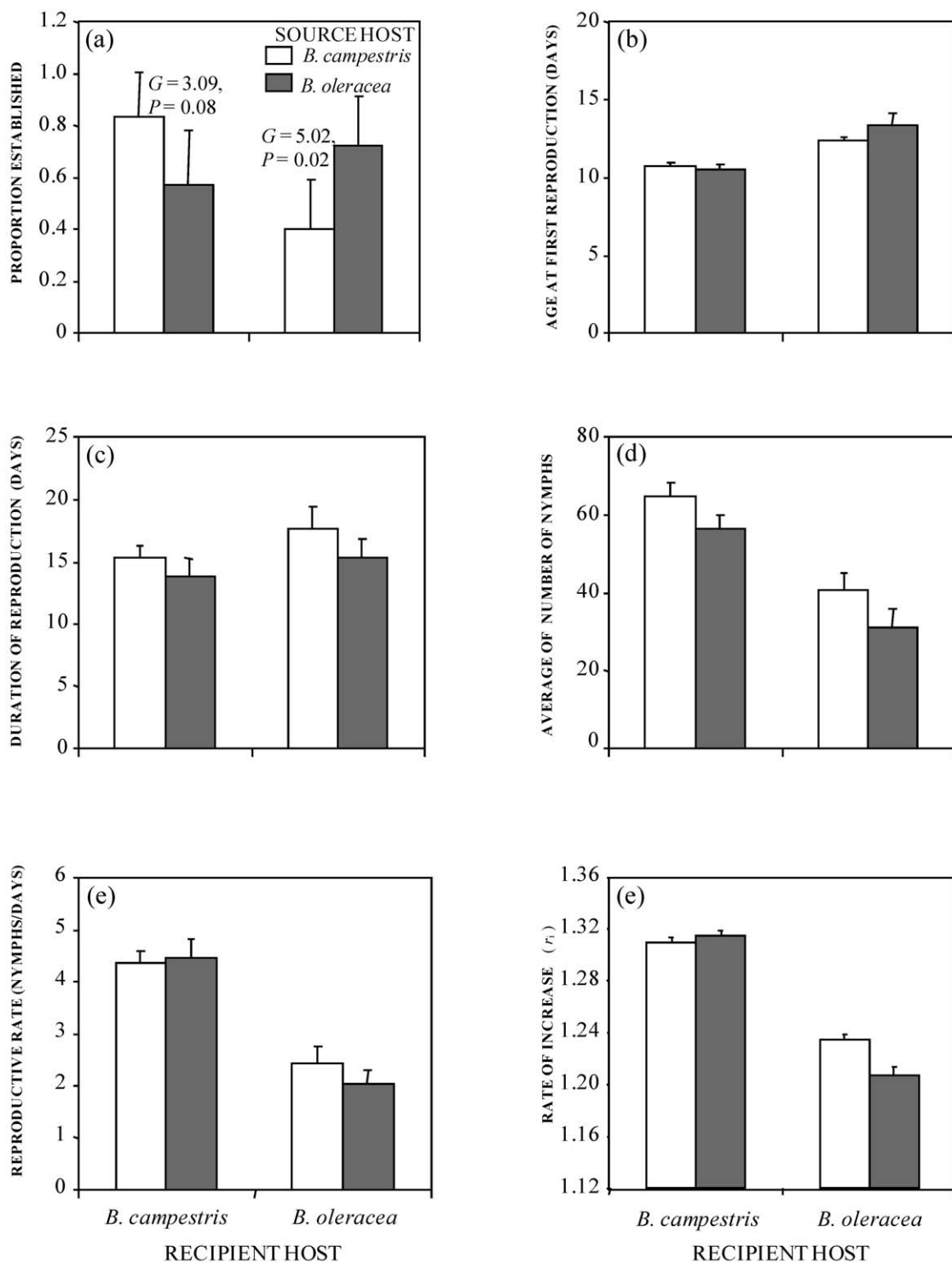


Fig. 2. Results of the experiment without considering maternal effects in the performance of *Brevicoryne brassicae*. (a) Average values of establishment (+ 1 confidence interval 95%), (b) age at first reproduction, (c) duration of reproduction, (d) average total number of nymphs, (e) reproductive rate, and (f) individual rate of increase [r_1] measured in a reciprocal transplant experiment. From B to E +1SE is shown.

TABLE 2. ANALYSIS OF VARIANCE OF 4 LIFE HISTORY TRAITS OF *BREVICORYNE BRASSICAE* ON 2 HOST SPECIES (*BRASSICA OLERACEAE* AND *BRASSICA CAMPESTRIS*) IN A RECIPROCAL TRANSPLANT EXPERIMENT WITHOUT CONSIDERING MATERNAL EFFECTS.

Variable	Source of variation	SS	df	F	P
Age at 1 st reproduction	Source host	0.001	1	0.192	0.66
	Recipient host	0.071	1	15.407	0.0003
	Source × Recipient	0.003	1	0.591	0.44
	Error	0.226	49		
Number of nymphs	Source host	0.188	1	3.925	0.05
	Recipient host	1.109	1	23.117	<<0.001
	Source × Recipient	0.051	1	1.070	0.31
	Error	2.351	49		
Duration of reproduction	Source host	0.064	1	2.379	0.13
	Recipient host	0.023	1	0.841	0.36
	Source × Recipient	0.002	1	0.079	0.78
	Error	1.321	49		
Reproductive rate	Source host	0.033	1	0.924	0.34
	Recipient host	1.449	1	41.01	<<0.001
	Source × Recipient	0.033	1	0.919	0.34
	Error	1.731	49		
Rate of increase (r_i)	Source host	1.48×10^{-3}	1	0.637	0.43
	Recipient host	0.107	1	45.93	<<0.001
	Source × Recipient	3.84×10^{-3}	1	1.65	0.20
	Error	0.114	49		

not affect any variable (Table 2). On average, aphids reproduced earlier, at a higher rate, and produced more nymphs on *Br. campestris* than on *Br. oleraceae* (Figs. 2b, d-f). No significant effects of source and recipient host and interaction were detected on duration of reproduction (Table 2, Fig. 2c).

A positive relationship between duration of reproduction and relative fitness was detected on both recipient hosts (Table 3 a-b). There were no differences in the selection gradients (i.e., equal slopes) between hosts for this character (ANCOVA, $F = 2.211.469$; $df = 1,44$, $P = 0.14$), indicating that selection favored those individuals with a longer reproductive period regardless of their recipient host. No selection was detected upon the age at first reproduction in *B. campestris* (Table 3a). In contrast, relative fitness is related to age at first reproduction on *Br. oleraceae* (Table 3 a-b), indicating that phenotypes that began reproduction earlier attained a higher relative fitness (Table 3a). Significant differences in the selection gradient on the age at first reproduction between recipient hosts were detected (ANCOVA, $F = 4.46$; $df = 1,44$; $P = 0.04$).

Natural Selection with Maternal Effects

Analyses of variance aimed to assess maternal effects upon life history traits of aphids indicated that the source host (on which the aphids spent 3

generations) did not explain a significant amount of variance (Table 4, Fig. 3a-d). However, a significant effect of the recipient host was detected for the number of nymphs, r_i , and marginally for age at first reproduction. The interaction source host x recipient host was not significant for all characters (Table 4). As before, fecundity (number of nymphs and r_i) was higher when aphids were grown on *Br. campestris*, irrespective of the source host (Fig. 3c-d).

Directional selection for duration of reproduction was detected on both recipient hosts (Table 5) and of similar magnitude as indicated by the not significant recipient host x duration of reproduction in an ANCOVA of fitness ($F = 1.128$; $df = 1, 69$; $P = 0.29$). No selection for the age at first reproduction was detected in both hosts (Table 5).

DISCUSSION

The present study demonstrates that *Br. campestris* and *Br. oleraceae* constitute 2 different environments for *B. brassicae*. The probability of establishment of the aphids was higher when they colonized a host similar to their original host in the field. Also, fecundity and rate of increase was consistently greater for aphids reared on *Br. campestris* than on *Br. oleraceae*, indicating that the former host constitutes a higher quality habitat. Differences in performance displayed by *B. brassicae* between host plants cannot be attribut-

TABLE 3. ANALYSIS OF SELECTION OF AGE AT FIRST REPRODUCTION AND DURATION OF *BREVICORYNE BRASSICAE* ON 2 HOST SPECIES (EXPERIMENT WITHOUT CONSIDERING MATERNAL EFFECTS). A. STANDARDIZED COEFFICIENTS (β) FROM LINEAR REGRESSION REPRESENT THE DIRECTIONAL SELECTION GRADIENTS. B. ANALYSIS OF VARIANCE AND ADJUSTED R^2 FOR THE MULTIPLE REGRESSION MODEL.

-A-							
Recipient host	Character	Coefficient β (SE)			T	P	
<i>Brassica campestris</i>	Intercept	1.000 (0.035)			27.93	<0.0001	
	Age first reproduction	-0.005 (0.035)			0.13	0.83	
	Duration of reproduction	0.109 (0.036)			2.97	0.01	
<i>Brassica oleraceae</i>	Intercept	1.00 (0.077)			12.10	<0.0001	
	Age first reproduction	-0.219 (0.080)			-2.58	0.01	
	Duration of reproduction	0.245 (0.080)			2.87	<0.01	
-B-							
Recipient host	Source	SS	MS	Df	F	P	r^2 adjusted
<i>Brassica campestris</i>	Model	0.306	0.153	2	4.42	0.023	0.21
	Error	0.830	0.034	24			
	Total	1.137					
<i>Brassica oleraceae</i>	Model	3.148	1.574	2	10.12	<0.001	0.42
	Error	3.578	0.156	23			
Total		6.726					

TABLE 4. ANALYSIS OF VARIANCE TO ASSESS EFFECTS OF THE MATERNAL HOST (SOURCE) AND RECIPIENT HOST ON LIFE HISTORY TRAITS OF *BREVICORYNE BRASSICAE* (EXPERIMENT IN THE PRESENCE OF MATERNAL EFFECTS).

Variable	Source of variation	Sums of Squares	df	F	P
Age at 1 st reproduction	Source host	0.023	1	1.713	0.19
	Recipient host	0.048	1	3.461	0.06
	Source \times Recipient	0.005	1	0.347	0.55
	Error	0.956	69		
Duration of reproduction	Source host	0.009	1	0.111	0.74
	Recipient host	0.019	1	0.242	0.62
	Source \times Recipient	0.015	1	0.196	0.65
	Error	5.409	69		
Number of nymphs	Source host	0.025	1	0.143	0.71
	Recipient host	0.810	1	4.572	0.03
	Source \times Recipient	0.024	1	0.138	0.71
	Error	12.224	69		
Rate of increase (r_i)	Source host	0.002	1	0.429	0.51
	Recipient host	0.028	1	6.938	0.01
	Source \times Recipient	1.6×10^{-3}	1	0.039	0.84
	Error		69		

able to the environment previously experienced by the mother on the source host. Thus, aphid performance depends mainly upon the chosen or available host plant.

Variation of aphid performance on different hosts is frequently interpreted in terms of differences in host plants phloem sap quality (Moran 1981; Sandström & Pettersson 1994; Dixon 1998).

Host quality can be defined as the plant's chemical or physical attributes affecting aphid individual fitness (Awmack & Leather 2002). *Brevicoryne campestris* possesses a higher concentration of glucosinolates (Kjaer 1976) and leaf nitrogen than *Br. oleraceae* (Leal-Aguilar et al. 2008). These differences between the 2 *Brassica* species may partly explain observed differences in aphid performance.

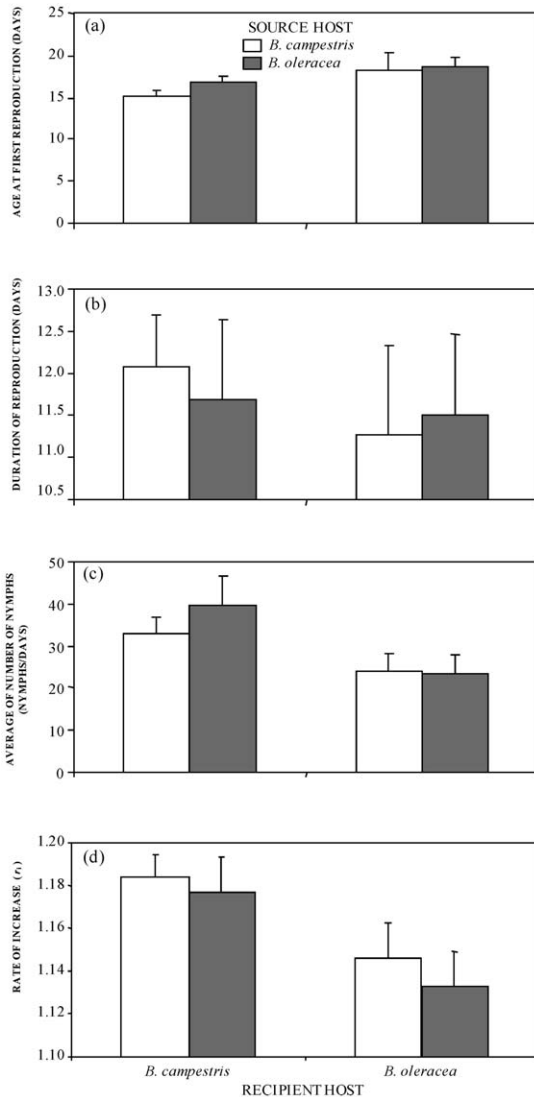


Fig. 3. Mean values of life history traits of *Brevicoryne brassicae* aphids grown for 2 generations on a source (maternal) host, and grown and measured at the third generation on the recipient host (experiment of maternal effects). (a) Age at first reproduction, (b) duration of reproduction, (c) average total number of nymphs, (d) rate of increase [r_1]. Bars are mean \pm 1SE.

On *Br. campestris*, the reproduction period is tightly linked to number of nymphs (fitness), whereas on *Br. oleracea*, duration of reproduction and, indirectly, age at first reproduction are related to fitness. The magnitude of directional selection (β) on life history traits detected in this study (range 0.109 to 0.256) is higher than the av-

erage magnitude estimated for plants and animals (0.08; Kingsolver et al. 2001), and is strong enough to promote both phenotypic differentiation and host specialization. However, the high gene flow between populations of *B. brassicae* associated with both hosts may limit differentiation of host related populations (Ruiz-Montoya et al. 2003).

The differences found between hosts in establishment, mean trait values, and selection on life history traits between recipients hosts (Table 3b) may suggest an initial stage of differentiation which could result in host race formation or host specialization in *B. brassicae*. The difference between hosts in the probability of aphid establishment is consistent with the expectation of local adaptation to the native host. If success in establishment is genetically correlated with fitness, further differentiation between host-associated populations may occur (Via 1991; Berlocher & Feder 2002; Drès & Mallet 2002). Our study offers a perspective on the role of selection and maternal effects in relation to host specialization in aphids. Yet, other potentially important factors in aphids like density dependence, predators, and parasitoids could play a role and need to be addressed in future studies. For instance, host plant biased predation and parasitoidism upon *B. brassicae* may prevent or even counter specialization.

Evidence of host specialization has been documented in the case of the aphid *Acyrtosiphum pisum* (Harris), (Homoptera: Aphididae) (Via 1991, 1999). In this species, it has been demonstrated that genetic correlations between resource use and mate choice (habitat acceptance) is the most parsimonious explanation for ecological specialization of *A. pisum* to their hosts (alfalfa and clover; Hawthorne & Via 2001). Since *B. brassicae* reproduces only by parthenogenesis in the highlands of Chiapas, this might limit further divergence between host associated populations of *B. brassicae*.

Clonal reproduction of *B. brassicae* and a high probability for an aphid to encounter different potential hosts could promote the evolution of phenotypic plasticity for resource use (Sultan & Spencer 2002). The evolution of host-specialization depends upon the type of environmental variation (fine- vs. coarse-grained; temporal vs. spatial), and the existence of genetic constraints (Via & Lande 1985; Fry 1996). Hence, various aspects of the *B. brassicae*-*Brassica* system warrant further study to test the Sultan and Spencer model (2002) in relation to the evolution of plasticity. First, at a fine scale, it is necessary to determine the existence of genetic constraints (trade-offs across host plants), reaction norms, and the extent of gene flow among aphid populations (i.e., between hosts; Ruiz-Montoya et al. 2003), which hypothetically could counteract the effect of local selection (Sultan & Spencer 2002).

TABLE 5. ANALYSIS OF SELECTION OF AGE AT FIRST REPRODUCTION AND DURATION OF *BREVICORYNE BRASSICAE* IN 2 HOST SPECIES AFTER 3 GENERATIONS (EXPERIMENT IN THE PRESENCE OF MATERNAL EFFECTS). A. STANDARDIZED COEFFICIENTS (β) FROM LINEAR REGRESSION REPRESENT DIRECTIONAL SELECTION GRADIENTS. B. ANALYSIS OF VARIANCE AND ADJUSTED R^2 FOR THE MULTIPLE REGRESSION MODEL.

-A-						
Recipient host	Character	Coefficient β (SE)		t	P	
<i>Brassica campestris</i>	Intercept	1.081 (0.096)		11.43	<0.0001	
	Age first reproduction	-0.067 (0.097)		-0.66	0.11	
	Duration of reproduction	0.343 (0.097)		3.52	0.001	
<i>Brassica oleraceae</i>	Intercept	1.000 (0.119)		8.39	<<0.001	
	Age first reproduction	-0.202 (0.134)		-1.51	0.14	
	Duration of reproduction	0.256 (0.134)		1.91	0.06	
-B-						
Recipient host	Source	SS	Df	F	P	r^2 adjusted
<i>Brassica campestris</i>	Model	5.331	2	6.718	0.003	0.21
	Error	15.868	40			
	Total	21.199	42			
<i>Brassica oleraceae</i>	Model	4.371	2	5.126	0.01	0.22
	Error	11.512	27			
	Total	15.883	29			

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