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Morphometric differences in the grasshopper *Cornops aquaticum* (Bruner, 1906) from South America and South Africa

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Abstract

The semi-aquatic grasshopper *Cornops aquaticum* is native to South America and inhabits lowlands from southern Mexico to Central Argentina and Uruguay. It is host-specific to aquatic plants in the genera *Eichhornia* and *Pontederia*. A quarantine population has existed in South Africa for 10 y, and it is planned to release it there as a biological control agent of water hyacinth, *E. crassipes*. Various studies of *C. aquaticum* are coordinated under HICWA (www.mpil-ploen.mpg.de). This paper compares the morphometry of the release population and 11 native populations in South America. We tested four hypotheses: 1) South African and South American populations of *C. aquaticum* differ in morphology; 2) the South African laboratory population is more similar to other isolated populations in South America than to nonisolated populations; 3) morphology differs across sites; 4) morphology differs with host plant. South African populations differed from continental nonisolated populations, but not from continental isolated ones. Isolated populations presented smaller individuals than nonisolated, but there was also a change in male morphology: while in nonisolated populations male wing length was similar to their body length, in isolated populations, male wings were smaller than body length. Females were larger when on *Eicchornia azurea* than on *E. crassipes*, while males presented larger wings than their body on *E. azurea*, and similar lengths on *E. crassipes*. These morphological changes may have resulted from phenotypic plasticity, selection for small size, or because of a loss of genetic diversity in quantitative traits..

Key words

geography, isolation, morphology, morphometrics, body size, wing, *Eichhornia*, *Pontederia*, water hyacinth, Neotropics

Introduction

The semi-aquatic grasshopper *Cornops aquaticum* (Bruner, 1906) is native to South America and inhabits lowlands from southern Mexico to Central Argentina and Uruguay (Adis *et al.* 2007). It is host- specific to aquatic plants in the genera *Eichhornia* and *Pontederia* (Adis & Junk 2003, Adis & Victoria 2001); however, different populations generally only have access to either *E. azurea* or *E. crassipes* (Silveira-Guido & Perkins 1975, Lhano *et al.* 2005, Ferreira & Vasconcelos-Neto 2001). Between 1996 and 1997, grasshoppers were collected from various South American sites and established in a quarantine laboratory in Pretoria, South Africa (Oberholzer & Hill 2001), for eventual release in South Africa as a biological control agent of water hyacinth, *E. crassipes* (Oberholzer & Hill 2001). Coevolution of the grasshopper and its host plant (Adis *et al.* 2004, Brede & Beebee 2005) is presently studied under the HICWA Project (Host-Insect Coevolution on Water Hyacinth), involving 10 countries (Argentina, Brazil, Colombia, France, Germany, Nicaragua, South Africa, Trinidad, United Kingdom and Uruguay), under the auspices of the Tropical Ecology Working Group of the Max Planck Institute for Limnology at Plön, Germany (www.mpil-ploen.mpg.de).

During our studies, we observed that body size in *C. aquaticum* appeared to vary with geography and host plant. In addition, we noticed that individuals in our laboratory colony appeared to have become increasingly smaller during 10 y in quarantine. Perhaps simple isolation stimulated this change in body size. If this were true, then we would expect the South African population to be more similar to other isolated populations than to nonisolated ones in South America. In this contribution, morphometric data obtained from 11 wild populations in South America and one 10-y-old laboratory population in South Africa are used to test the following hypotheses:

1. South African and South American populations of *C. aquaticum* differ in morphology.
2.The South African population is more similar to other isolated populations from South America than to nonisolated populations.
3. Morphology differs with geography.
4. Morphology differs with host plant (*E. azurea vs E. crassipes*).

Materials and methods

We collected 480 *C. aquaticum* from 11 sites in South America (see Table 1). The South African quarantine population at Pretoria represents a mixed population derived from Brazil, Mexico, Trini-

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Table 1a. Mean size (mm) of *C. aquaticum* from populations feeding on *E. crassipes* in South America and South Africa.

Country	Locality	Site	Coordinates	Sample	Number (n)		Total length [A]		Body length [B]		Wing length [I]	
					males	females	males	females	males	females	males	females
Argentina	Corrientes	Madrejón El Puente	27°26′S, 58°51′W	C	25	8	27.3 (1.22)	31.4 (1.22)	20.4 (1.02)	28.8 (0.53)	21.2 (0.98)	24.2 (1.16)
Argentina	Santa Fe	Rio Correntoso	31°41′S, 60°43′W	A	15	12	26.3 (1.47)	32.0 (1.58)	19.8 (0.65)	29.3 (0.99)	20.5 (1.20)	24.5 (1.07)
Argentina	Santa Fe	Rio Catarata	31°42′S, 60°45′W	B	11	18	26.6 (1.01)	32.3 (1.22)	20.1 (1.09)	28.2 (1.66)	20.5 (0.89)	25.0 (1.04)
Argentina	Santa Fe	Laguna El Puesto	31°43′S, 60°39′W	D	25	21	25.0 (1.29)	31.0 (1.59)	19.0 (0.85)	27.4 (1.90)	19.1 (1.07)	23.6 (1.37)
Brazil	Belém	City	15°26′S, 55°47′W	Q	40	40	24.1 (1.33)	30.0 (1.70)	19.9 (0.81)	26.4 (1.65)	18.0 (1.12)	22.6 (1.28)
Brazil	Manaus	Ilha de Marchantaria	03°14′S, 59°57′W	LM	20	26	26.5 (1.06)	30.6 (1.72)	20.9 (1.06)	27.3 (2.34)	19.9 (0.78)	22.7 (1.44)
Brazil	Pantanal	Fazenda Ipiranga	16°24′S, 56°37′W	GH	31	17	25.8 (0.94)	31.9 (1.77)	20.4 (0.86)	27.9 (1.29)	19.6 (0.80)	24.1 (1.59)
S. Africa	Pretoria	in captivity	25°43′S, 28°10′W	JK	18	19	23.8 (1.34)	28.9 (1.68)	20.1 (0.86)	26.1 (2.72)	18.2 (1.02)	21.8 (1.55)
Trinidad	Kernahan	Nariva Swamp	10°24′N, 61°03′W	xL	26	23	24.0 (1.06)	30.0 (1.37)	18.1 (1.06)	26.2 (1.43)	18.5 (0.97)	22.9 (1.19)
Uruguay	Piriapolis	Laguna del Sauce	34°50′S, 55°09′W	F	11	8	27.3 (1.57)	33.0 (2.18)	20.6 (1.07)	28.0 (1.50)	20.8 (1.15)	25.2 (2.84)

[ ] = measurements made *per* Carbonell (2001); ( ) = SD; [Brazil - Belém, S. Africa - Pretoria, Trinidad - Kernahan] = isolated populations.

Table 1b. Mean size (mm) of *C. aquaticum* from populations feeding on *E. azurea* in South America.

Country	Locality	Site	Coordinates	Sample	Number (n)		Total length [A]		Body length [B]		Wing length [I]	
					males	females	males	females	males	females	males	females
Argentina	Corrientes	Rio Paraná	27°29′S, 58°53′W	xM	32	9	28.1 (1.24)	33.0 (3.04)	20.4 (1.06)	30.2 (1.50)	22.0 (1.02)	26.3(1.22)
Argentina /Paraguay	Rio Paraguay	lower Rio Paraguay	27°15′S, 58°35′W	N	15	12	27.5 (0.80)	33.8 (2.14)	20.0 (1.08)	30.3 (2.81)	21.5 (0.64)	26.4 (1.74)

[ ] = measurements made *per* Carbonell (2001); ( ) = SD

dad and Venezuela (Hill & Oberholzer 2000). Populations from an agriculturally disturbed site in Trinidad, from within the city of Belém, and from S. Africa, represent geographically "isolated" populations (*cf*. Fig. 1). Total length, body length and wing length (as defined by Carbonell 2001) of adults (both sexes) were used as morphometric characters for data analysis (Fig. 2). The length of the hind femur, a valid character to define nymphal stages in *C. aquaticum* (Franceschini *et al.* 2005), was omitted, as adult specimens easily lose their hind legs when preserved in ≥70% ethanol.

Statistical analysis

To test Hypotheses 1, 3, and 4, we used univariate mixed-effects models (Crawley 2002a,b) to test statistically if morphology varied with geography and host plant (Manly 2000). We considered 'grasshopper individual' nested within 'sample' as random effects (Crawley 2002a) to avoid pseudoreplication (grasshopper individual) (Hurlbert 1984, Crawley 2002a), and to allow evaluation of the importance of variation among sampled sites (grasshopper populations) on morphometry (Buckley *et al.* 2003, Pinheiro & Bates 2000). Length was used as the response variable, while the corresponding morphological character (wing *vs* body length) was considered one of the explanatory factors, with two levels. Because total length included wing length (Fig. 2), these two measurements were statistically correlated. Therefore, we used only body length and wing length in the analyses, disregarding total length. Initially we adjusted a maximal model, and simplified it subsequently by deleting nonsignificant effects (Crawley 2002a). The fixed effects of the maximal tested model used to test Hypotheses 1 and 3, included gender, geography, morphological character (whether wing or body length) and their interaction terms. We used the interaction terms to test whether morphological characters responded differently to geography and gender. Geography was entered as a categorical variable with three levels: 'nonisolated', 'South Africa' and 'other isolated populations'.

To test hypotheses that the isolated S. African laboratory population is similar to other isolated, wild populations, but differs from nonisolated ones, we performed contrast analyses, pooling the geographical levels 'South Africa' with 'other isolated populations'. The use of contrasts instead of *a posteriori* comparisons allowed us to test explicit hypotheses with biological explanations.

We tested for the effect of random variation among grasshopper populations by deleting the random effect 'sample' from the minimal adequate model and noting the change in the log of the maximized restricted likelihood, as per Fox (2002). Significance of fixed effects was tested by deleting each explanatory variable from the model and noting the change in maximum likelihood (Crawley 2002a). Significance tests of fixed effects within the minimal model were shown as F-tests.

We tested the hypothesis that the variance of the isolated South African population is smaller than that of the nonisolated populations by using Fisher's F-test for each measured morphological character. We also tested the hypothesis that there are differences in grasshopper morphometry between host plants, by adjusting mixed-effects models with host plant, morphological character and their interaction terms as fixed effects. Because *C. aquaticum* grasshopper

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populations collected on *E. azurea* were all nonisolated, we compared them exclusively with other nonisolated populations using a subset of all available data (n = 319). All analyses were performed at a 5% significance level and assumed normal error distribution, (Fowler & Cohen 1996); they were performed with the statistical package R (R Development Core Team 2006).

Results

1. The inclusion of the sample site from which the grasshoppers were drawn as a random effect, increased significantly the amount of variation explained by the model (likelihood ratio = 86.58, $p < 0.0001$). This shows that there was random variation among grasshopper populations associated with a significant covariance within sites, *i.e.*, there were morphological differences among populations (Fig. 3), which must be considered in the mixed-effects model.

2. The pooling of the levels 'South Africa' with 'other isolated populations' did not reduce the variation explained by the fitted statistical model (likelihood ratio = 3.71, p = 0.45). This shows that there was no difference in the response between the geographical groups 'South Africa' and 'other isolated populations'. This allowed these two groups to be merged together as a third (named 'isolated populations').

3. The minimal adequate model (Table 2) presented highest order interactions of morphological characters with sex and geography. Wing length and body length did not respond in the same manner (Fig. 4). Females were always larger than males and always presented longer bodies than wings (Table 1, Fig. 4).

4. Both sexes were larger in nonisolated than in isolated populations (Fig. 4), but male and female morphology responded differently to geography. Females maintained similar morphological proportions in all populations, whereas males in isolated populations were not only smaller overall, but had smaller wing-to-body ratios (Fig. 4: Micropterous males).

5. The variance of morphological characters in the isolated S. African population did not differ from nonisolated populations (Table 3).

6. In the host-plant analyses, all interactions (morphological character, sex, and host plant) were significant (Table 4). Females that were collected on *E. azurea* were larger than those on *E. crassipes* (Fig. 5). In males, host plant influenced wing length, but not body length.

All four hypotheses are valid: morphology varies geographically, with degree of isolation, and with host plant. South African and South

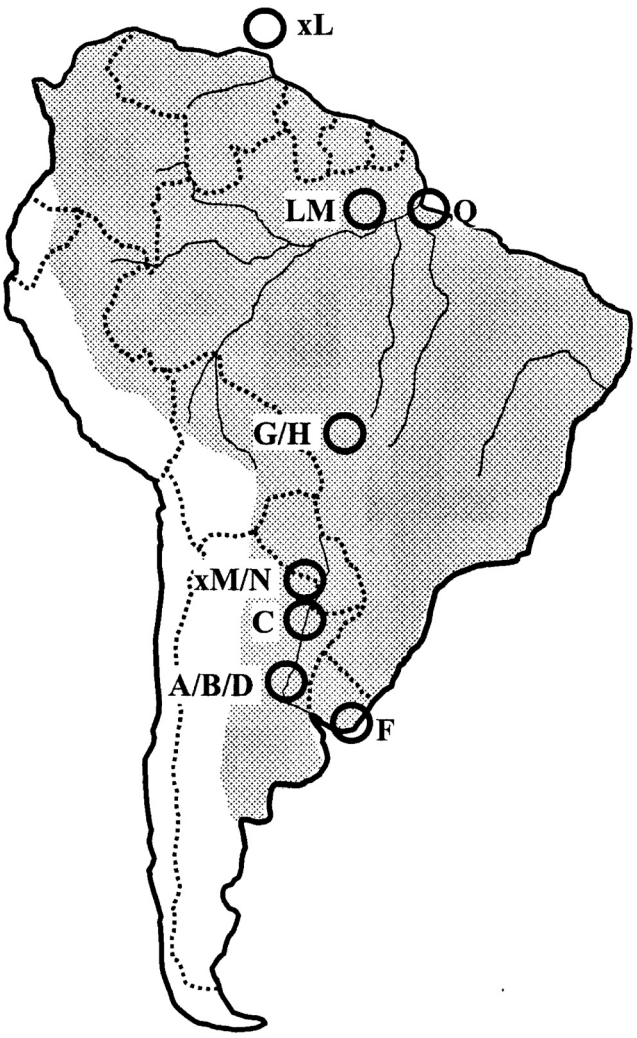


Fig. 1. Sampling locations and reference of *C. aquaticum* populations in South America. For location of populations see Table 1a/b. Shaded area indicates range of *C. aquaticum* in South America (according to Adis *et al.* 2007).

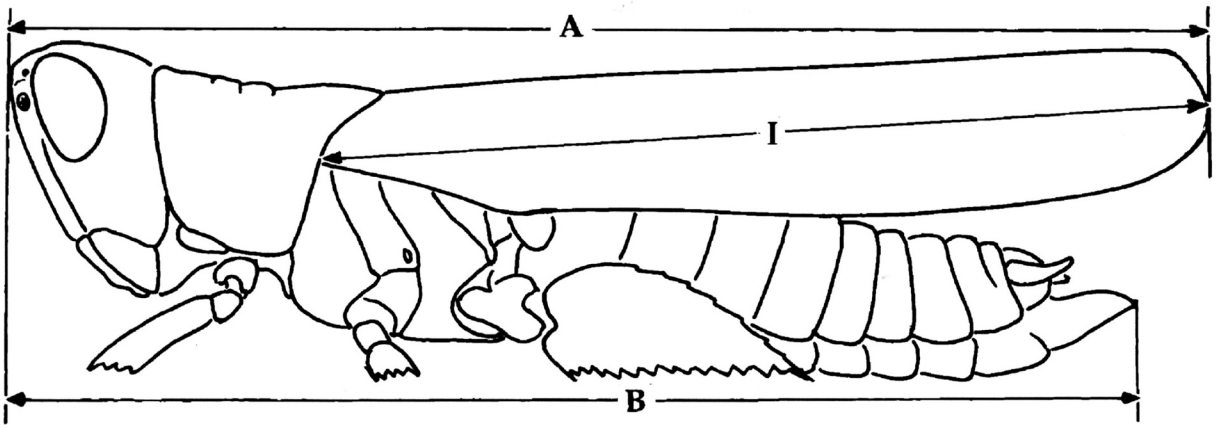


Fig. 2. Morphometric measurements on the grasshoppers, following Carbonell (2001). A: total length, I: wing length, B: body length (only undamaged specimens measured).

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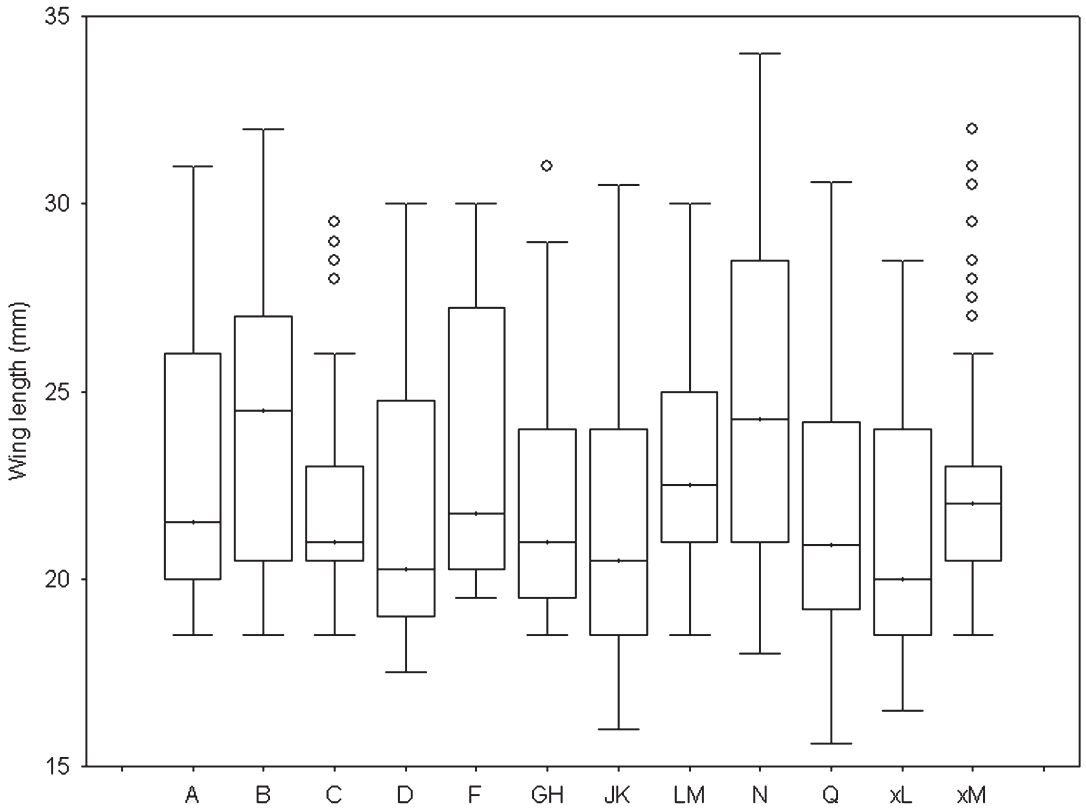


Fig. 3. Wing length (mm) of *C. aquaticum* among populations. "JK", "Q" and "xL" represent the isolated populations, "N" and "xM" the populations collected on *E. azurea*. All other populations were exclusively collected on *E. crassipes*. For location of samples see Table 1.

American populations differ in body size, with nonisolated South American grasshoppers being larger than the isolated populations (including the South African laboratory population). In addition, females maintain their morphological proportions irrespective of geographical situation and host plant, with those feeding on *E. azurea* being larger than those feeding on *E. crassipes*. In contrast, males alter the proportion of body to wing lengths according to geography and host plant. In isolated populations, male *C. aquaticum* change their morphology, with a greater proportional reduction in wing length in regard to their body size. Where males feed on *E. azurea* they present larger wings compared to those on *E. crassipes*, without altering their body length.

Table 2. Analysis of variance of the adjusted minimal mixed-effects model to explain length (mm) of *C. aquaticum* grasshoppers. Random effects were individuals (n = 480), nested within populations (n = 12). The factor Geography included nonisolated *vs* isolated populations; the South African population did not differ from the remaining isolated populations.

Source	numDF	denDF	F	P
Intercept	1	476	11577.76	<.0001
Morphological Character	1	476	601.73	<.0001
Sex	1	466	2592.83	<.0001
Geography	1	10	16.73	0.002
Morphol: Sex	1	476	638.74	<.0001
Morphol: Geog	1	476	18.11	0.0001
Sex: Geog	1	466	1.56	0.21
Morphol: Sex: Geog	1	476	15.12	0.0001

Fixed effects: Morphological character + Geography + Sex + Interaction terms. Random effects: individual grasshopper, nested within grasshopper population. Number of individual grasshoppers = 480, number of grasshopper populations = 12. numDF is numerator degrees of freedom; denDF is denominator degrees of freedom.

Discussion

In *C. aquaticum*, morphology varies with geography and host plant. This variation may be determined genetically or environmentally. The smaller overall size of *C. aquaticum* individuals in isolated populations may have resulted from selection for smaller size or due to a loss of genetic diversity in quantitative traits. A selective pressure for size reduction might be isolation *per se*, which can reduce the probability of far-dispersing individuals encountering mates, and hence, lower fitness for large individuals which might disperse further. This hypothesis is supported by the fact that island insects are often flightless and small (Diamond 1981, Roff 1994). Denno *et al.* (2002) tested a similar hypothesis but found no evidence that the low incidence of female macroptery in island populations of the delphicid planthopper *Toya venilia* was attributable to the effect of isolation.

Various hypotheses compete to explain the apparent reduction in body size of our South African laboratory colony. These include founder effect, inbreeding depression, outbreeding depression promoted by the heterogeneous composition of paternal lineages (Gerloff & Schmidt-Hempel 2005, Schaal & Leverich 2005), and selec-

Table 3. Results of independent Fisher's F-tests, comparing the variances of morphological characters between nonisolated South American and isolated South African grasshoppers.

Variable	F	N numerator	N denominator	critical F	P
♀ total	1.49	135	19	1.92	> 0.05
♂ total	1.32	179	18	7.95	> 0.05
♀ body	1.55	19	135	1.66	> 0.05
♂ body	1.63	18	179	1.66	> 0.05
♀ wing	1.52	135	19	1.92	> 0.05
♂ wing	1.80	179	18	1.95	> 0.05

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Table 4. Analysis of variance of the adjusted minimal mixed-effects model to evaluate if there were differences in *C. aquaticum* grasshoppers' morphology between the host plants *E. azurea* and *E. crassipes*.

Fixed-effect	numDF	denDF	F-value	P-value
Intercept	1	312	16230.87	<.0001
Host plant	1	7	5.32	0.054
Morphological Character	1	312	262.39	<.0001
Sex	1	312	1834.90	<.0001
Plant: Character	1	312	43.14	<.0001
Plant: Sex	1	312	22.68	<.0001
Character: Sex	1	312	447.23	<.0001
Plant:Character: Sex	1	312	16.77	0.0001

Fixed effects: Morphological character + host plant + sex + interaction terms. Random effects: individual grasshopper, nested within grasshopper population. Number of individual grasshoppers = 319, number of grasshopper populations = 9. numDF is numerator degrees of freedom; denDF is denominator degrees of freedom.

tion for small size. Continuous laboratory breeding may select for small, fast-breeding genotypes that can produce more generations per unit time than larger individuals. Isolation *per se* may also have influenced body size (Peer & Taborskyi 2005). Populations that are isolated for several generations may have lost genes for larger size because of inbreeding depression (Futuyma 1986, Eldrige *et al.* 2004) or genetic drift (Futuyma 1986, Escobar *et al.* 2005).

In contrast, our results might be explained by phenotypic plasticity. In some locusts, morphology is plastic and determined by population density (phase transformation) (Uvarov 1966, Sword & Simpson 2000, Simpson *et al.* 2001, Babah & Sword 2004). In this study, however, there is no straightforward relationship between population density and isolation. Isolated populations might be spatially constrained and densely packed, as could be the case for the Belém city *C. aquaticum* population, but could also have plenty of empty surrounding habitat, as in the low-density South African laboratory population, which has been maintained at a population size of ~ 100 individuals.

Our results indicate that geography and host plant influence body size more in males than in females. The smaller flexibility in female morphology may reflect developmental-reproductive constraints. Females may increase their individual fitness through a positive correlation between fecundity and body size (but see Barker *et al.* 2005). However, if a female has a minimum size requirement for successful production of oocytes, this could result in a lower level of resource being available for development of other morphological characters. Alternative explanations for differences in male-female morphological response might be differential linkage of certain genes influencing morphology, or the need for males to invest in large wings if they are the dispersing sex. Finally, adult size is frequently associated with nymphal developmental conditions, whereby well-fed larvae produce larger adults (Price 1997). If nymphal conditions are involved in the observed responses, this may mean that isolation, geography, and poor quality of host plants (*i.e.*, *E. crassipes*) might be responsible for less favorable conditions.

Conclusions

1. Morphology of *C. aquaticum* varies with sex, geography, host plant, and isolation.

2. Sex interacts with geography and with host plant to influence body size.

3. The smaller wings in isolated populations are in accordance with observations in other organisms. Several taxa have lost their

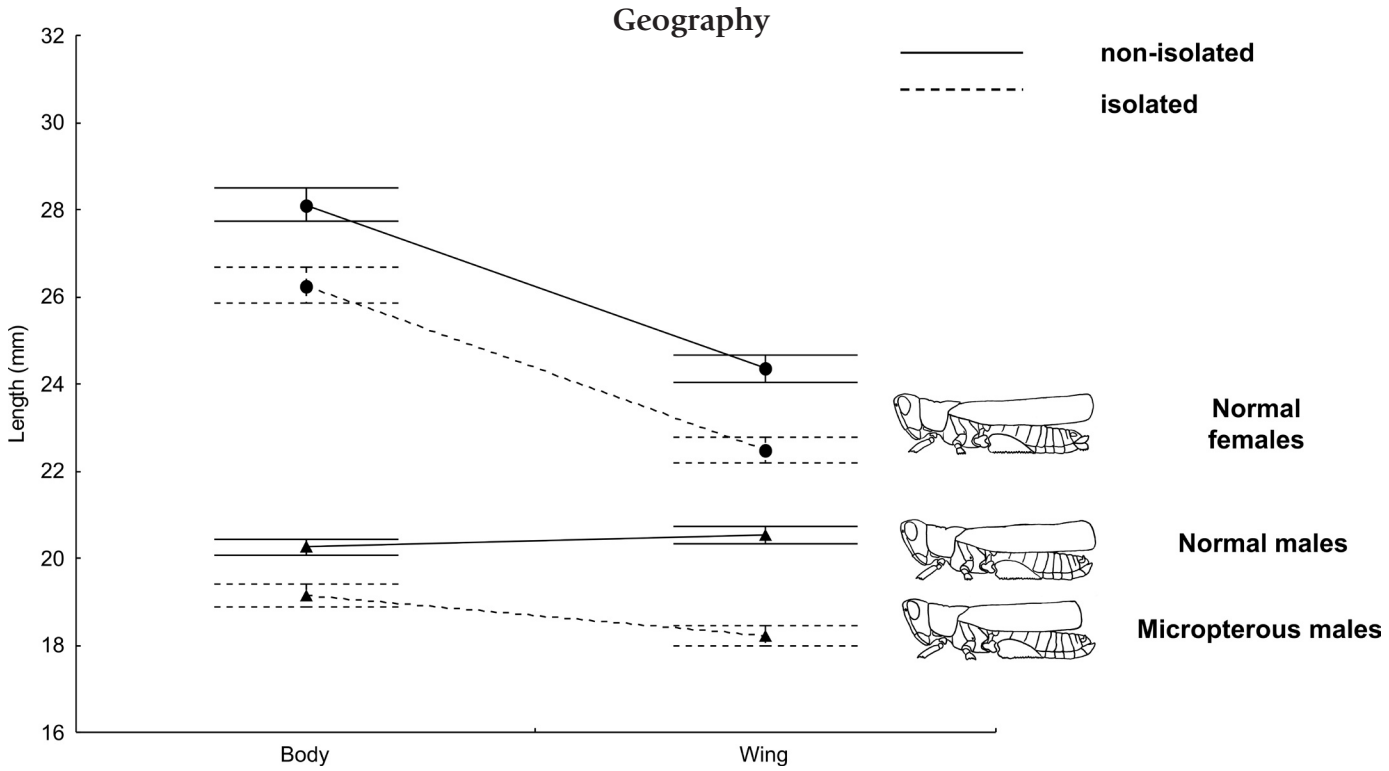


Fig. 4. Average *C. aquaticum* dimensions with 95% confidence interval bars, showing the interactions of morphology, sex and geography. Continuous lines: nonisolated populations; dashed lines: isolated populations. All interactions significant ($p < 0.05$), as in Table 2.

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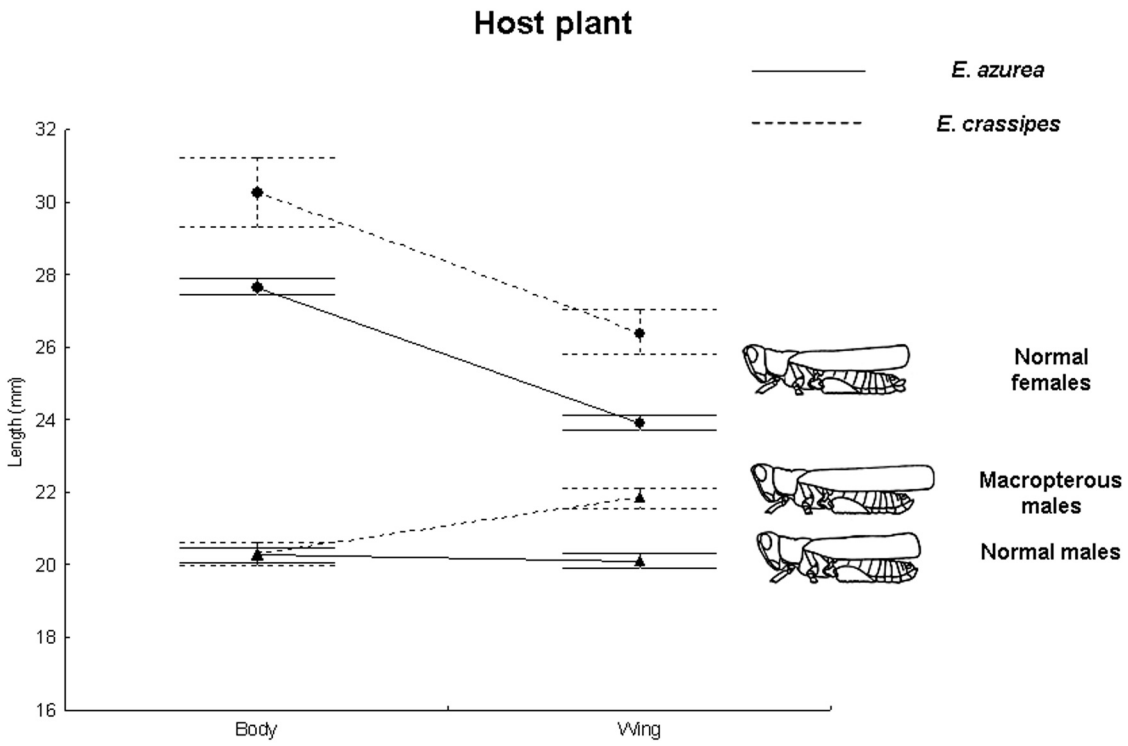


Fig. 5. Average ± 95% confidence interval of *C. aquaticum* grasshopper lengths (mm) from nonisolated populations, comparing two host plants: *E. azurea* (dashed lines) and *E. crassipes* (continuous lines). All interactions were significant (Table 4).

wings on islands compared to their continental sister groups (Diamond 1981, Roff 1994).

4. Body size in our *C. aquaticum* laboratory colony is smaller than that in the wild S. American source populations.

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