

**SPATIAL AUTOCORRELATION OF MORPHOMETRIC
VARIATION IN *Lutosa brasiliensis* (BRUNNER VON WATTENWYL,
1888) (ORTHOPTERA: GRYLLACRIDOIDEA: HENICIDAE)**

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ABSTRACT

Geographic differentiation and sexual dimorphism in eighteen morphometric characters of *Lutosa brasiliensis* (Orthoptera: Henicidae) collected in eight localities of the State of São Paulo (Brazil) were analysed. A two-way Multivariate Analysis of Variance (MONOVA) was used to assess simultaneously the effects of sex and geographic location (plus their interaction) on morphometric variability. The spatial patterns of variation were analysed by Factor and Spatial Autocorrelation Analyses (Moran's I coefficient in four distance classes). Both indicate that the main direction of variation is, for males and females, a north-south cline in overall body size. In females, however, ovipositor length is not correlated with overall body size and displays a different pattern of variation over geographic space, indicating that distinct evolutionary forces produced the geographic differentiation in the species.

INTRODUCTION

Henicidae is a small family of Gryllacridoidea which is composed of thirty-six genera described from throughout the world (Karny, 1937). Only two of these are found in Brasil: *Lutosa* Walker, 1869 and *Apotetamenus* Brunner v.W., 1888 (Levada, 1986). Like almost all Gryllacridoidea, the species of Henicidae are poorly known, which is usually attributed to their furtive habits (Levada, 1986). They are wingless and live burrowed in the ground most of the day, being active only at night (Rentz and Weissman, 1973).

The genus *Lutosa* is composed of several species (most of them still undescribed) which occur in southeastern Brazil (Levada and Diniz-Filho, in press). Levada (1986) did a taxonomic review of the Henicidae from Neotropical regions and detected a great amount of morphometric interpopulational variation in *L. brasiliensis* Brunner von Wattenwyl, 1888. This variation, however, was not analysed quantitatively.

Knowledge about geographic variation in morphological characters in Gryllacridoidea seems to be restricted to some species of Rhaphidophoridae from North America (Eades, 1964; Hubbell and Norton, 1978) and Italy (La Grega, 1961). These studies, however, were aimed to define infraspecific taxonomic categories in these species and did not analyse the evolutionary implications of geographic differentiation (Hubbell, 1956). In this context, population structure at the genetic level has recently been analysed by Cockley *et al.* (1977) and Sbordoni *et al.* (1981). However, nothing has been done in Henicidae, especially in Neotropical species.

This paper deals with multivariate morphometric analysis of geographic variation and sexual dimorphism in *L. brasiliensis*. The patterns of spatial variation for both sexes were analysed by spatial autocorrelation analysis, following the methodology proposed by Sokal and Oden (1978a,b) e Sokal (1986). With these techniques, three basic questions are addressed: 1) is there geographic differentiation in *L. brasiliensis*?; 2) is this differentiation randomly distributed in geographic space?; 3) what evolutionary processes could be involved in this differentiation?

MATERIAL AND METHODS

Material

One hundred and thirty males and females of *L. brasiliensis* were collected in eight localities of the State of São Paulo (Brazil) (Figure 1). Sample size and geographic position for each locality are given in Table I. Eighteen morphometric measurements for females and seventeen for males were made on each adult insect, which together with a short identification code, are described as follows: 1. greatest eye length (EYEL); 2. greatest eye width (EYEW); 3. interocular distance (INTE); 4. mandibular width measured in facial aspect (MANW); 5. distance from antennal alveolum to clipeus (DACL); 6. clipeus length (CLIP); 7. labrum length (LABL); 8. labrum width (LABW); 9. length of the last segment of maxillary palp (PAL1); 10. length of the last segment of labial palp (PAL2); 11. pronotum length (PRNL); 12. pronotum width (PRNW); 13. hind femur length (HFEL); 14. greatest hind femur width (HFEW); 15. hind tibia length (HTIB); 16. length of inner terminal spine in hind tibia (SPIN); 17. ovipositor length (in females) (OVIP); 18. length of subgenital plate (SGPL).

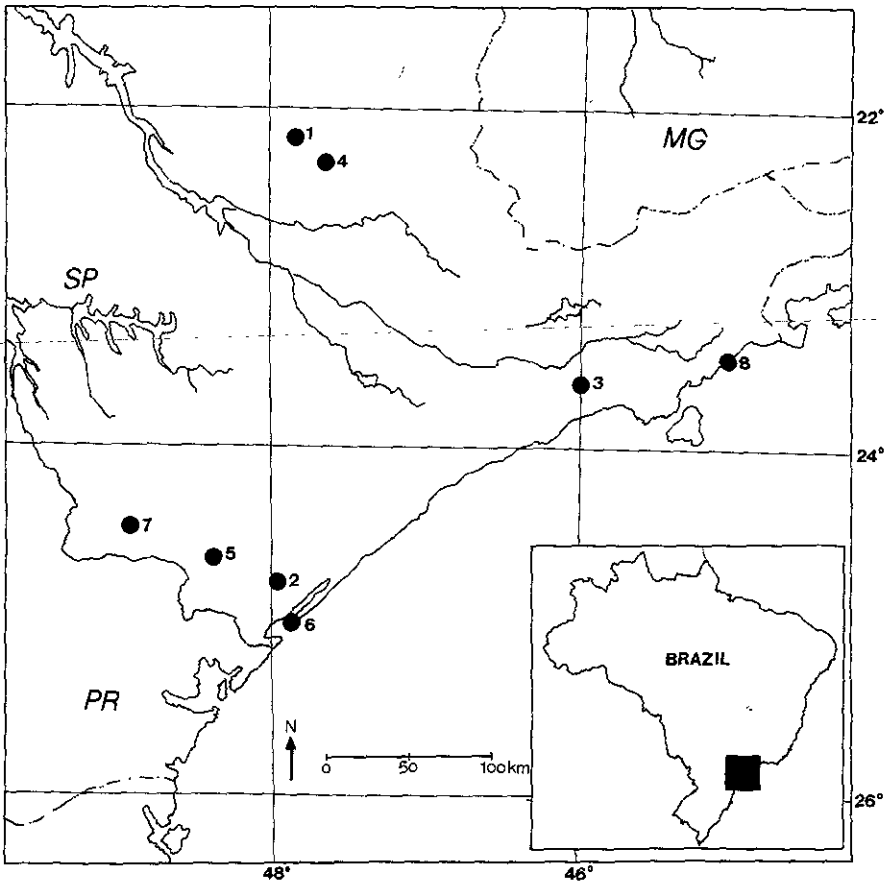


Figure 1 - Geographic position of the localities analysed.

These characters were measured with a micrometric ocular coupled to a stereomicroscope and transformed to decimal logarithms prior to analysis (Neff and Marcus, 1980). All individuals examined are deposited in the collection of the Departamento de Biologia, Instituto de Biociências, UNESP/Rio Claro.

Statistical procedures

The general patterns of statistical analyses are as follows. A two-way Multivariate Analysis of Variance (MANOVA) (Morrison, 1976) was used to assess

Table I - Geographic position and sample size for males and females in each locality analysed.

| Localities | Longitude | Latitude | Males | Females |
|-----------------|-----------|----------|-------|---------|
| 1. Corumbataí | 47°35'W | 22°14'S | 05 | 11 |
| 2. Jacupiranga | 48°00'W | 24°41'S | 09 | 17 |
| 3. Salesópolis | 46°05'W | 23°40'S | 20 | 18 |
| 4. Rio Claro | 47°33'W | 22°24'S | 06 | 08 |
| 5. Eldorado | 48°25'W | 24°38'S | 03 | 03 |
| 6. Cardoso Isl. | 47°57'W | 25°00'S | 02 | 08 |
| 7. Apiaí | 48°50'W | 24°30'S | 06 | 09 |
| 8. Ubatuba | 45°05'W | 23°25'S | 02 | 03 |

simultaneously the effects of sex (SEX) and geographic location (LOC), and their interaction (SEX*LOC), on the morphometric variability of *L. brasiliensis* (Neff and Marcus, 1980).

The mean values for each character in the localities were submitted to a Multiple Factor Analysis (Morrison, 1976). Factors with eigenvalues greater than one were extracted and subsequently rotated using Varimax solution (Harris, 1975). The most important character in each Factor was mapped.

Spatial autocorrelation summarizes the relationship between values for the same variable as a function of the distances between localities (Barbujani and Pigliucci, 1989). Inferences on the causal processes can sometimes be performed based upon spatial autocorrelation structure of several variables (Sokal and Oden, 1978a,b; Sokal *et al.*, 1986; Sokal, 1986).

An 8 x 8 matrix of topographic distances between pairs of localities (W) was constructed. The pairs of localities were then grouped in 4 distance classes: 0-100, 100-265, 265-290, 290-400 Km. For each character and for each class, Moran's I spatial autocorrelation coefficients (Cliff and Ord, 1973) were calculated, producing spatial correlograms (Sokal and Oden, 1978a,b). Moran's I is defined as

$$I = (n/K) [(\sum_i \sum_j Z_i Z_j W_{ij}) / \sum_i Z_i^2]$$

where n is the number of localities sampled, K is the sum of weights in the spatial relationship matrix W and Z is the variable analysed centered by the mean.

The values of Moran's I range from +1.0 to -1.0, and the expected value under the null hypothesis (absence of spatial autocorrelation) is $-(n-1)^{-1}$. Details of computation,

as well as standard errors of spatial autocorrelation coefficients, are furnished in Cliff and Ord (1973) and in Sokal and Oden (1978a). Considering the small number of localities sampled, the statistical significance of Moran's I was established using a randomization approach, based upon the Mantel test, as suggested by Hubert *et al.* (1981). Bonferroni criterion was used to establish the significance of the correlogram as a whole (Oden, 1984).

The similarity of spatial patterns (correlograms) for various characters was evaluated by constructing a matrix of Manhattan distances (Sneath and Sokal, 1973), non-significant correlograms excluding (Sokal, 1986). This matrix was compared with the correlation matrix between pairs of characters (surfaces) (Sokal, 1986). These matrices were also analysed by UPGMA (unweighted pair-group method - arithmetic average) clustering (Sneath and Sokal, 1973).

All statistical analyses were performed using a PC/AT microcomputer. Multivariate Analysis of Variance and Factor Analysis were performed using SAS-PC (SAS Institute Inc., 1988). Manhattan distances, UPGMA clustering and matrix correlations were done with the Numerical Taxonomy and Multivariate Analysis System (NTSYS-PC) (Rohlf, 1989). Spatial correlograms were obtained using the program IMCE (Diniz-Filho, 1991), written in Basic language and available from the author upon request.

RESULTS

In Table II are given the results of the two-way MANOVA. The F values, derived from Wilks' Lambda, indicate that there are significant differences ($P < 0.01$) among localities (geographic variation) and between sexes (sexual dimorphism). There is also an interaction between these two factors, which indicates that the amount and direction of sexual dimorphism are not the same in all localities (Neff and Marcus, 1980). Therefore, geographic differences in the intensity of sexual dimorphism are evident. Considering this, spatial pattern analysis was performed independently for each sex.

Table II - Results of the two-way MANOVA for testing effects of sex, locality and their interaction.

| Source of variation | Wilks' Lambda | F | D.F. |
|---------------------|---------------|----------|----------|
| Sex | 0.494 | 6.344** | 16, 99 |
| Locality | 0.001 | 11.335** | 112, 649 |
| Sex x Locality | 0.052 | 3.372** | 112, 649 |

** - $P < 0.01$.

The results of Factor Analysis, for males and females, can be seen in Table III and Table IV. For males, only one factor was extracted, which explains 93.3% of the variability in the data matrix. The communalities are all higher than 77%. Considering that this factor has all loads with high values and of the same signal, it can be interpreted as a general body size factor. The map of the character HFEW (Figure 2), which possesses the highest load for this factor, shows a north-south cline.

Table III - Factor Loads of Factor I (Varimax rotated) and Communalities, for males.

| Characters | I | Communalities (%) |
|------------|-------|-------------------|
| EYEL | 0.951 | 90.4 |
| EYEW | 0.961 | 92.3 |
| INTE | 0.974 | 94.8 |
| MANW | 0.983 | 96.7 |
| DACL | 0.971 | 94.3 |
| CLIP | 0.898 | 80.6 |
| LABL | 0.968 | 93.7 |
| LABW | 0.941 | 88.6 |
| PAL1 | 0.989 | 97.8 |
| PAL2 | 0.982 | 96.5 |
| PRNL | 0.991 | 98.3 |
| PRNW | 0.993 | 98.7 |
| HFEL | 0.972 | 94.5 |
| HFEW | 0.994 | 98.7 |
| HTIB | 0.984 | 96.9 |
| SPIN | 0.983 | 96.6 |
| OVIP | - | - |
| SGPL | 0.877 | 77.0 |

For females, three factors were extracted, which explain 92.0% of the variability of the data matrix. Factor I can be interpreted as general body size factor, Factor II possesses higher loads for characters related to the bucal apparatus and Factor III has high loads for OVIP and SGPL. The maps of the characters PAL1, CLIP and OVIP, with higher loads for these three factors, are shown in Figure 3. The character PAL1, related to the general size factor (Factor I), shows a north-south cline, as in males. The other characters do not show a clear spatial pattern.

Table IV - Factor Loads (Varimax rotated) and Communalities for females.

| Characters | I | II | III | Communalities (%) |
|------------|--------|-------|--------|-------------------|
| EYEL | 0.888 | 0.339 | -0.209 | 94.7 |
| EYEW | 0.772 | 0.568 | -0.175 | 94.9 |
| INTE | 0.698 | 0.379 | 0.468 | 84.9 |
| MANW | 0.521 | 0.640 | 0.496 | 92.7 |
| DACL | 0.861 | 0.230 | 0.325 | 90.0 |
| CLIP | 0.402 | 0.875 | -0.071 | 93.2 |
| LABEL | -0.373 | 0.832 | 0.199 | 87.0 |
| LABW | 0.263 | 0.851 | 0.329 | 90.2 |
| PAL1 | 0.944 | 0.307 | -0.023 | 98.6 |
| PAL2 | 0.901 | 0.425 | 0.073 | 99.8 |
| PRNL | 0.698 | 0.565 | 0.383 | 95.5 |
| PRNW | 0.656 | 0.652 | 0.172 | 88.5 |
| HFEL | 0.925 | 0.356 | 0.122 | 99.7 |
| HFEW | 0.808 | 0.537 | 0.131 | 95.5 |
| HTIB | 0.934 | 0.332 | 0.085 | 98.9 |
| SPIN | 0.744 | 0.527 | 0.320 | 93.4 |
| OVIP | -0.171 | 0.050 | 0.908 | 85.6 |
| SGPL | 0.496 | 0.440 | 0.632 | 82.8 |

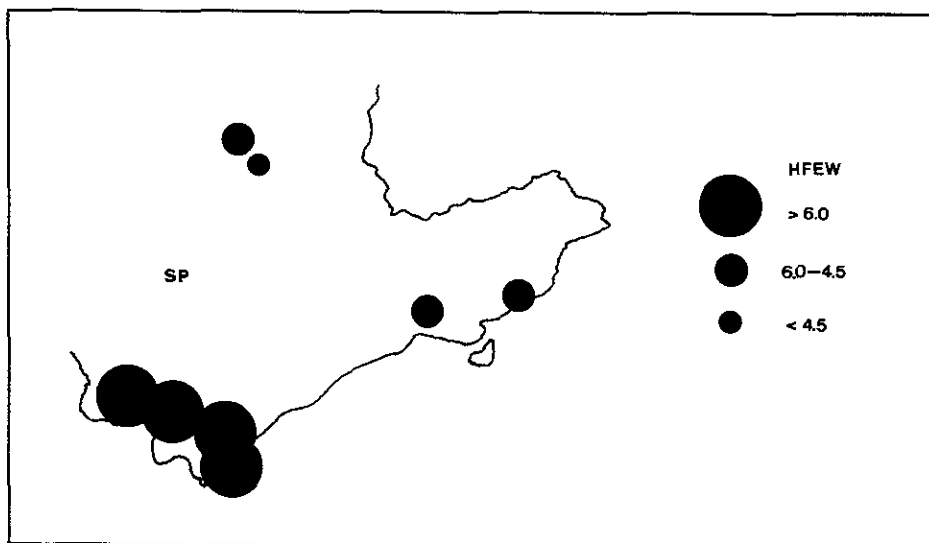


Figure 2 - Variation for character HFEW in males over geographic space (in milimeters).

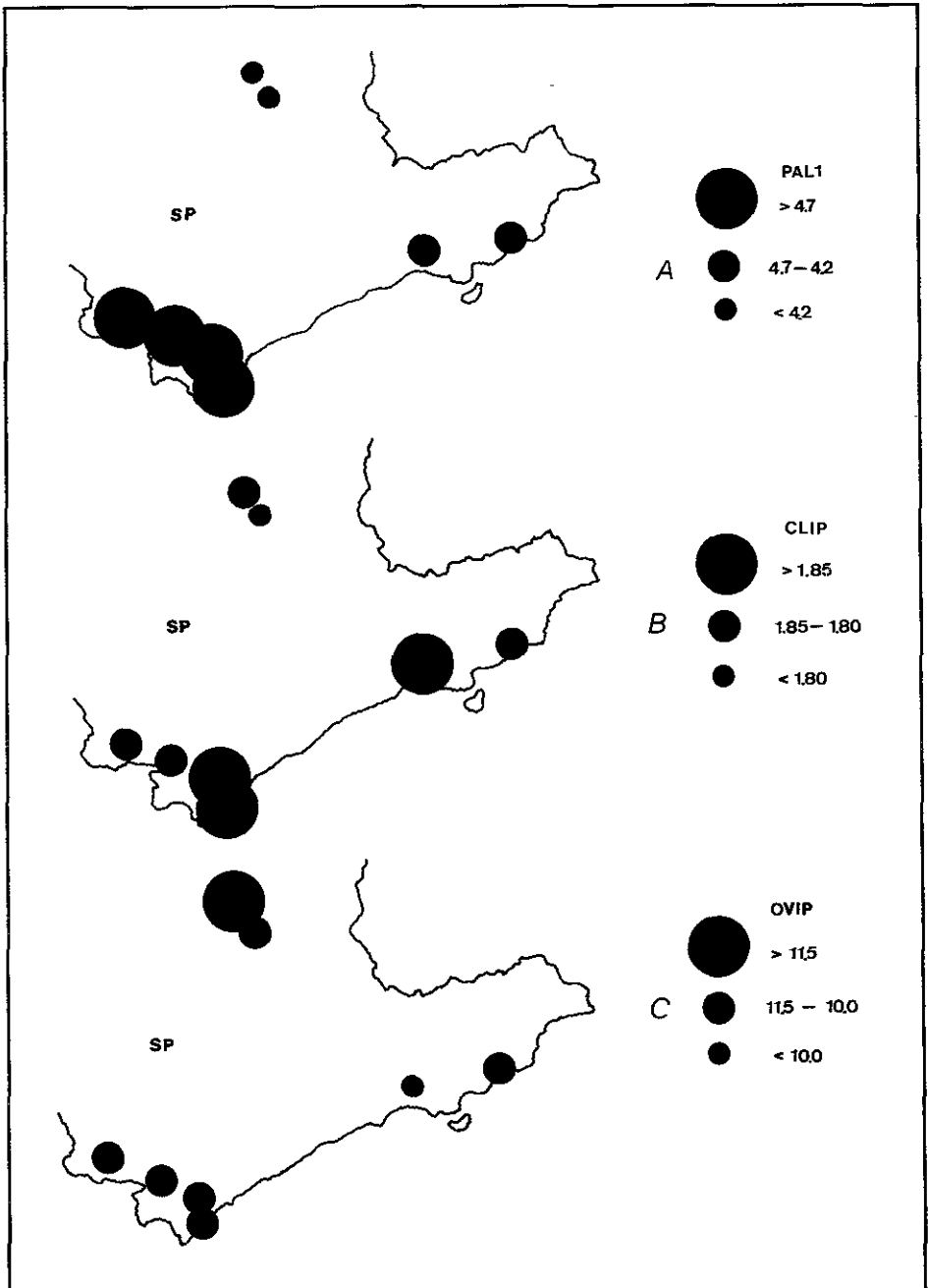


Figure 3 - Variation for three characters in females over geographic space (in millimeters).

Of 68 possible Moran's I coefficients for males (17 characters x 4 distance classes), 25 are significant at the 5% level. Using Bonferroni criteria, two characters (CLIP and SGPL) were singled out. The correlograms obtained can be seen in Figure 4. All show positive autocorrelations in the first distance class, followed by a decrease in the values of Moran's I up to the third distance class. Some characters show negatively significant autocorrelations in the third and fourth classes. The correlograms for males are all highly similar, and the comparison of Manhattan distances among them with correlations among surfaces (= characters) shows that similar correlograms tend to have correlated surfaces ($r = -0.59$).

For females, of 72 possible Moran's I coefficients (18 characters x 4 distances classes), 16 are significant at the 5% level. Bonferroni criteria singled out eight characters (EYEL, EYEW, MANW, CLIP, LABL, LABW, PRNW, SGPL). Characters related to Factor I show correlograms similar to those obtained for males (clines up to the third distance class) (Figure 5). Characters related to Factor II do not show significant correlograms based on Bonferroni criteria, and the character OVIP, which possesses the highest load for Factor III, shows a very distinct correlogram, with a significant negative autocorrelation for the second distance class (Figure 5). These aspects indicate correspondence between Factor and Spatial Autocorrelation analysis. The comparison of Manhattan distances among correlograms with correlations among surfaces also shows that similar correlograms tend to have correlated surfaces ($r = -0.91$).

DISCUSSION

The results show that there is a marked geographic differentiation in *L. brasiliensis*. There is a north-south cline in overall body size, as defined by Factor and Spatial Autocorrelation analyses. For females, there are other directions of variation, related to some characters of the bucal apparatus and ovipositor.

Causal explanations for geographic variation can usually be advanced when the evidence comes from genetic variables, such as gene frequencies. With morphometric characters, however, there are some problems related to the absence of knowledge about the proportion of genetic and environmental components in the morphometric variation (Gould and Johnston, 1972; Atchley, 1983). However, based on spatial autocorrelation analysis, some discussions about causal explanations are possible (Sokal and Wartenberg, 1981; Sokal, 1986).

Positive spatial autocorrelation in the short distance classes, as found in *L. brasiliensis*, can be interpreted in two basic ways: 1) selective agents patterned over the geographic space, which in distances greater than mean interlocality distances or: 2) there is migration among localities (Sokal and Oden, 1978b). Considering that there are also some negative spatial autocorrelations in the long distances classes, the correlograms

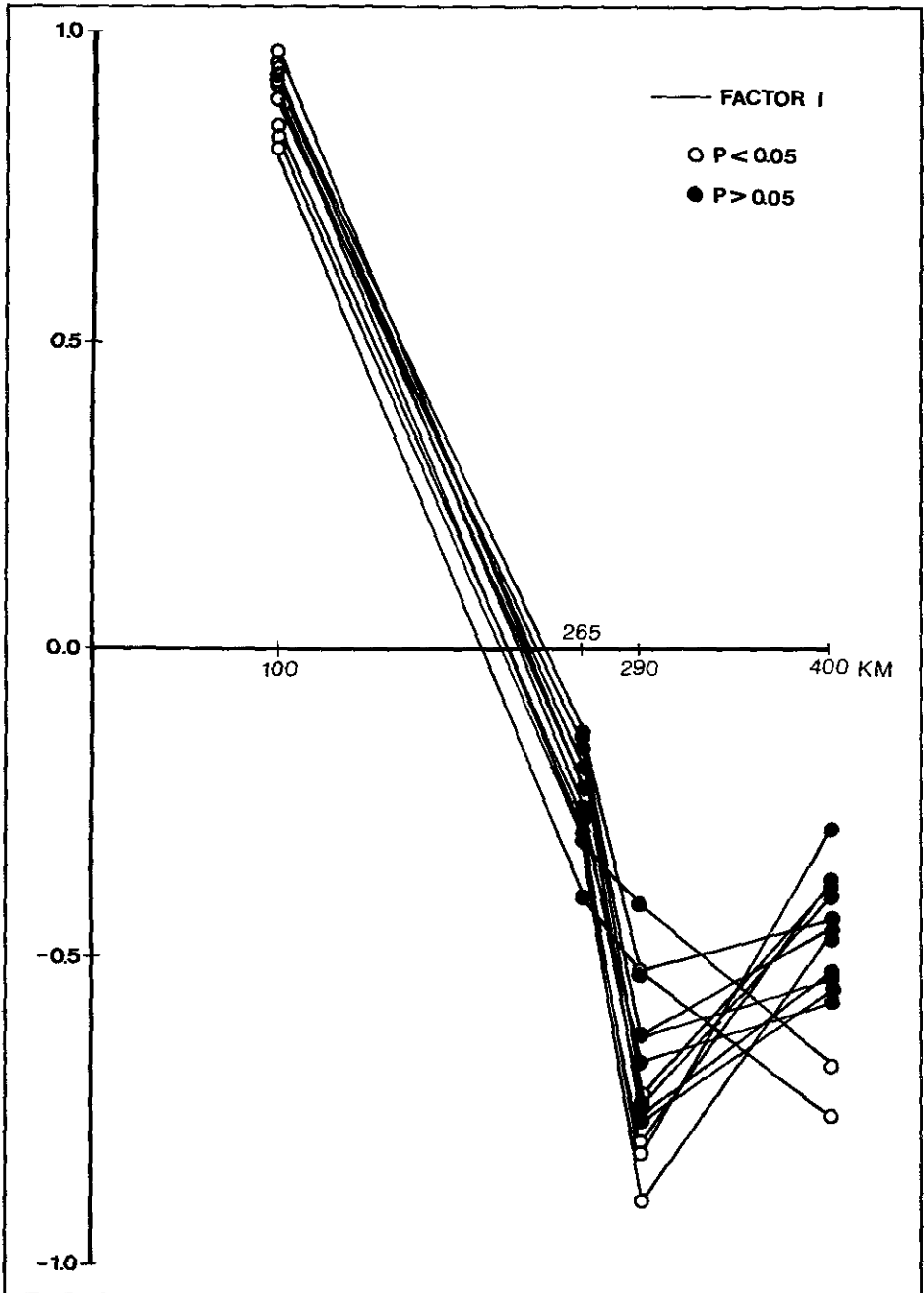


Figure 4 - Significant spatial correlograms for males.

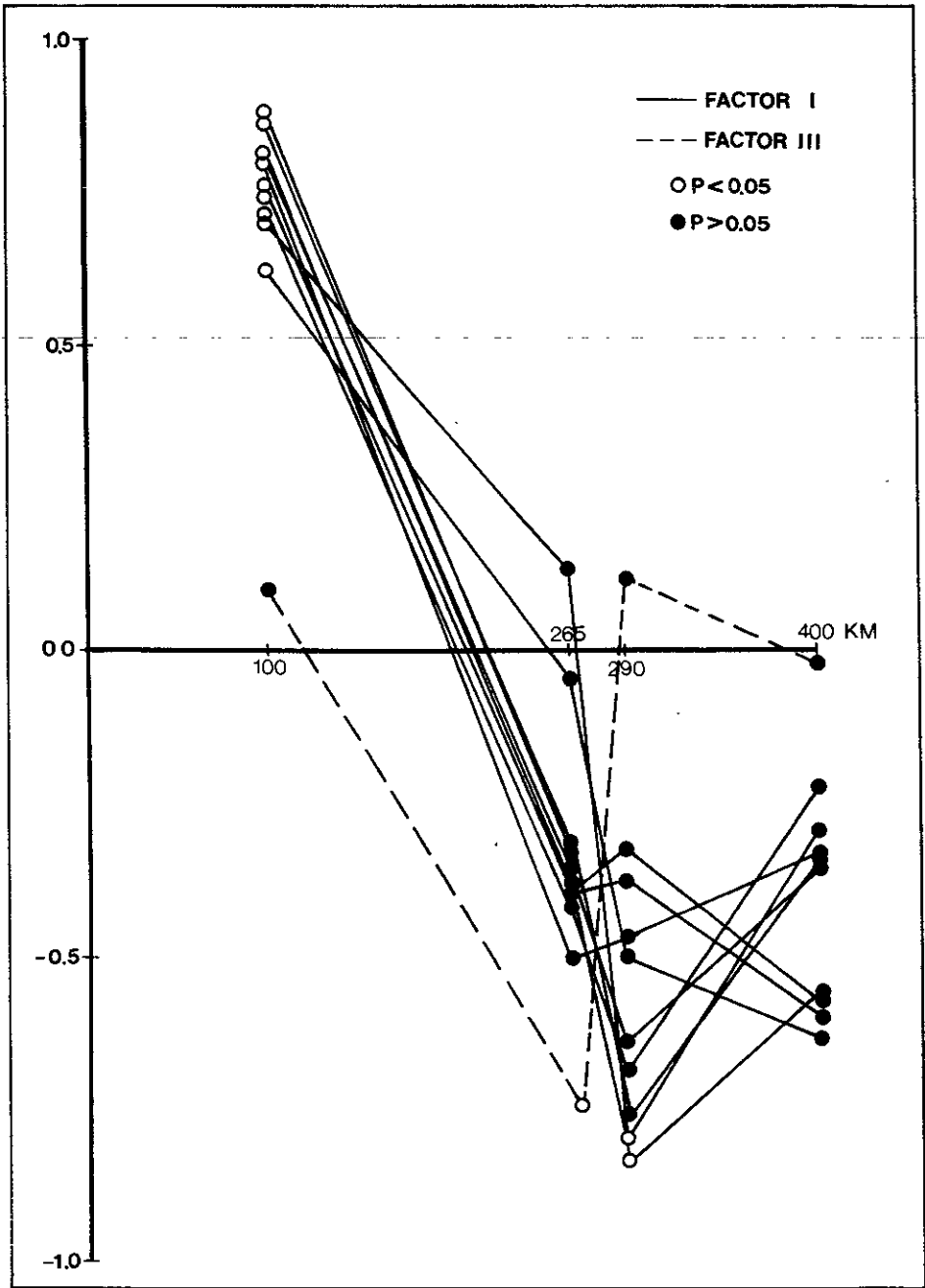


Figure 5 - Significant spatial correlograms for females.

indicate gradients and, indirectly, the action of natural selection. It is also important to remember that the low dispersion of *L. brasiliensis* (recall that they are wingless) should restrict migration among localities.

Characters related to overall body size show a north-south cline, which is common in insects (Daly, 1985). In some groups of Orthoptera (Grylloidea), these clines can be attributed to genetic adaptation to local climatic conditions (Masaki, 1967, 1978; Mousseau and Roff, 1989). Indeed, clinal variation patterns are frequently attributed to the action of natural selection and, hence, are presumed to reflect genetic adaptation of populations to local conditions (Mousseau and Roff, 1989). However, since natural selection acts upon phenotypic variation, and since a given genotype may express a variety of phenotypes depending upon its norms of reaction, adaptative variation among different environments may reflect phenotypic plasticity or genetic differentiation of populations (Via and Lande, 1985; Mousseau and Roff, 1989). So, if we eliminate an effect of phenotypic plasticity, there are indirect evidences for the action of natural selection affecting overall body size in *L. brasiliensis*. However, further investigation as to the environmental factors influencing this variation and concerning the genetic basis of the morphometric characters should be performed in order to reach a more exactly causal explanation for geographic variation in these characters.

In females, the characters related to Factor II present spatial heterogeneity of means, but no spatial pattern (Diniz-Filho, 1991). Following Sokal and Oden (1978b), this combination can be basically interpreted in two ways: 1) there are selective agents, patterned as patches in the geographic space, but acting on distances smaller than the mean interlocality distances or; 2) genetic drift determines the variation. The choice between these two hypothesis is not easy with morphometric characters, considering the absence of information about the values of genetic correlations among them (Atchley, 1983). The analysis of other morphometric and morphological characters should produce other independent axes of variation, and the comparison of patterns in these new axes with the patterns in Factor II should make possible the choice between these two hypotheses. If these axes provide similar correlograms and, like all axes in Varimax rotated Factor Analysis, are orthogonal, then the drift hypothesis would be more adequate (Sokal and wartenberg, 1981, 1983; Sokal, 1986).

It is possible to conclude that *L. brasiliensis* presents a very strong cline for overall body size, with increasing values from north to south, which can be attributed to local adaptation to climatic variation, assuming that an effect of phenotypic plasticity can be ruled out. However, there is another important direction of morphometric variation (ovipositor length), indicating that distinct evolutionary forces are responsible for the geographic differentiation in the species.

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RESUMO

Neste trabalho foram analisados os padrões de diferenciação geográfica e dimorfismo sexual em 18 caracteres morfométricos de *Lutosa brasiliensis* (Orthoptera: Hecanidae), coletados em oito populações do Estado de São Paulo (Brasil). Uma Análise de Variância Multidimensional (MANOVA) bifatorial permitiu avaliar simultaneamente o efeito do sexo e da posição geográfica dos indivíduos (mais sua interação) sobre a variabilidade morfométrica. Os padrões espaciais de variação, analisados através de Análises Fatoriais e de Autocorrelação Espacial, permitem concluir que a principal direção de variação morfométrica interpopulacional nesta espécie é um gradiente, com valores crescentes no sentido norte-sul, para os caracteres de tamanho geral do corpo. Nas fêmeas, entretanto, o comprimento do ovipositor está pouco correlacionado ao tamanho do corpo e possui um padrão espacial de variação distinto.

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