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CHROMOSOMAL POLYMORPHISM IN URBAN *Drosophila willistoni*[*]

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ABSTRACT

Urban populations of the wild species *Drosophila willistoni* were compared for chromosomal polymorphism. Populations were found to be less polymorphic for chromosome inversions nearer urban centers. Inversion IIL$_E$ showed higher frequencies associated with greater vegetation-cover. Frequency of chromosome arm inversions IIL, IIR and III however did not correlate with the degree of urbanization. More variation in inversion frequencies was found for chromosome IIL, while chromosomes IIR and III seemed to be more invariable.

INTRODUCTION

The potential of cities to promote evolutionary changes in *Drosophila* populations has not been extensively investigated. Exceptions are studies of Dubinin and Tiniakov (1945, 1946a,b, 1947), on the cosmopolitan *D. funebris* in Russian cities, Brncic (1989) on Chilean *D. pavani* and Singh and Das (1990) with *D. melanogaster* from urban and rural areas of India.

Fruit fly samples collected in the urban area of Porto Alegre, Rio Grande do Sul, south Brazil included large numbers of *D. willistoni*. They were found in conjunction with communities of the cosmopolitan species *D. immigrans, D. melanogaster, D. busckii* and *D. kikkawai. D. willistoni* is indigenous to neotropical forests and previously unknown from cities (review in Ehrman and Powell, 1982).

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[*] We dedicate this paper to Professor Warwick E. Kerr in honor of his 70th birthday.

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The aim of this study was to examine the relationship of chromosomal polymorphism of *D. willistoni* with this unusual habitat.

MATERIAL AND METHODS

A map of the urbanization gradient of Porto Alegre (30°2' S, 51°14' W; 1,000,000 inhabitants) was drawn from aerial photographs 1:20,000, from observations *in loco*, and with reference to a map showing the percentage of urban area covered by vegetation (Ruszczyk, 1987). Three characteristic zones can be identified in this gradient: high urbanization (mostly buildings at least four stories high; percentage of area covered by vegetation below 20%), medium (equal proportion of lower buildings and houses, vegetation between 20 and 40%) and low (mostly houses, also including open areas within the city, vegetation above 40%).

Flies were collected from 16 sites distributed through different zones of the urbanization gradient (Figure 1). For each sample site, the percentage of area covered by vegetation (including vacant lots, street trees, native vegetation as well as lawns and back yards) was determined for 100, 200 and 300 m diameter circles using 1:8,000 aerial photographs. The areas with buildings, houses or other constructions, streets and sidewalks, open areas between buildings and houses were calculated (100, 200 and 300 m diameters) by weighting the cuts of heliograph copies of 1:2,000 maps. For each site the "distance from the center of the city" (the geometric center of the high urbanization zone, Figure 1) was estimated.

Recording chromosome inversions

Drosophila were reared from fermenting fruit of native and exotic plants found growing in the city. Non-urban samples were collected in the Estação Experimental Agronômica de Guaíba, 40 km from Porto Alegre. Data from the same site in 1980 were also included. Collected fruits (see Table I) were placed in vials and kept at 25 ± 1°C, 60% r.h. for 15 days until imagos emerged. Flies were then identified and counted.

D. willistoni females which emerged were freely inseminated by males from the same samples and distributed as isofemale strains in vials, and F1 larvae were processed in the 3rd stage (Ashburner, 1967). Analysis of heterozygous inversions seen in salivary gland chromosomes was made on one larva per strain (Table II). Chromosome inversions were classified according to Dobzhansky (1950) and to our own records (Valente and Morales, 1985).

Data analysis

Absolute frequencies of heterozygotes of chromosome inversions were compared between urbanization zones using the Chi-square homogeneity test. For this

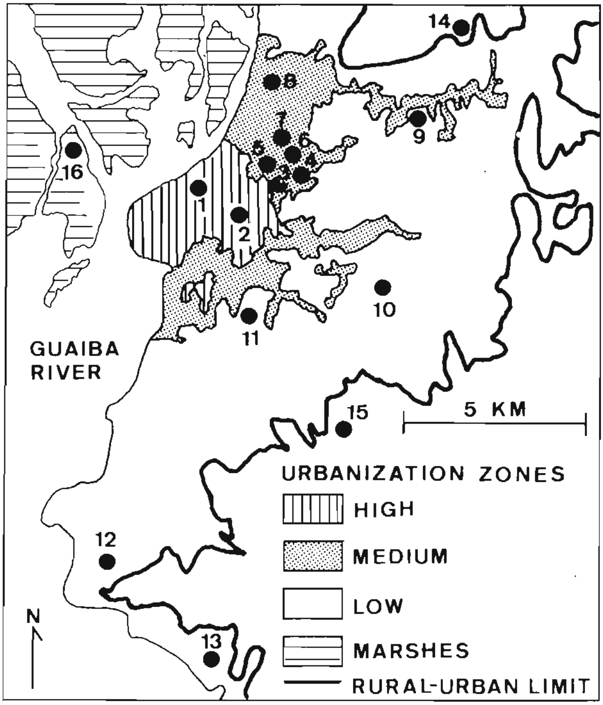

Figure 1 - Urbanization gradient of Porto Alegre with location of *Drosophila* sampling sites.

analysis, sampling sites were combined in four groups according to their location in the urbanization gradient: high, medium and low urbanization, and control (non-urban sites).

Multiple regression analysis (Kim and Kohout, 1975) was performed to investigate the relationship of the genetic constitution of *D. willistoni* populations (frequency of inversions individually considered, degree of chromosome heterozygosity, and mean number of inversions per female and per chromosome) with the urban variables of each sampling site.

RESULTS

Chromosome X (XL and XR arms) was virtually monomorphic in urban *D. willistoni* samples. The most polymorphic chromosome arms were the left and right of the second (IIL and IIR), and the third (III) which is acrocentric (Table II). Hence, the results refer to the variability of these arms only.

Table I - *Drosophila willistoni* collected (%) in urban Porto Alegre and in control sites.

Sample no./site	Urbanization zone	Date	Fruit Collected	% *Drosophila willistoni*	N
1 XV Square	High	01/86	Garbage	62.3	641
2 Farroupilha Park	High	05/87	Syagrus romanzoffiana	64.2	313
3 Goethe Sq.	Medium	05/87	Syagrus romanzoffiana	6.0	3383
4 Bordini Str.	Medium	03/87	Syagrus romanzoffiana	26.8	231
5a H. Ribeiro Str.	Medium	03/86	Syagrus romanzoffiana	2.4	5040
5b H. Ribeiro Str.	Medium	05/87	Syagrus romanzoffiana	4.5	2682
6 O.B. Viana Str.	Medium	04/86	Syagrus romanzoffiana	42.7	1371
7a M. Cardoso Sq.	Medium	06/85	Syagrus romanzoffiana	24.6	948
7b M. Cardoso Sq.	Medium	03/86	Syagrus romanzoffiana	38.4	877
8 P. Roosevelt Str.	Medium	07/86	Syagrus romanzoffiana	7.9	3266
9 D. Vignoly Sq.	Low	04/86	Syagrus romanzoffiana	1.1	6100
10a Botanic Garden	Low	07/86	Averrhoa carambola	15.6	2490
10b Botanic Garden	Low	07/86	Butia eriospatha	50.4	2192
11 Cemetery	Low	07/86	S. romanzoffiana	17.0	7059
12 M. Totta Str.	Low	04/87	A. carambola	62.0	793
13 O. Cruz Str.	Low	03/87	B. eriospatha	19.0	1083
14 Dique Av.	Low	03/86	B. eriospatha	10.4	2530
15a Cascata Hill	Low	01/86	Banana baits	95.5	355
15b Cascata Hill	Low	01/87	Eriobothrya japonica	25.8	814
16 Pintada Island	Low	07/86	Citrus sinensis	46.6	494
Control 1	Non-urban	03/80	S. romanzoffiana	17.0	690
Control 2	Non-urban	06/86	S. romanzoffiana	60.6	923
Control 3	Non-urban	04/87	S. romanzoffiana	11.1	4452

Frequencies of different inversions varied greatly. Examples are IIL_D and IIL_E which overlapped in the middle region of the left arm of the 2nd chromosome (Table II, A). These two inversions were very common in wild samples from Rio Grande do Sul, where their frequencies were virtually the same (Valente and Araujo, 1986a). In the city, however, this complex was broken up and the IIL_D frequencies seemed to vary erratically. Other inversions, such as IIL_F, which was present in all samples, showed less variability. The third chromosome showed relative uniformity in the frequencies of inversions III_J and III_B, which represented over 50% of the inversions in several samples from both control and the urban area (Table II, C). The other 12 inversions occurred in very low frequencies as well as the IIR inversions.

There were no differences between the degree of urbanization and the total number of inversions ($\chi^2 = 0.93$, DF = 2, p = 0.620) and those of the III chromosome ($\chi^2 = 1.25$, DF = 2, p = 0.535). With chromosome IIL, only values for medium and low urbanization were different ($\chi^2 = 9.77$, DF = 1, p = 0.002).

Mean percentages of heterozygotes per chromosomes per urbanization zones showed a gradient of heterozygosity increasing from the center towards the periphery (Figures 2 and 3B). In chromosome IIL, nearly all comparisons showed highly significant values ($p < 0.001$), except in those between low and medium urbanization. Also, in chromosome III, all comparisons resulted in highly significant values ($p < 0.001$), except for the low urbanization versus control ($\chi^2 = 2.410$, DF = 1, p = 0.117).

Table III summarizes the multiple regression analysis. The dependent variables mean number of inversions, percentage of B and D inversions of chromosome IIL, and B and J inversions of chromosome III were excluded because of the non-significant partial regression coefficients of all independent variables analysed. The inversion IIL_E attained the highest proportion of variance (73%) explained by the independent variables.

The standardized regression coefficient (variables were transformed to attain unit variance, allowing the comparison of variables measured in different units) indicated that each inversion had a particular relationship to different urban variables. For example, the variable open area between buildings had the opposite effect on inversions IIL_E and IIL_H. The same occurred with inversions III_C and III_H in relation to the area with buildings and houses. Also, the same inversion was related differently to the same independent variable, as a function of the size of the area used in the quantification (Table III, inversions IIL_E and IIL_A).

DISCUSSION

D. willistoni can be characterized by its tendency to colonize new environments including urban settings. Its outstanding ecological versatility, expressed by its capacity to exploit a large number of substrata both as feeding and breeding sites (Carson, 1965; Pipkin, 1965; Valente and Araujo, 1986b), is not always followed by substantial changes in the genetic structure characterized by a wide chromosomal polymorphism and large isoenzymatic variability (Ehrman and Powell, 1982).

The temperature in the city of Porto Alegre as in most cities is usually higher than in surrounding environments (Duckworth and Sandberg, 1954). During the winter months, *D. willistoni* is active in Porto Alegre (Valente *et al.*, 1989), but not in natural habitats in Rio Grande do Sul.

Table II. Frequency (%) of chromosome inversions, total heterozygosis, and mean number of inversions of the IIL (A), IIR (B) and III (C) chromosomes of urban *Drosophila willistoni*. Percentages above 100 after summation indicate more than one inversion per chromosome arm[a].

Chrom.	Invs.	Sample: 1	2	3	4	5a	5b	6	7a	7b	8	9	10a	10b	11	12	13	14	15a	15b	16	C1	C2	C3
A)	D	45	59	6	16	33	47	35	36	44	42	6.5	15	30	36	52	25	47	26	30	23	34	52	41.3
IIL	E	46	62	30.5	44	40	42	46	47	57	45	30.5	54	48	55	52	59	12	43	36	21	48	55	48.7
	F	0.6	33	24	38	13	40	37	14	25	21	24	34	29	31	30	37	5	39	42	21	29	29	21
	H	-	12	5	-	25	-	7.7	+	11	-	5	4	24	5	9	8.5	18	-	1.5	-	14	11	11
	B	0.6	5.9	5.5	-	+	29	10.7	22	11	23	5.5	16	17	6	6.8	3.8	1	1	28	15.4	1	17	17
	A	-	5.4	0.5	-	+	-	5.6	-	1	0.9	0.5	2	2	3	14	-	-	9	4.1	8	19	2	1
	I	0.3	-	2.5	-	3	-	4.7	-	-	0.4	2.5	-	0.3	2	-	-	-	9	0.5	-	2.1	1	2.4
	C	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-
	N++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-
Total heteroz.(%)		52	78	55	65	64	69	75	62	75	80	55	74	74	70	75	78	64	76	72	61	72	78	73
Flies analysed		352	186	200	114	149	163	232	205	326	233	200	180	376	384	44	130	192	274	196	207	97	382	402
X invs./chrom.		0.93	1.7	0.75	0.98	0.79	1.56	1.47	1.21	1.4	1.37	1.6	1.26	1.32	1.4	1.64	1.34	1.14	1.27	1.42	1.01	1.47	1.69	1.42
B)	B	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	5	-	-	3
IIR	C	1	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
	E	1	-	-	-	16	-	-	20	11	12	3	12	12	19	-	1	27	18	9	-	-	17	4
Total heteroz.(%)		1	0	0	2	11	0	0	11	3	5	1	3	7	5	0	7	14	9	3	2	0	5	2
Flies analysed		189	201	114	149	116	232	207	333	233	288	376	182	382	41	130	192	196	283	213	97	330	407	404
X invs/chrom.		0.01	0	0	0.02	0.11	0	0	0.11	0.03	0.05	0.8	0.07	0.03	0.05	0	0.07	0.14	0.03	0.09	0.02	0	0.08	0.02

Chrom.	Invs. Sample:	1	2	3	4	5a	5b	6	7a	7b	8	9	10a	10b	11	12	13	14	15a	15b	16	C1	C2	C3
C)	J	53	64	34	56	47	42	55.8	47	50	43	51	57	43	41	39	53	41	47	58	52	54	56	47
III	B	45	48	43	35	46	56	46	34	46	70	52	40	58	46	51	45	46	51	59	53	45	53	37
	C	27	26	12	6.1	18	37	16.4	18	17	28	12	20	17	19	20	27	15	25	21	56	32	19	24
	D	-	-	-	-	-	-	-	-	-	-	-	1	-	0.3	-	-	-	-	-	-	-	1	-
	H	9.2	1.6	11	38	13	28	17	13	18	46	14	19	27	23	10	9.2	14	24	23	2	12.3	17	7.4
	O	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
	F	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
	A	-	-	-	-	+	-	0.4	-	-	-	-	-	-	-	-	-	-	6	-	-	10	-	-
	M	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	0.5	-	-	0.7
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	E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	U	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-	1	-	2	0.5
	B1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-
	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-
	B2 + 1/2 91	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
Total heteroz.(%)		63	87	65	70	74	72	81	72	82	88	78	83	84	74	83	76	77	83	85	82	88	88	73
Flies analysed		370	191	201	114	149	165	232	207	329	234	287	182	377	379	41	131	192	286	193	202	97	327	404
X invs/chrom.		1.4	1.4	1.0	1.4	1.4	1.6	1.4	1.1	1.1	1.8	1.3	1.4	1.5	1.3	1.2	1.3	1.2	1.5	1.6	1.7	1.5	1.5	1.2
X invs/fem/sampl.		2.41	3.2	1.75	2.14	2.68	1.56	2.82	2.52	2.79	3.26	2.11	2.69	2.84	2.76	2.93	2.76	2.03	2.86	3.11	2.65	3.10	3.21	2.59

a) for sample date, name of the site and collected fruit see Table I. +) value below 0.1%. ++) probably a new, non described inversion, with break points in 42 and 52 sections, according to Dobzhansky's (1950) map.

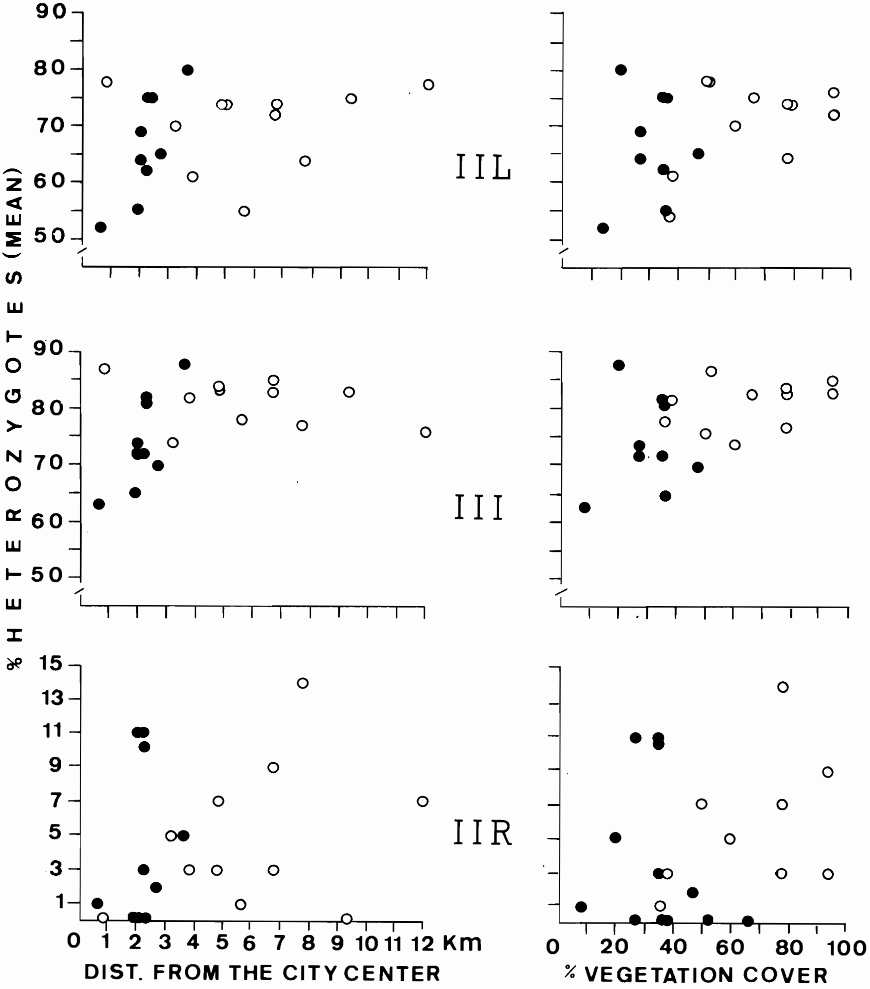

Figure 2 - Loss of heterozigosity in urban *D. willistoni*. Frequencies of heterozygotes for chromosomal inversions in three chromosomes (IIL, III and IIR) of *D. willistoni* and distance from the center of the city and percentage of area covered by vegetation of the sample sites. Black circles, sites located in the medium and high urbanization zones; clear circles, sites in the low urbanization zone.

Dubinin and Tiniakov (1946a,b, 1947) showed in *D. funebris* a gradient of loss of heterozygosity for paracentric inversions going from urban center to rural areas. This was interpreted as the effect of lowering of temperature as the sample sites were more

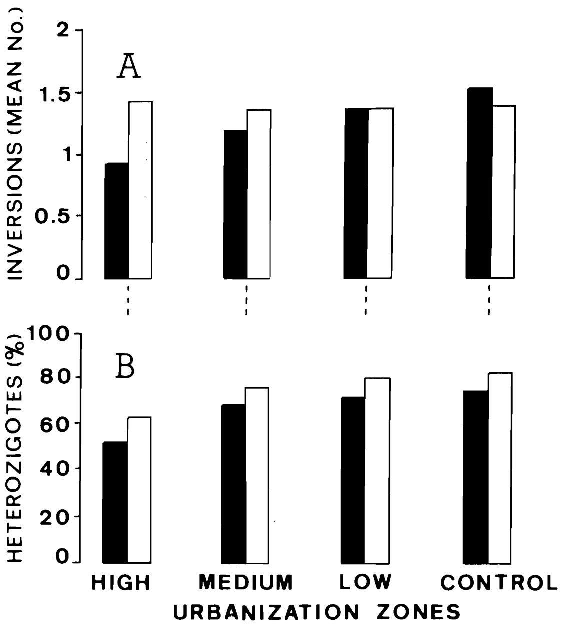

Figure 3 - Mean number of inversions per female per urbanization zone (A). Mean percentage of heterozygotes per chromosome per urbanization zone (B). Black bars, IIL chromosome; clear bars, III chromosome; control, non-urban sites.

distant from the city center. Our findings with wild *D. willistoni* was the exact opposite of those authors and Borisov (1969) with *D. funebris*. Increasing heterozygosity gradients from center to periphery could be related to gradual selective pressures imposed by urbanization on the amount of chromosome polymorphism.

Brncic (1989) did not find any significant differences in the arrangements of chromosome arms 4R and 4L in Santiago populations of *D. pavani* correlated with environmental changes due to urbanization of the area. *D. pavani* however, had a "rigid" chromosome polymorphism (Dobzhansky, 1962). Only some populations of *D. willistoni* may be considered to have "rigid" polymorphism. In others, the degree of polymorphism seems to vary considerably due to environmental pressures (Da Cunha *et al.*, 1950, 1959; Townsend, 1952, 1958; Sperlich and Pfriem, 1986) such as interspecific competition (Pavan *et al.*, 1957) and breeding sites (Valente and Araujo, 1985).

As suggested by Townsend (1952), and generalized by Carson (1965), there is a considerable loss of chromosome variability at the geographic margins of *Drosophila*. This would result from the action of selective factors in favor of structural homozygotes. Our data were compatible with this idea, since urban populations lose part of the inversion polymorphism when compared to non-urban populations of the species. The release of genetic variability linked to the inverted regions of the chromosomes could give origin

Table III - Multiple regression analysis. Proportion of variation explained (R^2) and standardized regression coefficient of independent variables. All variables arc sin transformed.

Dependent variable	Proportion of variation explained by all variables (R^2)	Standardized regression coefficients^a			
		% Open area between buildings and houses	% Area covered by vegetation	% Area with buildings and houses	% Area covered by streets and sidewalks
(Inversions)					
IIL$_E$	0.731	0.404^{+} -1.021^{++}	0.306^{+++}	N.S.	N.S.
IIL$_A$	0.586	0.522^{+} -0.847^{+++}	N.S.	N.S.	-0.849^{++}
IIL$_H$	0.335	-0.465^{+}	0.456^{+++}	N.S.	N.S.
IIL$_F$	0.265	0.515^{+}	N.S.	N.S.	N.S.
III$_C$	0.430	0.612^{+}	-0.923^{++}	N.S.	N.S.
III$_H$	0.364	N.S.	N.S.	0.987^{+++}	-0.762^{+}
(Heterozygosis)					
IIL	0.198	N.S.	0.445^{+++}	N.S.	N.S.
III	0.262	N.S.	N.S.	N.S.	-0.512^{+++}

a, variables were transformed to attain unit variance; +, ++, +++, respectively 100, 200 and 300 m (measurement diameter of the variable).

to new genetic combinations, some of which are capable of better exploitation of new resources and have more tolerance to high levels of environmental stress.

When the mean chromosome heterozigosity observed in *D. willistoni*, IIL = 69.21, SD = 8.31, N = 4136, III = 77.74, SD = 7.19, N = 4260 (in urban samples); IIL = 74.33, SD = 3.73, N = 841, III = 83.0, SD = 6.4, N = 828 (in control samples) was compared to that of samples from other wild sites in Rio Grande do Sul (Valente and

Araujo, 1985, 1986a) such as Parque de Itapuã (IIL = 82.78, SD = 4.27, N = 2955, III = 74.33, SD = 8.63, N = 2973) and Parque do Turvo (IIL = 83.30, SD = 4.42, N = 5289, III = 78.40, SD = 3.4, N = 5345), it appeared that the loss of certain chromosomal morphs was higher in chromosome IIL. The polymorphism in this chromosome arm seems to be more flexible in varying environmental conditions, producing more noticeable frequency gradients than in chromosome III (Figure 3B).

Nevertheless, stochastic factors such as founder effects or "bottlenecks" can also be responsible for the great frequency variations found in most inversions, such as IIL$_B$ (0.02 to 29) and III$_C$ (6.1 to 37). This reasoning is based on the observation that urban populations are small and isolated; extinction and recolonizations are probably frequent, and dispersion, which is low in its natural environment (Burla *et al.*, 1950), could be hampered by barriers such as buildings or fragmented vegetation.

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RESUMO

Populações urbanas da espécie selvagem *Drosophila willistoni* foram estudadas quanto ao seu polimorfismo cromossômico. Populações procedentes de locais mais próximos aos centros urbanos foram menos polimórficas para inversões cromossômicas. Maiores frequências da inversão III$_E$ foram encontradas em associação com maior cobertura vegetal. As frequências das inversões nos braços IIL, IIR e III, entretanto, não se correlacionaram com o grau de urbanização do sítio de coleta. Foi encontrada maior variação nas frequências de inversões para o cromossomo IIL, enquanto as do cromossomo III e do braço direito do segundo cromossomo (IIR) foram menos variáveis.

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