

# Two decades of colonization of the urban environment of Porto Alegre, southern Brazil, by *Drosophila paulistorum* (Diptera, Drosophilidae)

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**ABSTRACT.** *Drosophila paulistorum* Dobzhansky & Pavan, 1949 had initially been considered absent in anthropogenically disturbed environments, but in 1985 the detection of the species in Porto Alegre city, southern Brazil, suggested its potential to colonize new habitats and laid the foundations for ecologic studies on this species' populations. This study followed the variations in *D. paulistorum* populations in this town almost 20 years after its first local record. Drosophilid specimens were collected in sites with different urbanization grades and the results point to the expressive decline in *D. paulistorum* populations in Porto Alegre. This decline may be linked to urban growth and to naturally driven population decline, as imputed to climatic changes like variations in maximum and minimum temperatures as a consequence of a global climate warming. Also, the recent introduction of exotic species *Zaprionus indianus* Gupta, 1970 seems to play a role in this scenario, changing the interactions between native species.

**KEYWORDS.** Biological invasion, colonization, *Drosophila paulistorum*, urban ecology, *Zaprionus indianus*.

**RESUMO.** Duas décadas de colonização do ambiente urbano de Porto Alegre, sul do Brasil, por *Drosophila paulistorum* (Diptera, Drosophilidae). *Drosophila paulistorum* Dobzhansky & Pavan, 1949 era considerada inicialmente ausente em ambientes com influência antrópica, mas a detecção dessa espécie na cidade de Porto Alegre, sul do Brasil, em 1985, sugeriu seu potencial de colonização de novos ambientes e levou a fundação de estudos ecológicos com populações desta espécie. Este estudo acompanhou as variações populacionais de *D. paulistorum* nesta cidade quase 20 anos depois de seu primeiro registro neste local. Coletas de Drosophilidae foram realizadas em pontos com diferentes graus de urbanização e os resultados apontaram para uma expressiva diminuição dos tamanhos populacionais de *D. paulistorum* em Porto Alegre. Este declínio pode estar relacionado com o crescimento da cidade, assim como com retrações naturais no tamanho das populações devido a mudanças climáticas, tais como, variações nas temperaturas mínimas e máximas como consequência do aquecimento global. A introdução recente de *Zaprionus indianus* Gupta, 1970 também parece contribuir com esse quadro, uma vez que poderia estar modificando as interações entre as espécies nativas.

**PALAVRAS-CHAVE.** Invasão biológica, colonização, *Drosophila paulistorum*, ecologia de ambientes urbanos, *Zaprionus indianus*.

*Drosophila paulistorum* Dobzhansky & Pavan, 1949 is a superspecies of the *D. willistoni* subgroup, comprising six races or semispecies (DOBZHANSKY & SPASSKY, 1959; PÉREZ-SALAS *et al.*, 1970). The geographic distribution of the taxon is vast, stretching from Guatemala to southern Brazil, where only the Andean-Brazilian semi-species occurs. In southern Brazil, this semi-species coexists sympatrically with its sibling species, *D. willistoni* Sturtevant, 1916. In several tropical zones of the American continent, *D. paulistorum* comes second in abundance within the *D. willistoni* subgroup (SPASSKY *et al.*, 1971).

Until the publication of the study by SPASSKY *et al.* (1971), the southernmost limit of *D. paulistorum* geographic distribution was the city of Osório (29°54'S; 51°16'W), state of Rio Grande do Sul, southern Brazil. But in May 1985, *D. paulistorum* was captured in the urban environments of the city of Porto Alegre (30°02'S; 51°14'W), 90 km south of Osório (SANTOS & VALENTE,

1990). Though *D. paulistorum* had been considered incapable of surviving in anthropogenically disturbed environments (EHRMAN & POWELL, 1982) upon its capture in Porto Alegre city, the sampling of the species in urban environments suggests its high colonization potential, and certainly laid the foundations for ecologic studies about these populations.

The importance of studies on urban faunas lies in the fact that urbanization exposes organisms that formerly inhabited natural environments to a novel ecological dynamic. Among these disturbance factors is the depletion of forest areas observed as a consequence of the growth of cities to meet the needs of one single species, *Homo sapiens* (MCKINNEY, 2006). Another ecological consequence operated by the expansion of urbanization is pollution, which significantly alters the environment by impairing the quality of air, of water and of natural resources (MARCUS & DETWYLER, 1972). The massive disturbance set off by urban growth not only

spoils the natural habitat of native species, but also generates new environments that favour the establishment of exotic species capable of adapting to this new urban setting. The major consequence of urbanization progression for species conservation is that exotic species may actually enrich local biodiversity, as often observed (SAX & GAINES, 2003). Global diversity, nevertheless, is narrowed due to the subsequent extinction of endemic native species, lost to the overall species set (McKINNEY, 2006).

In the recent year of 2000, the systematic study of drosophilids within the urban environment of the city of Porto Alegre afforded to detect the introduction of *Zaprionus indianus* Gupta, 1970 (CASTRO & VALENTE, 2001). The arrival of this invader species to that environment seems to be promoting adjustments in the survival strategies of native species. Such adaptations are held to bring about certain changes in richness and abundance of the species that make up these drosophilid assemblies, as recently suggested by SILVA *et al.* (2005a,b).

Except for the studies focused on pest or epidemic control, research papers on arthropod populations in urban environments are scarce (McINTYRE, 2000). Although drosophilids constitute a suitable animal model to this line of research – an advantage imputed to the organism's abundance in cities – much is yet to be established regarding the ways urbanization affects the group (KREMEN *et al.*, 1993; VALIATI & VALENTE, 1996; LUCCHESI *et al.*, 2003). Studies on urban populations of *D. willistoni* and *D. paulistorum* using different genetic markers have revealed far-reaching genetic changes, seemingly forced upon species by urbanization (REGNER & VALENTE, 1993; VALENTE *et al.*, 1993; VALIATI & VALENTE, 1997; SAAVEDRA *et al.*, 2001).

Between 1991 and 1992, VALIATI & VALENTE (1996) carried out a second comprehensive study on the ecology of *D. paulistorum* in Porto Alegre city revealing that the species' frequency had increased since its first record in the city. Both the studies by SANTOS & VALENTE (1990) and by VALIATI & VALENTE (1996) indicated the preference expressed by *D. paulistorum* for exotic fruits as breeding and feeding sites, whereas *D. willistoni* was observed to settle for native fruits. These observations led to the inference that such tendencies may be part of a likely strategy adopted by species to avoid competition.

Such body of research has broadened the understanding of *Drosophila* adaptation to different environmental gradients. Also, these studies have demonstrated the particular importance of the genera as animal model in investigations of urbanization impact over the biodiversity of native species (PARSONS, 1991; POWELL, 1997; AVONDET *et al.*, 2003; FERREIRA & TIDON, 2005).

With a view to shedding new light on the path followed by *D. paulistorum* as a colonizing species, the present study monitored the occurrence and frequency of the species 20 years after the its first record in the urban environment of Porto Alegre, southern Brazil.

## MATERIALS AND METHODS

Specimens of Drosophilidae flies were collected throughout the year 2004 in four sites of Porto Alegre

city: Farroupilha Park (FAP – 30°02'4.7"S, 51°12'59.8"W; 37 hectares), Botanic Garden (BOG – 30°03'0.7"S, 51°10'34"W; 39 hectares), Mario Totta street (MTS – 30°06'46.7"S, 51°15'0.07"W; 2 hectares), and Gabriel Knijnik Park (GKP – 30°06'12.6"S, 51°12'10.5"W; 12 hectares). Collection sites exhibited different urbanization grades, based on a classification system defined by RUSZCZYK (1986) that considers the ratio of green areas to built areas. According to the system, FAP is classified as a high urbanization grade area (less than 20% vegetation cover and prevalence of buildings with more than four storeys), whereas BOG, MTS and GKP are all ranked as low urbanization grade areas (over 40% vegetation cover and predominance of one-storey houses and constructions). Samples were collected on three consecutive days in February (summer), April (autumn), July (winter), and October (spring), always between 9:00 and 11:00 am.

Two sampling methods were employed. In the first method, an entomological net was used to capture adult flies over different kinds of decomposing fruits found in the collection sites, as well as over banana and orange baits placed on the ground and topped with yeast. Bait amount was standardized as 5 Kg bananas and 5 Kg oranges at each collection site. Baits were distributed at different points 100 m away from one another along each collection site, in all sample collections. The second method used rotten fruits that were brought to the laboratory and kept in tubes containing vermiculite under controlled temperature and humidity (25°C ± 1°C, 60% R.H.) upon the emergence of the imagoes. Adult specimens were aspirated and transferred to bottles containing standard growth medium (MARQUES *et al.*, 1966). Adult flies were identified and counted using keys available from the *Drosophila* Laboratory, Federal University of the State of Rio Grande do Sul. In some cases, male genitalia were dissected. The sibling species *D. paulistorum* and *D. willistoni* were identified by electrophoresis of the Acid Phosphatase-1 enzyme (*Acp-1*), according to GARCIA *et al.* (2006).

Drosophilid populations were compared using the numeric and frequency records for the species studied. The records were made for sites BOG and MTS in years 1986 and 1987 by SANTOS & VALENTE (1990) and, for sites FAP, BOG and MTS in years 1991 and 1992, by VALIATI & VALENTE (1996). The data published by SANTOS & VALENTE (1990) list only *D. paulistorum* and *D. willistoni* frequencies; the other species were not discriminated and therefore could not be employed in some of the analyses carried out. Drosophilid data collected in years 2001 and 2002 and described by SILVA *et al.* (2005b), for the same places evaluated in this study, except MTS (Mario Totta street). Nevertheless, as specimens of the *D. willistoni* subgroup were not discriminated for species in this last paper mentioned, we resorted to these data only in the cases when *D. willistoni* and *D. paulistorum* clustered under the *D. willistoni* subgroup.

In order to evaluate the variations in species frequencies for the different collection sites and seasons, results were statistically analyzed using the Kruskal-Wallis Multiple Comparison Test. In turn, the Spearman's Correlation Test was used to assess the role played by

temperature in species frequency. Temperature records were obtained from the National Meteorology Institute (INMET), 8<sup>th</sup> District, a division of the Ministry of Agriculture, Cattle-Breeding and Supplies (MAPA), based in Porto Alegre, RS, Brazil.

## RESULTS AND DISCUSSION

Throughout 2004, 27,985 drosophilids were collected in the four sampling sites of Porto Alegre (Tab. I). Of these, 13,461 were classified as *Drosophila simulans* Sturtevant, 1919, 5,956 as *Z. indianus* and 4,365 as *D. willistoni*. These occurrence figures make them the three most abundant species, and taken together account for 85% of the total number of individuals captured. *Drosophila paulistorum*, with 246 specimens caught, represented a mere 0.9% of the total number of drosophilids collected.

Table II shows the data on drosophilid collections carried out in Porto Alegre city in year 2004, complemented by the records in SANTOS & VALENTE (1990) and VALIATI & VALENTE (1996) for the same collection sites. Samples were sorted for collection site, year and season. Trophic resources employed to capture specimens were in turn organized under the categories native fruits (from Neotropical plants), and exotic fruits.

For years prior to 2004, *D. paulistorum* frequency had always been higher than *D. willistoni* frequency in exotic fruits such as *Averrhoa carambola* (L.) (Oxalidaceae) and *Maclura pomifera* (Raf.) C. K. Schneider (Moraceae). Oppositely, *D. willistoni* had constantly been more abundant in native fruits, as *Syagrus romanzoffiana* (Cham.) Glassmann (Arecaceae), for that same period. In 2004, *D. paulistorum* was basically not observed in native fruits, and sustained its preference for some exotic fruits, as *Eriobotrya japonica* (Lindl.)

Table I. Species and total number of specimens sampled in the four collection sites in Porto Alegre city, southern Brazil, in 2004 (FAP, Farrroupilha Park; BOG, Botanic Garden; MTS, Mario Totta Street; GKP, Gabriel Knijnik Park; (\*), frequency under 0.1%).

Species	Author and year	Collection sites				Total (%)
		FAP	BOG	MTS	GKP	
<i>D. simulans</i>	Sturtevant, 1919	6,896	4,065	2,128	372	13,461 (48.1)
<i>Z. indianus</i>	Gupta, 1970	1,821	2,637	1,403	95	5,956 (21.3)
<i>D. willistoni</i>	Sturtevant, 1916	709	1725	1412	519	4,365 (15.6)
<i>D. mercatorum</i>	Patterson & Wheller, 1942	627	614	104	4	1,349 (4.8)
<i>D. mediopunctata</i>	Dobzhansky & Pavan, 1943	66	88	79	302	535 (1.9)
<i>D. immigrans</i>	Sturtevant, 1921	108	216	188	6	518 (1.9)
<i>D. cardinoides</i>	Dobzhansky & Pavan, 1943	317	8	19	0	344 (1.2)
<i>D. maculifrons</i>	Duda, 1927	110	127	49	14	300 (1.1)
<i>D. paulistorum</i>	Dobzhansky & Pavan, 1949	0	27	189	30	246 (0.9)
<i>D. kikkawai</i>	Burla, 1954	122	27	45	0	194 (0.7)
<i>D. nebulosa</i>	Sturtevant, 1916	52	57	11	10	130 (0.5)
<i>D. polymorpha</i>	Dobzhansky & Pavan, 1943	27	58	25	13	123 (0.4)
<i>D. griseolineata</i>	Duda, 1927	19	53	11	20	103 (0.4)
<i>D. neocardini</i>	Streisinger, 1946	16	14	26	1	57 (0.2)
<i>D. paraguayensis</i>	Duda, 1927	0	11	6	34	51 (0.2)
<i>D. sturtevanti</i>	Duda, 1927	1	28	15	3	47 (0.2)
<i>D. bandeirantorum</i>	Dobzhansky & Pavan, 1943	3	12	12	6	33 (0.1)
<i>D. nappae</i>	Vilela <i>et al.</i> , 2004	0	8	3	16	27 (0.1)
<i>D. paramediotriata</i>	Townsend & Wheller, 1955	7	12	2	0	21 (0.1)
<i>D. capricorni</i>	Dobzhansky & Pavan, 1943	0	0	1	18	19 (0.1)
<i>D. parabocainensis</i>	Carson, 1954	0	1	1	17	19 (0.1)
<i>D. cardini</i>	Sturtevant, 1916	15	0	0	0	15 (0.1)
<i>D. hydei</i>	Sturtevant, 1921	2	2	8	0	12 (*)
<i>D. melanogaster</i>	Meigen, 1830	0	0	0	12	12 (*)
<i>D. zottii</i>	Vilela, 1983	0	0	0	11	11 (*)
<i>D. onca</i>	Sene <i>et al.</i> , 1977	0	1	7	0	8 (*)
<i>D. mediopicta</i>	Frota-Pessoa, 1954	0	3	1	3	7 (*)
<i>D. meridionalis</i>	Wasserman, 1962	0	6	0	0	6 (*)
<i>D. buzzatii</i>	Carson & Wasserman, 1965	2	3	0	0	5 (*)
<i>D. neoguaramunu</i>	Frydenberg, 1956	1	0	1	0	2 (*)
<i>D. pallidipennis</i>	Dobzhansky & Pavan, 1943	0	1	0	1	2 (*)
<i>D. roehrae</i>	Pipkin & Heed, 1964	0	0	0	2	2(*)
<i>D. ananassae</i>	Doleschall, 1858	0	0	0	1	1 (*)
<i>D. annulimana</i>	Duda, 1927	0	0	0	1	1 (*)
<i>D. caponei</i>	Pavan & Da Cunha, 1947	0	1	0	0	1 (*)
<i>D. malerkotliana</i>	Parshad & Paika, 1964	0	0	1	0	1 (*)
<i>D. ornatifrons</i>	Duda, 1927	0	0	0	1	1 (*)
Total (%)		10,921(39.0)	9,805 (35.0)	5,747 (20.5)	1,512 (5.4)	2,7985

(Rosaceae), verified in the GKP spring record. In this particular trophic resource, the species frequency was substantially high as compared to *D. willistoni* (28.4% and 5.4%, respectively). Nevertheless, a significant alteration was observed in *A. carambola* as compared to records of previous years, made clear by the most surprising observation that *D. paulistorum* frequencies were actually lower than *D. willistoni* frequencies (exception is made for the MTS spring collection). It may be hypothesized that this change in trophic resource preference by *D. willistoni* has interfered in the composition of drosophilid assemblies that feed on these fruits, thus affecting *D. paulistorum* abundance. Apart from this, the decrease in *D. paulistorum* frequency values may also be the result of the pressure exerted by *Z. indianus*. This last species was present in 13 of the 14 trophic resources available (the species was not observed in *E. japonica*, exclusively). Further investigations should be conducted to ascertain whether these notions are correct or not.

Figure 1 illustrates the variation of mean frequencies of *D. paulistorum*, *D. willistoni*, *Z. indianus* and of the other drosophilid species collected between the years 1986 and 2004 in sites BOG and MTS. The analytic panorama obtained suggests that *D. paulistorum* successfully started the colonization of Porto Alegre at some moment in years 1986 and 1987, with a mean baseline frequency of 11% within drosophilid assemblies (SANTOS & VALENTE, 1990). The species managed to maintain frequencies round that value (13%) in samples collected five years later (VALIATI & VALENTE, 1996); yet, a considerable decrease in abundance was observed in 2004, as revealed by the maximum frequency of 1.4%.

Figure 1 also shows that *Z. indianus* was not observed in collections carried out between 1986 and 1992. In fact, the species was recorded in Porto Alegre for the first time only in the year 2000 (CASTRO & VALENTE, 2001). *Zaprionus indianus* is an invader species native to Africa, which very speedily has been colonizing South America (DE TONI *et al.*, 2001; GONI *et al.*, 2001; TIDON *et al.*, 2003; SILVA *et al.*, 2005a,b) since its first record in the continent, made in São Paulo city (Brazil) in March 1999 (VILELA, 1999).

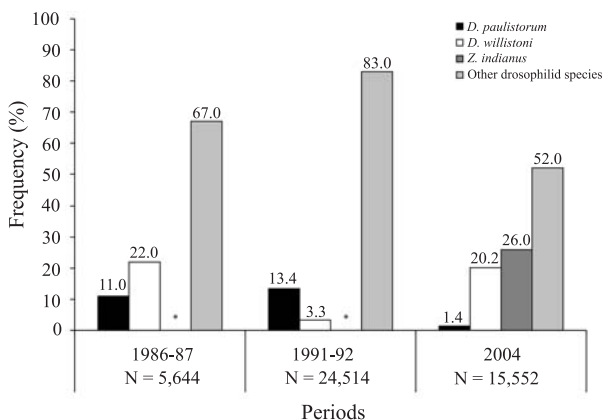


Fig. 1. Mean percent frequencies of *D. paulistorum*, *D. willistoni*, *Z. indianus* and of the other drosophilid species collected in sites BOG and MTS in Porto Alegre, southern Brazil, in three periods: 1986 to 1987 (SANTOS & VALENTE, 1990); 1991 to 1992 (VALIATI & VALENTE, 1996), and in 2004 (present study). (N, total number of specimens; \*, absence of *Z. indianus* in southern Brazil).

Figure 2 illustrates the mean frequencies of drosophilid assemblies sampled between 1986 and 2004, irrespective of geographic site, season, and trophic resource used. The most representative groups were *D. melanogaster* Meigen, 1830 subgroup (represented by *D. melanogaster* and by *D. simulans*, this last with abundance over 90%), *D. willistoni* subgroup (represented by *D. willistoni* and by *D. paulistorum*), followed by the species *Z. indianus*. Noticeable is the fact that the frequencies of cosmopolitan *D. melanogaster* subgroup species and those of *Z. indianus* varied in reverse order. It was thus that the *D. melanogaster* subgroup came to represent 75% of the total number of individuals collected in 1991, when *Z. indianus* had not yet been recorded in Porto Alegre. However, this frequency was lowered to 16.7% in 2001, contrasting with the 44.2% frequency then recorded for *Z. indianus*. Still another reversal in abundance values was observed in 2004, when *D. melanogaster* subgroup frequency rose again (49%), accompanied by a decrease in *Z. indianus* frequency (21%). An explanation for these oscillating frequencies may lie in a likely competition between these species, as *Z. indianus* records in Brazil were carried out in disturbed environments (TIDON *et al.*, 2003; SILVA *et al.*, 2005a,b; TIDON, 2006), which is similar to what has been observed for the *D. melanogaster* subgroup (PARSONS & STANLEY, 1981).

On the other hand, the oscillations observed for the *D. willistoni* subgroup were small as compared to *D. melanogaster* subgroup values (Fig. 2). The presence of *Z. indianus* in Porto Alegre did not affect the frequency of the *D. willistoni* subgroup as a whole, since the frequency recorded for the subgroup in 2004 was 17% – very similar to the 1991 record (14.2%), one decade before *Z. indianus* got into Porto Alegre environments. However, this does not necessarily mean that the frequencies of each species of the subgroup (*D. willistoni* and *D. paulistorum*) were constant either before or after the invasion by *Z. indianus*. As shown in figure 3, *D. willistoni* was more frequent in 1986-1987, and in 2004, while *D. paulistorum* was far more numerous in 1991 and 1992.

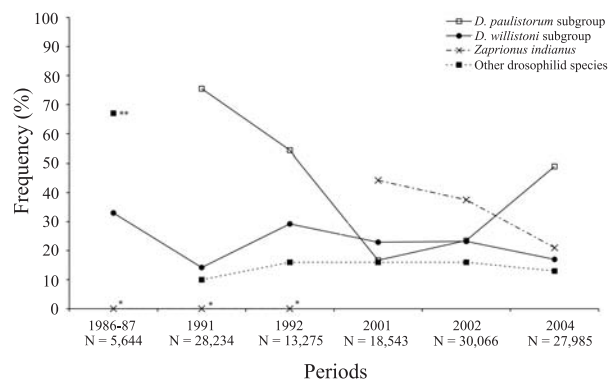


Fig. 2. Mean percent frequencies of subgroups *D. melanogaster* and *D. willistoni*, *Z. indianus* species, and other drosophilid in years 1986 to 2004 in Porto Alegre city, southern Brazil, irrespective of collection site, season and trophic resource of collection (N, total number of specimens; \*, absence of *Z. indianus* in southern Brazil; \*\*, species of the *D. melanogaster* subgroup were not discriminated by the authors (SANTOS & VALENTE, 1990)).

Table II. Collection sites, urbanization levels, periods, trophic resources of collection and frequency of *D. paulistorum*, *D. willistoni*, *Z. indianus* and other drosophilid species collected in Porto Alegre, southern Brazil, in years 1986 to 1987 (SANTOS & VALENTE, 1990), 1991 to 1992 (VALIATI & VALENTE, 1996), and in the present study (FAP, Farroupilha Park; BOG, Botanic Garden; MTS, Mario Totta Street; GKP, Gabriel Knijnik Park.; U.L., urbanization level; N, native fruit; E, exotic fruit. Fruit and baits: 1, *Maclura pomifera* (Raf.) (Moraceae); 2, *Syagrus romanzoffiana* (Cham.) (Arecaceae); 3, *Butia eriospatha* (Becc) (Palmae); 4, Banana bait; 5, Orange bait; 6, *Hovenia dulcis* (Thunb) (Rhamnaceae); 7, *Syagrus coronata* (Martius) Beccari (Arecaceae); 8, *Averrhoa carambola* (L.) (Oxalidaceae); 9, *Psidium guajava* (L.) (Myrtaceae); 10, *Britoa guazumaefolia* (Cambessedes) Legrand (Myrtaceae); 11, *Eugenia jambolona* (Lam.) (Myrtaceae); 12, *Psidium araca* (Raddi) (Myrtaceae); 13, *Passiflora edulis* (Sims) (Passifloraceae); 14, *Eriobotrya japonica* (Lindl) (Rosaceae)).

Collection site	U.L.	Year/Season	Trophic resources	<i>D. willistoni</i> subgroup			Other species (%)	Total	References
				<i>D. paulistorum</i> (%)	<i>D. willistoni</i> (%)	<i>Z. indianus</i> (%)			
FAP	High	1991/Autumn	1 (E)	4.65	0	0	95.35	129	VALIATI & VALENTE (1996)
		1991/Autumn	2 (N)	0	4.79	0	95.21	313	VALIATI & VALENTE (1996)
		1992/Summer	1 (E)	43.33	24.87	0	31.80	616	VALIATI & VALENTE (1996)
		1992/Autumn	1 (E)	25.98	5.12	0	68.90	1,913	VALIATI & VALENTE (1996)
		1992/Autumn	3 (N)	1.08	25.63	0	73.29	1,951	VALIATI & VALENTE (1996)
		2004/Summer	1 (E)	0	1.15	5.36	93.49	522	Present study
		2004/Summer	2 (N)	0	20.74	21.79	57.47	1,051	Present study
		2004/Summer	4	0	11.09	40.22	48.70	460	Present study
		2004/Summer	5	0	9.62	28.02	62.36	364	Present study
		2004/Autumn	1 (E)	0	0	47.83	52.17	23	Present study
		2004/Autumn	2 (N)	0	7.59	64.06	28.35	843	Present study
		2004/Autumn	4	0	12.86	50.00	37.14	70	Present study
		2004/Autumn	5	0	12.12	33.33	54.55	33	Present study
		2004/Autumn	6 (E)	0	11.96	71.74	16.30	92	Present study
		2004/Autumn	7 (N)	0	4.92	80.33	14.75	366	Present study
		2004/Winter	2 (N)	0	14.66	7.48	77.86	962	Present study
		2004/Winter	4	0	11.01	5.79	83.20	363	Present study
		2004/Winter	5	0	19.42	6.61	73.97	484	Present study
		2004/Spring	2 (N)	0	0.19	4.08	95.73	4,638	Present study
		2004/Spring	4	0	1.82	0.45	97.73	220	Present study
2004/Spring	5	0	1.16	1.16	97.68	430	Present study		
BOG	Low	1986/Winter	3 (N)	3.92	46.53	0	49.54	2,192	SANTOS & VALENTE (1990)
		1986/Winter	8 (E)	8.03	7.55	0	84.42	2,490	SANTOS & VALENTE (1990)
		1991/Summer	3 (N)	1.42	3.50	0	95.08	8,764	VALIATI & VALENTE (1996)
		1991/Summer	8 (E)	8.83	1.32	0	89.85	3,782	VALIATI & VALENTE (1996)
		1991/Autumn	2 (N)	0	0.88	0	99.12	1,016	VALIATI & VALENTE (1996)
		1991/Autumn	8 (E)	17.48	0	0	82.52	978	VALIATI & VALENTE (1996)
		1991/Winter	4	0.35	5.94	0	93.71	780	VALIATI & VALENTE (1996)
		1991/Winter	2 (N)	0	2.33	0	97.67	86	VALIATI & VALENTE (1996)
		1991/Spring	4	0	0	0	100	182	VALIATI & VALENTE (1996)
		1991/Spring	5	0	0	0	100	273	VALIATI & VALENTE (1996)
		1992/Summer	3 (N)	0	3.40	0	96.60	589	VALIATI & VALENTE (1996)
		1992/Summer	9 (N)	11.90	5.95	0	82.15	381	VALIATI & VALENTE (1996)
		1992/Autumn	8 (E)	27.80	10.03	0	62.17	1,525	VALIATI & VALENTE (1996)
		2004/Summer	3 (N)	0.12	20.06	35.15	44.67	1,630	Present study
		2004/Summer	4	0.70	11.16	20.70	67.44	430	Present study
		2004/Summer	5	0	27.91	18.60	53.49	43	Present study
		2004/Summer	8 (E)	0	0	30.88	69.12	68	Present study
		2004/Summer	10 (N)	0	19.88	71.08	9.04	166	Present study
		2004/Summer	9 (N)	0	5.52	79.55	14.94	308	Present study
		2004/Summer	11 (E)	0	2.01	27.76	70.23	299	Present study
		2004/Summer	12 (N)	3.23	37.10	43.55	16.13	62	Present study
		2004/Autumn	2 (N)	0	16.28	46.48	37.25	639	Present study
		2004/Autumn	3 (N)	0	1.61	54.50	43.90	934	Present study
		2004/Autumn	4	0.38	31.38	30.77	37.54	325	Present study
		2004/Autumn	5	0	21.88	35.16	42.97	128	Present study
		2004/Autumn	8 (E)	2.53	20.54	55.06	21.88	672	Present study
		2004/Winter	2 (N)	0	31.23	4.04	64.74	1,313	Present study
		2004/Winter	3 (N)	0	18.89	1.11	80.00	90	Present study
2004/Winter	4	0	12.11	6.77	81.13	355	Present study		
2004/Winter	5	0.33	36.46	4.54	58.70	661	Present study		
2004/Winter	8 (E)	0	72.84	0	27.16	81	Present study		
2004/Spring	2 (N)	0	7.14	3.57	89.30	981	Present study		
2004/Spring	4	0	2.03	0.68	97.29	295	Present study		
2004/Spring	5	0	7.29	0.99	91.72	302	Present study		
2004/Spring	8 (E)	0	17.39	17.39	65.22	23	Present study		

Table II. (cont.)

Collection U.L. site	Year/Season	Trophic resources	<i>D. willistoni</i> subgroup			Other species (%)	Total	References	
			<i>D. paulistorum</i> (%)	<i>D. willistoni</i> (%)	<i>Z. indianus</i> (%)				
MTS	Low	1987/Autumn	8 (E)	45.65	16.39	0	37.96	793	SANTOS & VALENTE (1990)
		1991/Summer	8 (E)	11.46	0.16	0	88.38	5,467	VALIATI & VALENTE (1996)
		1991/Autumn	8 (E)	25.79	2.16	0	72.06	4,033	VALIATI & VALENTE (1996)
		1991/Winter	8 (E)	8.47	2.45	0	89.08	2,821	VALIATI & VALENTE (1996)
		1992/Autumn	8 (E)	64.84	0.94	0	34.22	640	VALIATI & VALENTE (1996)
		2004/Summer	4	0	4.42	22.79	72.79	452	Present study
		2004/Summer	5	0	10.14	26.09	63.77	207	Present study
		2004/Summer	8 (E)	1.36	19.01	24.43	55.20	221	Present study
		2004/Autumn	2 (N)	0	34.99	26.58	38.43	1,772	Present study
		2004/Autumn	4	0	18.02	49.75	32.23	605	Present study
	High	2004/Autumn	5	0	21.17	44.97	33.86	378	Present study
		2004/Autumn	8 (E)	5.18	39.65	23.30	31.88	734	Present study
		2004/Autumn	13 (N)	0	26.73	37.63	35.64	101	Present study
		2004/Winter	4	0	10.23	3.26	86.51	215	Present study
		2004/Winter	5	0.77	23.66	0	75.57	131	Present study
		2004/Winter	8 (E)	0	8.43	0	91.60	238	Present study
		2004/Spring	4	0	4.26	0	95.74	94	Present study
		2004/Spring	5	4.12	8.25	0	87.63	97	Present study
		2004/Spring	8 (E)	28.49	23.31	6.77	41.43	502	Present study
		GKP	Low	2004/Summer	4	0.35	32.87	3.85	62.94
2004/Summer	5			0.76	65.02	4.56	29.66	263	Present study
2004/Autumn	4			0	35.58	28.84	35.58	163	Present study
2004/Autumn	5			1.57	65.75	9.84	22.84	254	Present study
2004/Winter	4			0	2.01	0	97.99	249	Present study
2004/Winter	5			0	5.88	0	94.12	119	Present study
2004/Spring	4			1.89	7.55	0	90.57	53	Present study
2004/Spring	5			1.96	17.65	0	80.39	51	Present study
2004/Spring	14 (E)			28.38	5.41	0	66.22	74	Present study

Yearly variations in the frequencies of several insect groups have also been recorded by WOLDA (1992), in a 14-year study conducted in a Panamanian forest. The author verified that some populations remained notably constant, while others suffered marked fluctuations. Furthermore, some species were extinguished, at the same time that others – initially rare or even absent from that environment – became abundant with time. Such observations unveil the fundamental importance of the long-term screening of drosophilid populations in Porto Alegre to assess the alternating trends in *D. willistoni* and *D. paulistorum* abundances, as well as in *D. melanogaster* subgroup and *Z. indianus* frequencies.

The present study afforded, for the first time, to detect the oscillations in *D. paulistorum* frequencies since the organism's arrival in Porto Alegre, before and after the arrival of *Z. indianus*. Figure 4 illustrates the occurrences of *D. paulistorum*, *D. willistoni*, *Z. indianus*, and of the remaining species for the 2004 seasons, irrespective of collection site. The highest *D. paulistorum* frequency (2.2% in spring) matches the lowest *Z. indianus* frequency (3.5%), and specially the lowest *D. willistoni* frequency (3.4%). It may be advocated that the low 2004 *D. paulistorum* frequency relates indirectly with the presence of *Z. indianus*. This assumption is based on the probable interaction between *Z. indianus* and *D. willistoni*, as the latter species and *D. paulistorum* are not found in different trophic resources – an observation made by SANTOS & VALENTE (1990) and by VALIATI & VALENTE (1996).

Figure 5 illustrates *D. paulistorum* and *D. willistoni* frequencies for years 1986 to 1992 in three Porto Alegre

sites with different urbanization grades. We observe that *D. paulistorum* was differentially distributed in these environments. The species preferred low urbanization grade sites, specially MTS, in which the number of individuals collected was significantly higher in contrast with BOG values ( $Z=2.98$ ;  $p<0.01$ ) and FAP ( $Z=2.08$ ;  $p<0.05$ ). Figure 6 is a representation of the 2004 frequencies of *D. paulistorum*, *D. willistoni*, and *Z. indianus* for the collections made in sites FAP, BOG, and MTS, which were also evaluated in previous years, and in GKP, likewise investigated by SILVA *et al.* (2005b). The distribution pattern of *D. paulistorum* frequencies in low urbanization grade sites was observed to have been constant throughout 2004; however, a marked decrease in the species' abundance is now observed in all environments studied (Figs. 5 and 6). The Kruskal-Wallis analysis revealed that this decrease in *D. paulistorum* abundance was significant in sites FAP ( $Z=3.16$ ;  $p<0.01$ ), BOG ( $Z=3.24$ ;  $p<0.01$ ), and MTS ( $Z=4.44$ ;  $p<0.01$ ) throughout 2004. It is remarkable that *D. paulistorum* had previously been sampled in MTS at a frequency that reached 43.3% (Tab. II).

Several aspects may lie behind this decline in *D. paulistorum* populations. For instance, the urban growth experienced in Porto Alegre city since the 1980's might have altered urbanization grades after its first classification, made by RUSZCZYK (1986). Perhaps the area where BOG is located – in which tall buildings have been erected and a wide avenue has recently been built – should be re-classified as a medium urbanization grade area, while MTS and GKP are still low urbanization grade sites.

Contrary to what was observed for *D. paulistorum*, the likely alterations in urbanization grades in Porto Alegre have not affected *D. willistoni* frequencies to a significant extent ( $p < 0.05$ ), since the species has been shown to inhabit all these different collection sites. DOBZHANSKY (1965) compared *D. willistoni* and *D. paulistorum* capacities to explore novel environments, and suggested that *D. willistoni* alone, due to the species' genetic characteristics, revealed a trend to become a colonizing species. Though this notion has been challenged by the data in SANTOS & VALENTE (1990) and in VALIATI & VALENTE (1996) – obtained when *D. paulistorum* expansion was clearly taking place in Porto Alegre – our present findings have led us to consider the DOBZHANSKY (1965) hypothesis, as *D. paulistorum* is once again found in less urbanized environments only.

Just like *D. willistoni*, *Z. indianus* has been captured in almost all Porto Alegre collection sites, with almost all trophic resources. This evinces its success as invader species in the town (Fig. 6 and Tab. II). FERREIRA & TIDON (2005), while studying drosophilid potentials to colonize sites of different urbanization grades, came to similar results for *Z. indianus*.

Among the sites evaluated in the present study, special attention is due to GKP, where the lowest *Z.*

*indianus* frequencies were observed. Even so, this difference was statistically significant only when the species frequency were compared to its occurrence in the highest urbanization grade site, FAP ( $Z = 3.06; p < 0.01$ ). Among the places investigated, GKP has some thickly forested spots that may explain the decreased *Z. indianus* frequencies there observed. In Central Brazil, TIDON *et al.* (2003) have reported higher abundance values for the species in disturbed environments limited to the outer stretches of gallery forests. FERREIRA & TIDON (2005) verified that the majority of endemic Drosophilidae species are not capable of colonizing urban environments. The conclusion was similar to that in the study by AVONDET *et al.* (2003): some Drosophilidae species may indicate not only the occurrence of environmental changes, but also the degree of environmental disturbance revealed by the alterations in species frequencies. Thus, these species are efficient indicators of ecological changes brought about by urbanization.

According to PARSONS (1987), cities are relatively unfavourable habitats to native species. This is because these species cannot rely on the adaptive conditions necessary to thrive in a disturbed setting which, as a consequence, is suitable to the colonization by exotic species. The decline in arthropod richness observed with

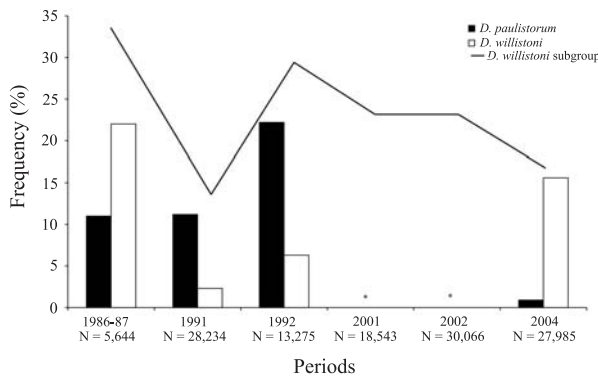


Fig. 3. Mean percent frequencies of the *D. willistoni* subgroup in years 1986 to 2004 (represented by a line), and of *D. paulistorum* and *D. willistoni* in years 1986 to 1992 and in 2004 year in Porto Alegre city, irrespective of collection site, season and trophic resource (N, total number of specimens; \*, species of the *D. willistoni* subgroup were not discriminated by the authors (SILVA *et al.*, 2005a, b)).

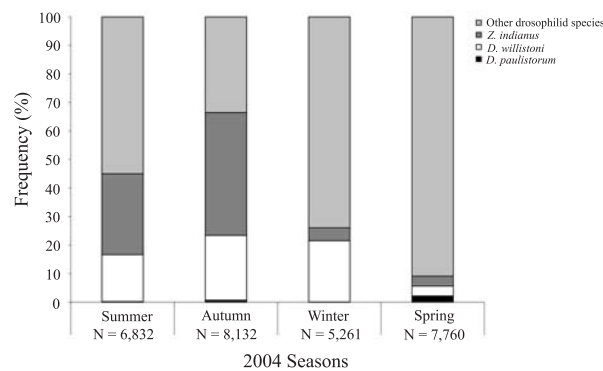


Fig. 4. Mean percent frequencies of *D. paulistorum*, *D. willistoni*, *Z. indianus*, and other drosophilid species collected in the four seasons of 2004, in the four collection sites of Porto Alegre city, southern Brazil (N, total number of specimens).

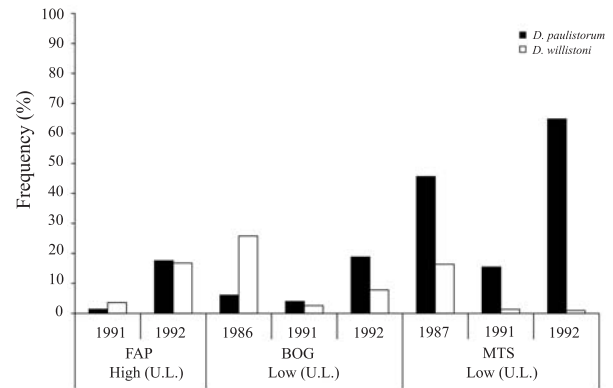


Fig. 5. Mean percent frequencies of *D. paulistorum* and *D. willistoni* in years 1986 to 1992 in collection sites FAP, BOG, and MTS, Porto Alegre, southern Brazil, irrespective of season and trophic resources of collection (U.L., urbanization level).

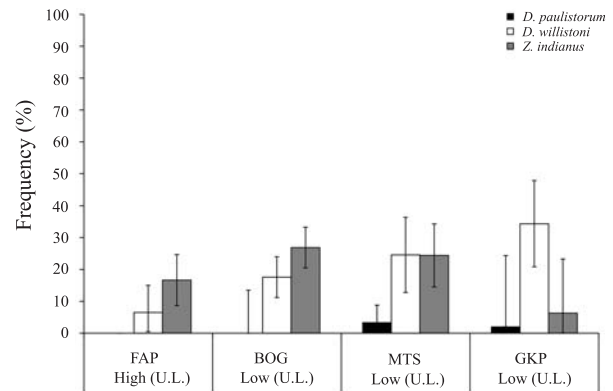


Fig. 6. Means and standard deviations of *D. willistoni*, *D. paulistorum* and of *Z. indianus* in year 2004, in four collection sites in Porto Alegre city, southern Brazil, irrespective of the season and trophic resources of collection (U.L., urbanization level).

increased urbanization grades has been imputed to a series of factors, such as the isolation of native populations into smaller zones within their natural environment, as well as to pollution and to the destruction of feeding and breeding sites (McINTYRE, 2000). This drop in species richness within an urbanization gradient has also been observed for birds (MARZLUFF, 2001), mammals (MACKIN-ROGALSKA *et al.*, 1988), and butterflies (BLAIR & LAUNER, 1997). As a rule, more intensely urbanized areas are the home of a small group of exotic species and of an even smaller number of native species, as compared to the suburbs. In our study, the only high urbanization grade site (FAP) presented the lowest species diversity (20), with 16 native and 4 exotic species captured. In low urbanization grade sites (BOG, MTS, GKP), the number of exotic species oscillated between 4 and 5. *Drosophila simulans*, *D. immigrans* Sturtevant, 1921, and *Z. indianus* were common to all these sites, and were also captured in FAP. Nevertheless, native species diversity (21 to 23) in less urbanized locations was over 30% higher (31.2% to 43.7%) than in FAP. These suburban areas have green spots, remnants of the natural habitats of these native species and that may work as ecological refuges, which diminish local extinctions and contribute to greater richness of native species.

Figure 7 shows the frequency oscillations for *Z. indianus* and for the *D. willistoni* subgroup, as well as the mean maximum and minimum temperatures and respective standard deviations for the seasons in years 2001, 2002, and 2004 in Porto Alegre city. In 2001 and 2002, *D. willistoni* subgroup frequency was observed to decrease significantly ( $r=0.91$ ;  $p<0.01$ ) in the seasons when *Z. indianus* frequency increased, which however was not observed in 2004 ( $r=0.60$ ;  $p<0.05$ ). The growth of *Z. indianus* populations was observed in summer and spring, when mean temperatures were higher. Yet, *Z. indianus* frequencies are more intimately correlated to mean minimum temperatures ( $r=0.61$ ;  $p<0.01$ ) than to mean maximum temperatures ( $r=0.32$ ;  $p<0.05$ ); still, when global mean temperatures are considered, such correlation is not always observed. For instance, it was only in the 2002 collections that a correlation between mean temperatures and higher *Z. indianus* frequencies was

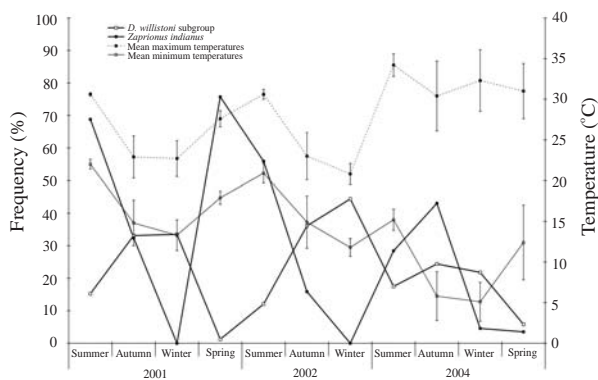


Fig. 7. Mean percent frequencies of the *D. willistoni* subgroup and of *Z. indianus*, and mean maximum and minimum temperatures and respective standard deviations in 11 seasons in years 2001, 2002, and 2004, in Porto Alegre city, southern Brazil.

established ( $r=0.99$ ;  $P<0.01$ ). TIDON *et al.* (2003) did not find any correlation between *Z. indianus* frequencies and mean temperatures, while TIDON (2006) reported a significant though low correlation with the temperature in some study sites in the Brazilian Cerrado biome. So, mean temperatures do not always reflect what actually happens with temperature extremes (maximum and minimum values), which may be more informative to evaluate oscillations in drosophilid assemblies. Therefore, very low temperatures constitute limiting factors to the population size of *Z. indianus*, as observed in winters, specially in 2004, when minimum temperatures were the lowest recorded throughout the study period. In like manner, *D. willistoni* subgroup frequencies are temperature-dependent also in Porto Alegre city. However, differently from what was observed for *Z. indianus*, the subgroup presented a negative correlation with maximum temperatures ( $r=0.72$ ;  $p<0.01$ ), and had the lowest frequencies in hotter seasons. In a recent paper that studied drosophilid composition across an urban gradient in Florianópolis city, state of Santa Catarina, southern Brazil, M. S. Gottschalk (pers. comm.), observed exotic species to predominate in periods of moderate and high temperatures, while native species prevailed in colder weather.

As a final point, the expressive decrease in population size suffered by *D. paulistorum* in the past few years is also reflected in chromosomal inversion polymorphisms. In the study by SANTOS & VALENTE (1990), the number of different heterozygous chromosomal inversions detected in all populations of Porto Alegre was 18; but VALIATI & VALENTE (1997) detected 23, of which only six had been found in the first study mentioned. In the present study, the analysis of chromosomal polymorphism in *D. paulistorum* populations in Porto Alegre revealed the occurrence of only three heterozygous chromosomal inversions (data not shown).

The temperature of the planet has risen roughly 0.8°C in the past 100 years, and around 0.2°C every decade in the past 30 years (HANSEN *et al.*, 2006). Recent studies have shown that several genetic changes in different organisms seem to be associated to these climate changes, called global warming (PARMESAN & YOHE, 2003; COTTON, 2003; LEVITAN & ETGES, 2005; BRADSHAW & HOLZAPFEL, 2006). BALANYÀ *et al.* (2006, 2007) studied 26 populations of *D. subobscura* Collin & Gordon, 1936 (COLLIN, 1936) distributed across Europe and South and North Americas. The data obtained for the past 24 years demonstrate that the temperature has risen in 22 of the places investigated. The authors verified that the frequency of chromosomal inversions typically observed in species inhabiting low latitudes, i.e., warmer regions, has increased swiftly in 25 populations studied. These fast alterations in chromosomal arrangement frequency reflect the adaptation response by some genes to climate change across the geographic distribution of *D. subobscura* (HEERWAARDEN & HOFFMANN, 2007) and *D. melanogaster* (UMINA *et al.*, 2005).

All in all, there appears to be a decrease in the colonizing potential of *D. paulistorum* in Porto Alegre, made evident by the drop in the species' frequency in



recent years. This fact may be linked to the city's growth, as well as to the natural population decline that may possibly take place in the long run. This decline may also bear a relationship with climatic changes, such as variations in minimum and maximum temperature amplitudes. Moreover, the presence of *Z. indianus* seems to contribute to this scenario, as the species might be interfering in the interactions between native species.

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