

# Breeding sites of drosophilids (Diptera) in the Brazilian Savanna. I. Fallen fruits of *Emmotum nitens* (Icacinaceae), *Hancornia speciosa* (Apocynaceae) and *Anacardium humile* (Anacardiaceae)

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**ABSTRACT.** Breeding sites of drosophilids (Diptera) in the Brazilian Savanna. I. Fallen fruits of *Emmotum nitens* (Icacinaceae), *Hancornia speciosa* (Apocynaceae) and *Anacardium humile* (Anacardiaceae). In this study, drosophilids that bred in fruits of three common plant species of the Brazilian Savanna were investigated: *Emmotum nitens*, *Hancornia speciosa* and *Anacardium humile*, along with the temporal and spatial distribution of these insects among fruits obtained from six individuals of *E. nitens*. Fallen fruits were collected in natural environments, placed on moist sand in individual containers and all drosophilids that emerged from these resources during 15 days were collected, counted and identified. From 3,651 fruits collected (3,435 of *E. nitens*, 179 of *A. humile* and 37 of *H. speciosa*) 4,541 flies emerged and were classified into 19 species of Drosophilidae. Their distribution was unequal among the three resources, also over time, and among the six individuals of *E. nitens*. Such fluctuations probably reflect the availability of resources in time and space and probably the action of selective factors such as larval competition.

**KEYWORDS.** Biodiversity; Cerrado biome; *Drosophila*.

**RESUMO.** Sítios de criação de drosofilídeos (Diptera) no bioma Cerrado. I. Frutos caídos de *Emmotum nitens* (Icacinaceae), *Hancornia speciosa* (Apocynaceae) e *Anacardium humile* (Anacardiaceae). Neste estudo, são investigados os drosofilídeos que se criam em frutos de três espécies de plantas comuns do Cerrado brasileiro: *Emmotum nitens*, *Hancornia speciosa* e *Anacardium humile*, juntamente com a distribuição temporal e espacial desses insetos entre os frutos obtidos de seis indivíduos de *E. nitens*. Frutos recolhidos sobre a serrapilheira, em ambientes naturais, foram mantidos no laboratório e os drosofilídeos que deles emergiram foram contados e identificados. Dos 3.651 frutos coletados (3.435 de *E. nitens*, 179 de *A. humile* e 37 de *H. speciosa*) emergiram 4.541 drosofilídeos, classificados em 19 espécies. A distribuição dessas espécies foi desigual entre os três tipos de recursos, ao longo do tempo, e também entre os seis indivíduos de *E. nitens*. Essas flutuações refletem a disponibilidade dos recursos no tempo e no espaço, e provavelmente a ação de forças seletivas como a competição entre as larvas.

**PALAVRAS-CHAVE.** Biodiversidade; *Drosophila*; savana brasileira.

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The distribution of organisms varies in space and time, and is strongly influenced by environmental heterogeneity. Changes in temperature, humidity, and resource availability, among other factors, can alter the size, density, and distribution of populations. A portion of these variations has evolutionary meaning, because it can alter the structure and genetic composition of the populations. However, although the relationships between organisms and environments are a central issue in ecology, they are still poorly understood (Begon *et al.* 2006).

Drosophilids are considered excellent models for biological research (Powell 1997), but little is known about their ecology, especially in tropical environments (Val *et al.* 1981; Tidon 2006). These flies breed in a wide variety of organic substrates, including fallen fruits, flowers, slime fluxes, and fleshy fungi (Carson 1971). During their decomposition, these substrates attract flies due the presence of microorganisms, principally yeasts, which constitute the alimentary base for these insects

(Powell 1997). Tropical zones appear to be characterized by an “unlimited” supply of available fruits for drosophilids, and previous papers identified the drosophilid species associated with different fruits in Africa (Lachaise & Tsacas 1983) and Southern South America (Brncic & Valente 1978; Araújo & Valente 1981; Pereira *et al.* 1983; Valente & Araújo 1986; Bonorino & Valente 1989; Valente & Araújo 1991; Rohde & Valente 1996; Vilela 2001). In the Brazilian Savanna, however, the only fruit studied thus far was *Solanum lycocarpum* (Solanaceae) (Leão & Tidon 2004). Valente & Araújo (1986) have investigated two species in the family Anacardiaceae (*Mangifera indica* and *Spondias mombin*) as breeding sites for drosophilids, but this is the first study investigating drosophilids associated with species of Apocynaceae and Icacinaceae in the Neotropical Region.

The Brazilian Savanna, locally known as the Cerrado biome, is the largest region of savanna in a single country, covering approximately 2 million km<sup>2</sup> (Oliveira & Marquis 2002). It is

considered a biodiversity hotspot, because it is one of the least known and most endangered areas in the world, having had more than 60% of its native vegetation destroyed, mainly in consequence of human activities (Myers *et al.* 2000). Its climate is seasonal, wet from October to March and dry from April to September, with temperatures ranging from 22 °C to 27°C (Klink & Machado 2005). This savanna is a mosaic of physiognomic vegetation forms, ranging from dense grassland, usually with a sparse cover of shrubs and small trees, to almost closed woodland, with a canopy height of 12–15 m (Ratter *et al.* 1997). These vegetation types have different structures and species composition, and the transition between them varies from sharp to gradual.

The drosophilid assemblages of the Brazilian Savanna vary in space and time, but the causes of these fluctuations are still unknown (Tidon 2006). According to Wolda (1988), insect populations can respond to micro and macroclimatic changes, as well as to alterations in resource availability. Therefore, understanding the feeding and breeding habits of these flies is important to explain their relationship to the environment (Toda 1973; Tidon 2006). This study is part of a broader project, aimed at investigating the relationship between drosophilid flies and the environment where they occur in the Brazilian Savanna. The objectives here were (1) to characterize the assemblages of drosophilids breeding in fallen fruits of three common plants of the Brazilian Savanna: *Emmotum nitens* (Icacinaeae), *Hancornia speciosa* (Apocynaceae) and *Anacardium humile* (Anacardiaceae) and (2) to evaluate the spatial and temporal distribution of these insects among fruits obtained from individuals of *E. nitens*.

## MATERIAL AND METHODS

Fallen fruits of the focal species were collected in fragments of natural vegetation at two sites in the municipality of Sobradinho, a town of Distrito Federal located in the vicinity of Brasilia. At site 1 (ca. 37.2 ha, located at 15° 37' S; 47° 47' W), fallen fruits were obtained around six trees of *Emmotum nitens* and 14 trees of *Hancornia speciosa*, in environments of dystrophic *cerradão* and *cerrado sensu stricto*, respectively. At site 2 (ca. 96.5 ha, located at 15° 38' S; 47° 44' W), fallen fruits were collected around 32 trees of *Anacardium humile*, in an area with a predominance of *campo sujo*. Detailed descriptions of these vegetation types can be found in Oliveira & Marquis (2002). The geographic locations were obtained with a Garmin II GPS. Fruits were collected weekly, from October 2005 to February 2006, which covered the dispersal period of the focal plants. We collected all fruits found on the ground around each focal individual. The sample size of each collection, however, varied in accordance with the availability of fruits.

*Emmotum nitens* Miers belongs to the pantropical family Icacinaceae, which includes 12 American genera whose center of origin is the Amazon basin (Barroso *et al.* 1984). It is popularly known as *sobre* or *faia*, and can reach 10m in height. This species is considered an indicator of dystrophic

*cerradões*, which are areas with nutrient poor soil and predominately evergreen vegetation (Ratter *et al.* 1973). The fruits are fleshy, about 2 cm in diameter and 5 g in weight, and have an unpleasant odor. They are resistant due to a woody endocarp involving the seed that acts as a barrier against insects, fire and other external factors.

*Hancornia speciosa* Gomez belongs to the widely distributed family Apocynaceae, which includes more than 4,500 species classified into 415 genera. Commonly known as *mangaba*, this fruit is berry, ellipsoid to globoid, yellowish green or rosy green, with viscous, whitish pulp, from 2.6 to 4 cm in diameter (Almeida *et al.* 1998).

*Anacardium humile* St. Hil. is classified in the family Anacardiaceae, which includes 70 genera and about 600 species of tropical and subtropical distribution, with some representatives in temperate areas. Popularly known as *cajuzinho-do-cerrado*, this is a typical plant of *campo sujo* and *cerrado*. Its fruit is a true nut, and its comestible part is the pseudofruit, located at the apex of the fruit, approximately 1.5 cm in diameter, which is red, claviform, and has white and succulent pulp (Almeida *et al.* 1998).

All fruits found on the ground in the vicinity of each individual were collected, placed in a separate labeled plastic bag and taken to the laboratory where each bag was weighed and the number of fruits counted. After counting, fruits obtained from the same tree were placed on a bed of moist sand in individual containers plugged with synthetic foam stoppers. The containers were maintained at constant temperature (25±1 °C) and photoperiod (13 h: 11 h, Light: Dark). Water was added when necessary to prevent desiccation using a manual plant sprayer. All emerged insects were removed daily with a small vacuum cleaner. After the first emergence this procedure was continued for only 15 days in order to avoid overlapping of generations since if any individual was not collected on the first day this is the minimum interval for the second generation to emerge. The captured specimens were identified using keys, descriptions and, in some cases, by the analysis of the male terminalia (Freire-Maia & Pavan 1949; Pavan & Nacur 1950; Frota-Pessoa 1954; Magalhães 1962; Val 1982; Vilela 1983; Vilela & Bächli 1990; Chassagnard & Tsacas 1993). The species were classified into three groups: 1: *Zaprionus indianus* (ZAP) which was recently introduced into the South America (Vilela 1999), 2: other exotic species (EXO), and 3: endemic species of the Neotropical Region (NEO). References to the taxonomic authorities can be found in the Drosophilidae taxonomy database compiled by Bächli (2008) and Brake & Bächli (2008). Voucher specimens of the captured insects were deposited in the collection of the Laboratório de Biologia Evolutiva of the Instituto de Ciências Biológicas of the Universidade de Brasília.

Weekly-based accumulation curves for drosophilid species were compiled separately for each plant species, to assess sample representivity. Species accumulation curves, Chao 1, were generated using Estimate S 7.5 (Colwell 2005). The drosophilids that emerged from each resource were analyzed by composition and relative abundance of species and by the

density of flies per gram of fruit. Tests for statistically significant differences in the relative abundance of Neotropical and exotic species among the three plant species were done using a Chi-square test at  $\alpha=0.01$  significance level. For *Emmotum nitens*, the density of flies was tested for spatial (six trees) and temporal (five months) variables by simple linear regression.

## RESULTS

From the 3,651 fruits collected (3,435 of *Emmotum nitens*, 37 of *Hancornia speciosa*, and 179 of *Anacardium humile*) 4,541 drosophilids emerged and were classified into 16 species of *Drosophila* Fallén and one species of each of the following genera: *Rhinoleucophenga* Hendel, *Scaptodrosophila* Duda and *Zaprionus* Coquillett (Table I). Specimens of coleoptera, lepidoptera and species of the families Tephritidae (Diptera) and Vespidae (Hymenoptera) also emerged.

Although the accumulation curves did not reach an asymptote, the highest species richness seemed to be associated with *Emmotum nitens* and the lowest with *Anacardium humile* (Fig. 1). *Drosophila nebulosa* and *D. simulans* emerged from fruits of all plant species and were the only drosophilids registered in *A. humile*. The remaining fly species usually emerged from a single substrate type (Table I). The proportion of Neotropical and exotic species also varied among the three resources ( $\chi^2 = 6.63$ ;  $df = 1$ ;  $p < 0.01$ ): the

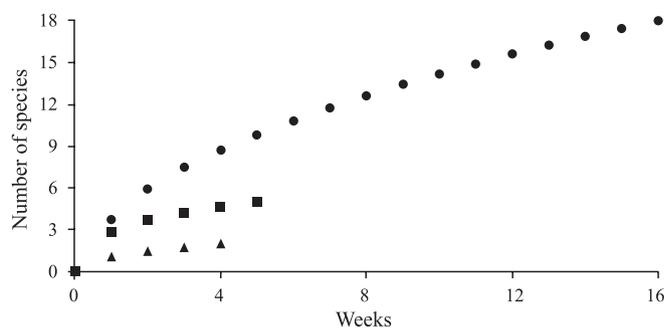


Fig. 1. Accumulation curves for drosophilid species that emerged from *Emmotum nitens* (●;  $n = 3435$ , from October 2005 to February 2006), *Hancornia speciosa* (■;  $n = 37$ , November 2005) and *Anacardium humile* (▲;  $n = 179$ , October 2005). Data randomized 1,000 times using Estimate S 7.5 (Colwell 2005).

fauna associated with *E. nitens* was dominated by Neotropical species, whereas in *A. humile* and *Hancornia speciosa* the exotics *D. simulans* and *Zaprionus indianus*, predominated respectively (Fig. 2).

The distribution of drosophilids in *Emmotum nitens* varied among the six trees and in successive months of collection (Fig. 3). Three of the six studied trees showed the highest richness, abundance and density of drosophilids (Table II). The abundance of flies was related to the weight of fruits of each tree ( $r^2 = 0.98$ ) as well as to the total number of fruits

Table I. Drosophilids emerged in laboratory from fallen fruits of *Emmotum nitens*, *Hancornia speciosa* and *Anacardium humile* collected from October 2005 to February 2006 in the municipality of Sobradinho, Distrito Federal, Brazil.  $n$  = number of fruits.

Drosophilid species	Plant species			Total
	<i>E. nitens</i> ( $n=3,435$ )	<i>H. speciosa</i> ( $n=37$ )	<i>A. humile</i> ( $n=179$ )	
<i>Drosophila nebulosa</i> Sturtevant, 1916	2,032	118	1	2,151
<i>Zaprionus indianus</i> Gupta, 1970	1,024	222	-	1,246
<i>D. willistoni</i> Sturtevant, 1916	875	-	-	875
<i>D. simulans</i> Sturtevant, 1919	117	2	19	138
<i>D. bocainensis</i> Pavan and da Cunha, 1947	57	-	-	57
<i>D. mediotriata</i> Duda, 1925	23	-	-	23
<i>D. cardini</i> Sturtevant, 1916	12	4	-	16
<i>Rhinoleucophenga</i> sp. A	-	12	-	12
<i>D. immigrans</i> Sturtevant, 1916	6	-	-	6
<i>D. cardinoides</i> Dobzhansky and Pavan, 1943	3	-	-	3
<i>D. paraguayensis</i> Duda, 1927	3	-	-	3
<i>Drosophila</i> sp. A	3	-	-	3
<i>D. sturtevanti</i> Duda, 1927	2	-	-	2
<i>D. arauana</i> Pavan and Nacur, 1950	1	-	-	1
<i>D. mercatorum</i> Patterson & Wheeler, 1942	1	-	-	1
<i>D. mesostigma</i> Frota-Pessoa, 1954	1	-	-	1
<i>D. ornatifrons</i> Duda, 1927	1	-	-	1
<i>D. polymorpha</i> Dobzhansky and Pavan, 1943	1	-	-	1
<i>Scaptodrosophila latifasciaeformis</i> Duda, 1940	1	-	-	1
Total number of drosophilids	4,163	358	20	4,541
Total fruit weight (g)	14,969	753	606	16,328
Drosophilids/g fruit	0.278	0.476	0.033	0.278

\* Singleton species were represented by males, except *S. latifasciaeformis*.

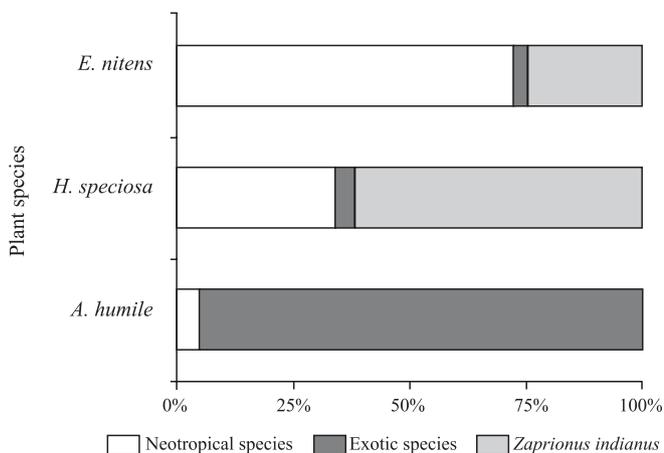


Fig. 2. Percentage of emergence of three categories of drosophilids in fruits of *Emmotum nitens*, *Hancornia speciosa*, and *Anacardium humile*.

produced along the months ( $r^2 = 0.95$ ). Trees that produced more fruits had longer fruiting periods, about three months. The population peak of drosophilid in fruits of *E. nitens* was in January, when the availability of fruits was also higher (Fig. 3).

## DISCUSSION

The drosophilid assemblages of the Brazilian Savanna vary in space and time, and can respond to micro and macroclimatic changes, as well as to alterations in resource availability. The fruits evaluated here are exploited by these flies in different manners.

An increase in the density of these flies does not necessarily correspond to an increase in species diversity. The highest density of drosophilids was recorded in fruits of *Hancornia speciosa*, but the highest richness occurred in *Emmotum nitens*. Rotting fruits of *E. nitens* were available in the environment for these insects throughout five months, and were used as breeding site by 18 species of drosophilids. *H. speciosa* and *Anacardium humile*, on the other hand, presented relatively briefer periods of fructification, one month each, and had fewer drosophilid species associated with them. These last two species of plant seems to be ephemeral resources that are exploited mainly by opportunistic species, such as *Drosophila nebulosa*, *D. simulans* and *Zaprionus indianus*, that belong to introduced and/or widely distributed species in South America (Tidon *et al.* 2003; Tidon 2006).

The highest diversity of drosophilids in *Emmotum nitens* is probably due to the type of environment where these plants live. Most species of these flies avoid environments that are too dry, bright or hot (Grossfield 1978), and are associated with forest habitats, such as the *cerradões* where *E. nitens* occurs. Therefore, we suggest that fallen fruits of *E. nitens* are an important resource for the maintenance of drosophilid populations, since this species produces fruits in habitats well suited for many species of drosophilids and for a relative long period of time.

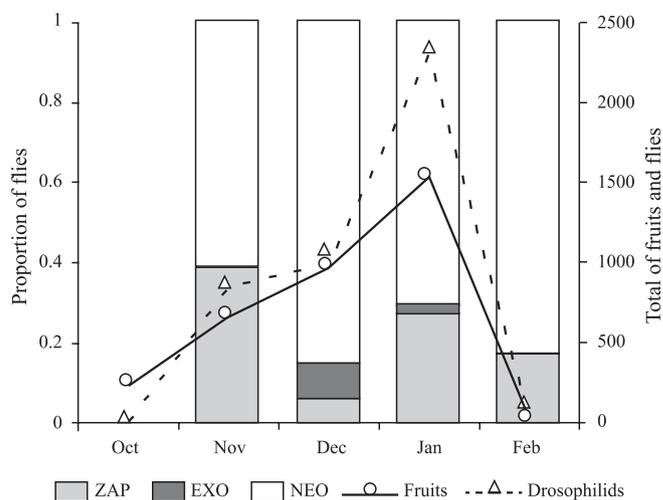


Fig. 3. Temporal fluctuation of the drosophilid assemblage breeding in *Emmotum nitens*, from October 2005 to February 2006. Bars represent the relative abundance of *Zaprionus indianus* (ZAP), Neotropical drosophilids (NEO) and exotic drosophilids, except *Z. indianus* (EXO). Lines represent the absolute abundance of flies and fruits over time.

Several drosophilid species avoid laying eggs on substrates with high densities of larvae (Medina-Muñoz & Godoy-Herrera 2005; Wertheim *et al.* 2006). Competition among larvae is probably higher in such substrates and as result this behavior would tend to decrease species richness. This may have occurred in *Hancornia speciosa*, from whose fruits emerged 222 individuals of *Zaprionus indianus*, 118 of *Drosophila nebulosa*, and 18 individuals classified into three other species. *Z. indianus* is a recently introduced species into South America (Vilela 1999), probably from African savannas very similar to the habitats where *H. speciosa* occurs. It is possible that the presence of eggs of this species is preventing the oviposition of Neotropical drosophilids, and therefore contributes to the low richness in this resource, where the density of flies was the highest. The association between *H. speciosa* and drosophilids may be a good model to test the hypothesis of competition between endemic and exotic species, and we intend to perform future studies to study this mechanism.

The distribution of drosophilid assemblages in *E. nitens* also seems to reflect the availability of fruits in space and time since the abundance of flies varied with the availability of fruits under each tree and over time. The population peak of drosophilids in *E. nitens* was at the height of the wet season (January) when the availability of fruits in general is higher (Almeida *et al.* 1998). The high availability of resources in this period certainly contributed to the growth of the drosophilid populations, which are consumers of the yeasts and bacteria that decompose these fruits. These results support those obtained by Souza-Silva *et al.* (2001), which showed that the largest flower-visiting flies' densities also occur when resource availability is high, given appropriate environmental conditions.

Table II. Relative abundance (%) of drosophilids emerging from fallen fruits from six trees of *Emmotum nitens*, from October 2005 to February 2006, in the municipality of Sobradinho, Distrito Federal, Brazil.

Drosophilid species	Trees						Total
	1	2	3	4	5	6	
<i>Drosophila nebulosa</i>	43.69	59.08	53.33	71.33	100	-	48.81
<i>Zaprionus indianus</i>	24.10	24.66	28.03	18.18	-	100	24.60
<i>D. willistoni</i>	30.19	0.27	8.72	9.09	-	-	21.02
<i>D. simulans</i>	1.31	9.76	1.71	-	-	-	2.81
<i>D. bocainensis</i>	0.26	3.66	3.76	0.70	-	-	1.37
<i>D. mediotriata</i>	-	0.54	3.25	-	-	-	0.55
<i>D. cardini</i>	-	0.95	0.85	-	-	-	0.29
<i>D. immigrans</i>	0.19	-	-	0.70	-	-	0.14
<i>Drosophila</i> sp. A	0.04	0.27	-	-	-	-	0.07
<i>D. cardinoides</i>	-	0.41	-	-	-	-	0.07
<i>D. paraguayensis</i>	0.07	-	0.17	-	-	-	0.07
<i>D. sturtevantii</i>	0.04	-	0.17	-	-	-	0.05
<i>D. arauna</i>	0.04	-	-	-	-	-	0.02
<i>D. mercatorum</i>	0.04	-	-	-	-	-	0.02
<i>D. mesostigma</i>	0.04	-	-	-	-	-	0.02
<i>D. ornatifrons</i>	-	0.14	-	-	-	-	0.02
<i>D. polymorpha</i>	-	0.14	-	-	-	-	0.02
<i>Scaptodrosophila latifasciaeformis</i>	-	0.14	-	-	-	-	0.02
Total number of drosophilids	2,680	738	585	143	11	6	4,163
Total number of fruits	1,855	526	705	231	81	37	3,435
Total fruit weight (g)	8,419	2,317	2,827	1,050	202	154	14,969
Drosophilids/g fruit	0.318	0.319	0.207	0.136	0.054	0.039	0.278

Regarding the drosophilid assemblage composition in *Emmotum nitens*, the relative abundance of Neotropical species was always higher than that of exotics throughout the period of this study. These data confirm the idea that fallen fruits of this plant species represent an important resource for the maintenance of native drosophilids in the Cerrado biome.

In the tropics, where seasonal variation in temperature tends to be low, seasons usually reflect variations in precipitation and/or intensity of radiation. Understanding how tropical insect populations respond to seasonal variation is fundamental to explain their phenological patterns and life histories (Braby 1995; Pinheiro *et al.* 2002).

In conclusion, this study showed that drosophilid assemblages vary in space and time among resources, that the abundance of flies responds to resource availability, and that decaying fruits of *Emmotum nitens* are important breeding sites for Neotropical drosophilids.

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## REFERENCES

- Almeida, S. P.; C. E. B. Proença; S. M. Sano & J. F. Ribeiro. 1998. **Cerrado: espécies vegetais úteis**. Planaltina. Embrapa-CPAC. xiii+464 p.
- Araújo, A. M. & V. L. S. Valente. 1981. Observações sobre alguns lepidópteros e drosofilídeos do Parque do Turvo, RS. **Ciência e Cultura** 33: 1485–1490.
- Bächli, G. 2008. TaxoDros: The database on taxonomy of Drosophilidae. Consulted November 2008. URL: <http://taxodros.unizh.ch/>.
- Barroso, G. M.; A. L. Peixoto; C. G. Costa; C. L. F. Ichaso & E. F. Guimarães. 1984. **Sistemática de angiospermas do Brasil**. Viçosa. Imprensa Universitária-UFV. 377 p.
- Begon, M.; C. R. Townsend & J. L. Harper. 2006. **Ecology: From Individuals to Ecosystems** (4th edition). Oxford. Blackwell Publishing. xii+738 p.
- Bonorino, C. B. C. & V. L. S. Valente. 1989. Studies on wild and urban populations and breeding sites of *Drosophila nebulosa*. **Revista Brasileira de Biologia** 49: 771–776.
- Braby, M. F. 1995. Seasonal changes in relative abundance and spatial-distribution of Australian lowland tropical satyrine butterflies. **Australian Journal of Zoology** 43: 209–229.
- Brake, I. & G. Bächli. 2008. Drosophilidae (Diptera). In: **World Catalogue of Insects** 9: 1–412.
- Brcic, D. & V. L. S. Valente. 1978. Dinâmica de comunidades de *Drosophila* que se estabelecem em frutos silvestres no Rio Grande do Sul. **Ciência e Cultura** 30: 1104–1111.
- Carson, H. L. 1971. **The ecology of Drosophila breeding sites**. Harold L. Lyon Arboretum Lecture. Honolulu. University of Hawaii Press. 28 p.
- Chassagnard, M. T. & L. Tsacas. 1993. The subgenus *Zaprionus* s.str. Definition of species groups and revision of the *Vittiger* subgroup (Diptera, Drosophilidae). **Annales de la Societe Entomologique de France** 29: 173–194.
- Colweel, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Freire-Maia, N. & C. Pavan. 1949. Introdução ao estudo da drosófila. **Cultus** 1: 1–171.
- Frota-Pessoa, O. 1954. Revision of the tripunctata group of *Drosophila* with description of fifteen new species (Drosophilidae, Diptera). **Arquivos do Museu Paranaense** 10: 253–304.

- Grossfield, J. 1978. Non-sexual behavior of *Drosophila*, p. 1–126. In: Ashburner, M. & T. R. F. Wright (eds.). **The genetics and biology of *Drosophila***, v. 2b. London and New York. Academic Press. 452 p.
- Klink, C. A. & R. B. Machado. 2005. Conservation of the Brazilian Cerrado. **Conservation Biology** 19: 707–713.
- Lachaise, D. & L. Tsacas. 1983. Breeding-sites in tropical African Drosophilids, p. 221–332. In: Ashburner, M.; H. L. Carson & J. N. Thompson (eds.). **The genetics and biology of *Drosophila***, v. 3a. London. Academic Press. 382 p.
- Leão, B. F. D. & R. Tidon. 2004. Newly invading species exploiting native host-plants: the case of the African *Zaprionus indianus* (Gupta) in the fruits of the native Brazilian Cerrado (Diptera, Drosophilidae). **Annales de la Societe Entomologique de France** 40: 285–290.
- Magalhães, L. E. 1962. Notes on the Taxonomy, Morphology, and Distribution of the *saltans* group of *Drosophila*, with Descriptions of four new Species. **The University of Texas Publications** 6205: 134–154.
- Medina-Muñoz, M. C. & R. Godoy-Herrera. 2005. Dispersal and pupation behavior of Chilean sympatric *Drosophila* species that breed in the same site in nature. **Behavioral Ecology** 16: 316–322.
- Myers, N.; R. A. Mittermeyer; C. G. Mittermeyer; G. A. B. Fonseca & J. Kent. 2000. Biodiversity spots for conservation priorities. **Nature** 403: 853–858.
- Oliveira, P. S. & R. J. Marquis. 2002. **The Cerrados of Brazil**. New York. Columbia University Press. x+398 p.
- Pavan, C. & J. Nacur. 1950. Duas novas espécies de *Drosophila* (Diptera) do grupo *annulimana*. **Dusenya** 1: 263–274.
- Pereira, M. A. Q. R.; C. R. Vilela & F. M. Sene. 1983. Notes on breeding and feeding sites of some species of the repleta group of the genus *Drosophila* (Diptera, Drosophilidae). **Ciência e Cultura** 35: 1313–1319.
- Pinheiro, F.; I. R. Diniz; D. Coelho & M. P. S. Bandeira. 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. **Austral Ecology** 27: 132–136.
- Powell, J. R. 1997. **Progress and Prospects in Evolutionary Biology: The *Drosophila* Model**. Oxford. Oxford University Press. xiv+562 p.
- Ratter, J. A.; J. F. Ribeiro & S. Bridgewater. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. **Annals of Botany** 80: 223–230.
- Ratter, J. A.; P. W. Richards; G. Argent & D. R. Gifford. 1973. Observation on northeastern Mato Grosso. I The woody vegetation types of the Xavantina - Cachimbo expedition area. **Philosophical Transactions of the Royal Society of London (B)** 66: 449–492.
- Rohde, C. & V. L. S. Valente. 1996. Ecological characteristics of urban populations of *Drosophila polymorpha* Dobzhansky and Pavan and *Drosophila cardinoides* Dobzhansky and Pavan (Diptera, Drosophilidae). **Revista Brasileira de Entomologia** 40: 75–79.
- Souza-Silva, M.; J. C. R. Fontenelle & R. P. Martins. 2001. Seasonal abundance and species composition of flower-visiting flies. **Neotropical Entomology** 30: 351–359.
- Tidon, R. 2006. Relationships between drosophilids (Diptera, Drosophilidae) and the environment in two contrasting tropical vegetations. **Biological Journal of the Linnean Society** 87: 233–247.
- Tidon, R.; D. F. Leite & B. F. D. Leão. 2003. Impact of the colonization of *Zaprionus* (Diptera: Drosophilidae) in different ecosystems of the Neotropical Region: 2 years after the invasion. **Biological Conservation** 112: 299–305.
- Toda, M. J. 1973. Seasonal activity and microdistribution of drosophilid flies in Misumai in Sapporo. **Journal of Faculty of Sciences, Hokkaido University** 18: 532–550.
- Val, F. C. 1982. The male genitalia of some Neotropical *Drosophila*: notes and illustrations. **Papéis Avulsos de Zoologia** 34: 309–347.
- Val, F. C.; C. R. Vilela & M. D. Marques. 1981. Drosophilidae of the Neotropical region, p. 123–168. In: Ashburner, M.; H. L. Carson & J. N. Thompson (eds.). **The genetics and biology of *Drosophila***, v. 3a. London. Academic Press. 429 p.
- Valente, V. L. S. & A. M. Araújo. 1986. Comments on breeding sites of *Drosophila willistoni* Sturtevant (Diptera, Drosophilidae). **Revista Brasileira de Entomologia** 30: 281–286.
- Valente, V. L. S. & A. M. Araújo. 1991. Ecological aspects of *Drosophila* species inhabiting wild environments in Southern Brazil (Diptera: Drosophilidae). **Revista Brasileira de Entomologia** 35: 237–253.
- Vilela, C. R. 1983. A revision of the *Drosophila repleta* species group (Diptera, Drosophilidae). **Revista Brasileira de Entomologia** 27: 1–114.
- Vilela, C. R. 1999. Is *Zaprionus indianus* Gupta 1970 (Diptera, Drosophilidae) currently colonizing the Neotropical region? **Drosophila Information Service** 82: 37–39.
- Vilela, C. R. 2001. Breeding sites of Neotropical Drosophilidae (Diptera). III. Rotting infructescences of *Philodendron bipinnatifidum* (Araceae). **Revista Brasileira de Entomologia** 46: 339–344.
- Vilela, C. R. & G. Bächli. 1990. Taxonomic studies on Neotropical species of seven genera of Drosophilidae (Diptera). **Mitteilungen der Schweizerischen Entomologischen Gesellschaft** 63: 1–332.
- Wertheim, B.; R. Allemand; L. E. M. Vet & M. Dicke. 2006. Effects of aggregation pheromone on individual behaviour and food web interactions: a field study on *Drosophila*. **Ecological Entomology** 31: 216–226.
- Wolda, H. 1988. Insect seasonality: Why? **Annual Review of Ecology and Systematics** 19: 1–18.