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Small-Scale Elevational Variation in the Abundance of *Eufriesea violacea* (Blanchard) (Hymenoptera: Apidae)

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Variação Altitudinal em Pequena Escala na Abundância de *Eufriesea violacea* (Blanchard) (Hymenoptera: Apidae)

RESUMO - Machos de *Eufriesea violacea* (Blanchard) foram amostrados em um pequeno gradiente altitudinal no Sudeste do Brasil e apresentaram picos seqüenciais de abundância do ponto mais baixo (700 m) para o ponto mais alto (1.100 m) do gradiente durante o período de amostragem. A influência da temperatura sobre a duração do período de ovo-a-adulto e nas épocas de florescimento de plantas fornecedoras de alimento (néctar) sugere que esse seja um dos fatores que determinam a distribuição da abundância dos machos ao longo do gradiente altitudinal. Os resultados ressaltam a importância de se obter amostras estratificadas em função da altitude quando populações de Euglossini são estudadas, especialmente em localidades com grande variação topográfica.

PALAVRAS-CHAVE: Distribuição altitudinal, Euglossini, Floresta Atlântica

ABSTRACT - *Eufriesea violacea* (Blanchard) males were sampled in a small-scale elevational gradient in Southeastern Brazil and showed sequential peaks of abundance from lowest (700 m) to highest (1,100 m) altitudes during the sampling period. The influence of the temperature on the length of the egg-to-adult period and flowering dates of plants producing food (nectar) suggests that it may be one of the factors determining the distribution of male abundance along the altitudinal gradient. The results emphasize the importance of obtaining altitudinal stratified samples when studying Euglossini populations, especially when the studies are done at sites with marked topographical variation.

KEY WORDS: Altitudinal distribution, euglossine bee, Atlantic Forest

A large part of research in ecology is interested in understanding what determines the abundance of species in their areas of occurrence (Begon *et al.* 1996). One way to verify the importance of some factor(s) in the spatial distribution of an organism is to examine the abundance variation of this organism where those factors vary in a predictable way, such as in ecological gradients. It is well known that the distribution and abundance of several bee species differ along various types of gradients, reflecting responses to changes in biotic and abiotic factors in these gradients (Linsley 1958). In this context, elevational gradients are particularly suitable to explore, because many features that potentially influence the distribution of bees, such as temperature and resource availability, vary with altitude (Michener 1979).

The Euglossini (Hymenoptera: Apidae), with nearly 200 species in five genera, occur from northern Mexico to Argentina and Paraguay (Dressler 1982). In Brazil, the distribution of these bees extends to 30ºS, where it is abruptly interrupted by the transition from forest environments to pampas (Wittmann *et al*. 1988). Male euglossine bees collect floral fragrances mainly from orchids but also from many other plant families (Ramírez *et al*. 2002, Braga & Garófalo 2003), and from some extrafloral sources (Whitten *et al*. 1993). According to the most accepted hypothesis, males collect fragrances because these may influence mate choice by females (e.g. Eltz *et al*. 1999). Since the late 1960's, synthetic fragrances have been used for obtaining, in a few days, large samples of euglossine communities at given localities (e.g. Roubik & Ackerman 1987, Rebêlo & Garófalo 1997, Tonhasca *et al*. 2002a). As most such sampling has been done at single locations within habitats, some authors

(Ackerman 1983, Becker *et al*. 1991, Armbruster 1993, Tonhasca *et al*. 2002b) have discussed if those results would represent the habitat or only particular habitats, and how would be they related to spatial distribution of euglossine bees.

In this work we report a small-scale elevational variation in the abundance of *Eufriesea violacea* (Blanchard) and discuss how the temperature could be responsible for the observed distribution. *E. violacea* is distributed in southern, south-eastern and part of western central Brazil and reaches Argentina and Paraguay (Kimsey 1987, Wittmann *et al*. 1988). This species is often present in inventories in Brazil (Peruquetti *et al*. 1999), but information about its biology remains scarce (Peruquetti & Campos 1997).

Material and Methods

Study site. The study was carried out in the São Sebastião do Ribeirão Grande farm (22º45' S, 45º28' W), Pindamonhangaba, São Paulo State, Brazil. The farm has 1,700 ha with altitudes ranging from 600 m to 1,900 m. Seventy percent of the total area is still covered by native Atlantic Forest, mainly ombrophylous montane forest. In the low altitude sections of the farm (ca 600-1,200 m), abandoned eucalyptus plantations with secondary-growth native understory predominate. A well-preserved riparian forest has been maintained, forming an uninterrupted network of vegetation throughout the area. The farm is connected to a fairly well-preserved vegetation continuum through the Mantiqueira mountain range. The local climate is seasonal moist (Cwa, Köppen 1948), with a mean annual rainfall of 1,260 mm, and mean annual temperature of 22.1ºC, ranging from 9.6ºC in July to 32.4ºC in February (meteorological data for 1952-2000).

Sampling procedures and data analyses. Sampling was done at three points of the Cedro stream riparian forest, at altitudes of 700, 900 and 1,100 m, separated from each other by about 1,000 m. To attract euglossine males, three aromatic compounds (eucalyptol, eugenol and vanillin) were used (following Garófalo *et al*. 1998). Cotton balls of standard size were soaked with these baits and hung on strings that were tied to vegetation. The baits were placed in the shade, 1.5 m above the ground and 5 m apart in a straight line. The cotton balls were replenished hourly with the respective compounds in order to maintain a high, homogeneous attractiveness. Bees attracted to these sampling stations were captured with an entomological net, killed with ether and placed in individual plastic containers. The bait being visited and the time of the visit were registered. Bees were collected during a four-hour period, between 9 a.m. and 1.30 p.m.

To determine whether the abundance of the bees was dependent on the air temperature of the sampling station, we recorded the local temperature with a thermometer every 30 min, and every bee captured. Mean monthly temperature and total rainfall were obtained from a meteorological station located near the study area (22º 58' S, 45º 27'W), and are shown in Fig. 1. The bait position at each sampling station and the station sampling sequence were randomized. The stations were sampled monthly on three consecutive sunny days, from July 1998 to June 1999. Voucher specimens were deposited in the entomological collection of the Departmento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto/USP.

The chi-square test was used to examine for abundance differences among sample stations. We used analysis of variance (ANOVA) to test for differences in mean values of temperature obtained from November to January on the sampling days in each station. The Tukey post-hoc comparison method was used to identify significant differences among the means. Pearson's correlation analysis was performed to determine whether there was an association between bees' abundance and sample station air temperature (Zar 1984).

Results

***E. violacea* abundance.** Three hundred and twenty seven *E. violacea* males were captured at the three sampling stations, 18.6% at 700 m, 39.8% at 900 m and 41.6% at 1,100 m. Seven additional euglossine species were sampled (Appendix I), but at a frequency that does not justify further comments. *E. violacea* males occurred from October 1998 to February 1999. Since 320 of the 327 males were caught from November to January, the data were analyzed only for this period.

E. violacea males were attracted to eucalyptol and vanillin, and the frequency of visits always favored eucalyptol (November: 85.3% vs. 14.7%; December: 97.1% vs. 2.9%; January: 83.8% vs. 16.2%). The number of individuals attracted to each compound did not differ among altitudes ($\chi^2 = 1.23$, P = 0.540, N = 320).

Considering all *E. violacea* males sampled in the period, the number of individuals at the lowest station (700 m, 60 individuals) was significantly smaller than at the intermediate and highest stations (900 m, 127 individuals; 1,100 m, 133 individuals) ($\chi^2 = 30.79$, P < 0.001, N = 320). The difference in the number of individuals was also observed when the analysis was done for each month separately (Fig. 2). The abundance of *E. violacea* showed

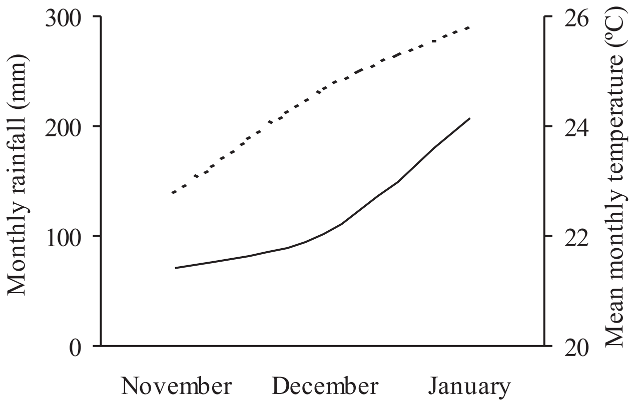

Figure 1. Mean monthly temperature (solid line) and monthly rainfall (dashed line) in November and December 1998, and January 1999 in the study site.

uphill sequential peaks along the elevational gradient from November to January, with a peak at 700 m in November, at 900 m in December and at 1,100 m in January (Fig. 2).

Local temperature. The local air temperatures (i.e., measured on the days of sampling) clearly characterized the elevational gradient in our study area, with lower temperatures in higher altitudes during the sampling period (Table 1). However, temperatures showed fairly different patterns along the gradient. In November, temperatures showed a clear uphill decrease, with a mean difference of ca. 3ºC among sample station. In December, temperatures showed a less marked uphill decrease, and only the 700 m and the 1,100 m stations were significantly different. In January, the temperature was significantly higher in the 700 m station, but did not differ among the 900 m and 1,100 m stations. When temperatures were compared in the same sample station through the months, the 700 m station showed no difference, while the 900 m and 1,100 m stations showed a significant increase in December, maintaining similar temperatures in January (Table 1).

***Eufriesea violacea* abundance *vs.* local temperature.** In November, the abundance of *E. violacea* decreased from the lowest station towards the highest station (Fig. 2) following the decrease of the temperature (Table 1). In December and January, however, the largest abundances occurred at cooler stations. No significant correlation was found between the temperature on sampling days and the frequencies of males collected (r = 0.30; P = 0.44).

Discussion

The high seasonal variation showed by *E. violacea*, with adults appearing only during a short period of the year, has also been reported by other authors (Wittmann *et al*. 1989; Rebêlo & Garófalo 1991, 1997; Peruquetti & Campos 1997; Garófalo *et al*. 1998; Sofia *et al*. 2004). This activity pattern reflects the occurrence of only one generation per year and, as observed for other species of the genus (Garófalo *et al*. 1993), such bees spend most of the annual cycle as diapausing pre-pupae.

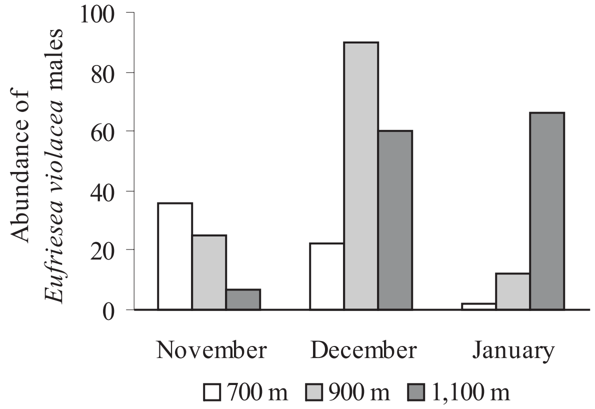

Figure 2. Monthly abundance variation of *E. violacea* in November and December 1998, and January 1999. Abundance differed significantly among altitudes in November ($\chi^2 = 18.91$, P < 0.001, N = 68), December ($\chi^2 = 40.51$, P < 0.001, N = 172) and January ($\chi^2 = 88.90$, P < 0.001, N = 80).

As observed in this study, eucalyptol was also the fragrance favored by most of the males at Estação Experimental de Zootecnia, Sertãozinho, SP (Rebêlo & Garófalo 1997) and at Parque Estadual Mata dos Godoy, Londrina, MG (Sofia *et al*. 2004). Vanilin, however, attracted most of the males at Santa Carlota Farm, Section Itaoca, Cajuru, SP (Rebêlo & Garófalo 1997), in Viçosa, MG (Peruquetti *et al*. 1999), and in Rio Grande do Sul, the initial preference for vanilin shifted towards eucalyptol throughout each season (Wittmann *et al*. 1989). This intraspecific variation in fragrance preferences may be attributed to either age, as suggested by Ackerman (1989), Wittmann *et al*. (1989) and Rebêlo & Garófalo (1991), or genetic differences among populations, or differences in the availability of fragrances resources (Ackerman 1989).

The presence of males of *E. violacea* at baits since October indicates the beginning of the emergence of local bees as adults. Thus, the increase in the number of males sampled in the following months would reflect an increase in the number of emerging bees. Besides the increase in the number of males at baits, the abundance of them showed uphill sequential peaks along the elevational gradient from November to January. One of the factors that could be determining those uphill sequential peaks would be the temperature.

It is known that an increase in altitude of 100 m entails a fall in mean temperature of 0.6°C to 0.7°C (Pearsall 1950). As the egg-to-adult period is influenced by temperature (Garófalo *et al*. 1993), individuals produced in nests established in lowest altitudes would be the first to emerge and those reared from nests found in higher altitudes would have a slower development and, therefore, would emerge later, as described by Whittaker & Tribe (1996) for *Neophilaenus lineatus* (L.) (Auchenorrhyncha: Cercopidae). Similarly, the increase in the mean monthly temperature at our study site over the months (Fig. 1) can also have acted as a sequential "trigger" for the emergence of the bees by keeping the temperature above a threshold for some period of time ('physiological time' - see Begon *et al*. 1996). So, this gradual increase in temperature from lower to higher altitudes together with the differences in the duration of the egg-to-adult period would result in the uphill sequential distribution of the abundance peaks of males along the elevational gradient.

Another aspect that is sensitive to temperature changes and probably influenced the variation in the abundance distribution of euglossine males would be the availability of food and fragrances resources along the elevational gradient. Temperature is considered an important physical factor identified as a cue that may initiate flowering onset (Rathcke & Lacey 1985). Fitter *et al*. (1995) found a very high degree of dependence of first flowering date on mean monthly temperatures of the preceding month for 219 of 243 species of angiosperms and gymnosperms in southern central England. If this dependence also occurs in seasonal tropical environments, it could provide an uphill synchronous

Table 1. Comparison of the sample station temperatures (mean ± standard error) on the sampling days in three consecutive months.

	Sample station temperature (ºC)			P[1]	Post-hoc comparisons[2]
	700 m	900 m	1,100 m		
November	23.1 ± 0.65	20.0 ± 0.37	17.3 ± 0.49	< 0.001	700^{a} 900^{b} $1{,}100^{c}$
December	23.1 ± 0.55	22.7 ± 0.69	21.2 ± 0.24	0.036	700^{a} 900^{ab} $1{,}100^{b}$
January	22.5 ± 0.17	21.4 ± 0.26	21.3 ± 0.27	0.002	700^{a} 900^{b} $1{,}100^{b}$
P[1]	0.620	0.03	< 0.001		
Post-hoc comparisons[2]	-	Nov^{a} Dec^{b} Jan^{ab}	Nov^{a} Dec^{b} Jan^{b}		

[1] ANOVA

[2] Tukey's test. An altitude (within a row) and a month (within a column) followed by different letters is significantly different ($P < 0.05$).

flowering for some plant species in the elevational gradient of our study site. Consequently, this flowering pattern would lead to uphill sequential peaks in the abundance of males since they may be collected in higher frequency near the sites from which they obtain food or fragrances (Ackerman 1983, Armbruster 1993) although the local concentration of resources does not prevent bees from accessing nearby areas (Tonhasca *et al*. 2002b). According to Otero & Sandino (2003), as the males do not collect fragrances everyday, but do feed frequently, it seems logical to suppose nectar distribution as a main, but not sole, causal factor of the capture frequencies.

If the hypothesis presented here is correct, the variation in the abundance distribution observed in this study agrees with the hot spot hypothesis (Armbruster 1993), which suggests that the local distribution of Euglossini is determined by a network of habitual foraging routes, with convergence of the routes of some species at points with a high concentration of resources ('hot spots'). In our study site, these routes could have gradually moved from the lowest to the highest portions of the riparian forest as euglossine males emerged and migrated uphill in pursuit of available resources.

A similar dispersal behavior as the suggested for the males of *E. violacea* was reported for females of *Euphilotes enoptes* (Boisduval) (Lepidoptera: Lycaenidae), the larvae of which feed on inflorescences of *Eriogonum compositum* (Polygonaceae) (Peterson 1997). This species showed an uphill bias in movement that resulted from higher emigration from senescing low-elevation patches than from phenologically delayed, high-elevation patches (Peterson 1997).

Elevational variation in euglossine abundance over a short period of time may occur also in less markedly seasonal, low-latitude environments. A similar pattern to that described here was found when we analyzed the abundance distribution of *Euglossa viridissima* Friese (Hymenoptera: Apidae) using data from Janzen *et al*. (1982). This species was sampled simultaneously at altitudes of 5 m and 300 m in Santa Rosa National Park, Costa Rica, and also showed sequential variation in abundance throughout the sampling months; there were more individuals in the upland in August 1977 ($\chi^2 = 23.54$, $P < 0.001$, $N = 239$), a similar number at the two altitudes in December 1977 ($\chi^2 = 1.82$, $P = 0.178$, $N = 291$) and more individuals in the lowland in March 1978 ($\chi^2 = 75.63$, $P < 0.001$, $N = 181$). Additional studies with Euglossini species in elevational gradients could confirm if this is a general pattern.

We are aware that the lack of elevational replicates reduces the generalization power of our results; however, considering that the observed pattern of abundance distribution occurred over a small elevational gradient, our results show the importance of obtaining altitudinally stratified samples when studying orchid bees populations (as pointed out by Armbruster 1993, and reaffirmed by Tonhasca *et al*. 2002a), especially when these studies are done in environments with high topographical variation. In such locations, sampling within a single altitude level might miss such elevational abundance variation.

Appendix I. Additional euglossine species captured in the São Sebastião do Ribeirão Grande farm, Pindamonhangaba, State of São Paulo, Brazil.

Euglossa annectans Dressler (one male at 900 m and two males at 1,100 m), *Euglossa fimbriata* Rebêlo & Moure (one male at 700 m), *Euglossa truncata* Rebêlo & Moure (one male at 700 m, two males at 900 m and one male at 1,100), *Eulaema nigrita* Lepeletier (seven males at 700 m, nine males at 900 m and three males at 1,100 m), *Eulaema cingulata* (Fabricius) (one male at 700 m and two males at 900 m), *Exaerete smaragdina* (Guérin) (one male at 700 m) and *Eufriesea danielis* (Schrottky) (one male at 900 m).

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References

Ackerman, J.D. 1983. Diversity and seasonality of male euglossine bees (Hymenoptera: Apidae) in central Panama. Ecology 64: 274-283.

Ackerman, J.D. 1989. Geographic and seasonal variation in fragrance choices and preferences of male euglossine bees. Biotropica 21: 340-347.

Armbruster, W.S. 1993. Within-habitat heterogeneity in baiting samples of male euglossine bees: Possible causes and implications. Biotropica 25: 122–128.

Becker, P., J.S. Moure & F.J.A. Peralta. 1991. More about euglossine bees in Amazonian forest fragments. Biotropica 23: 586-591.

Begon, M., J.L. Harper & C.R. Townsend. 1996. Ecology. 3rd ed., Oxford, Blackwell Science, 1068p.

Braga, A.K. & C.A. Garófalo. 2003. Coleta de fragrâncias por machos de *Euglossa townsendi* Cockerell (Hymenoptera, Apidae, Euglossini) em flores de *Crinum procerum* Carey (Amaryllidaceae), p.201-207. In G.A.R. Melo & I. Alves-dos-Santos (eds.), Apoidea Neotropica: Homenagem aos 90 anos de Jesus Santiago Moure. Criciúma, Editora UNESC, 320p.

Dressler, R.L. 1982. Biology of the orchid bees (Euglossini). Ann. Rev. Ecol. Syst. 13: 373-394.

Eltz, T., W.M. Whitten, D.W. Roubik & K.E. Linsenmair. 1999. Fragrance collection, storage, and accumulation by individual male orchid bees. J. Chem. Ecol. 25: 157-176.

Fitter, A.H., R.S.R. Fitter, I.T.B. Harris & M.H. Williamson. 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. Funct. Ecol. 9: 55–60.

Garófalo, C.A., E. Camillo, J.C. Serrano & J.M.M. Rebêlo. 1993. Utilization of trap nests by Euglossini species (Hymenoptera, Apidae). Rev. Bras. Biol. 53: 177-187.

Garófalo, C.A., E. Camillo, S.C. Augusto, B.M.V. Jesus & J.C. Serrano. 1998. Diversidade e abundância sazonal de Euglossini (Hymenoptera, Apidae) na Serra do Japi, Jundiaí, SP, p.72-79. Anais do IV Simpósio de Ecossistemas Brasileiros. Águas de Lindóia, SP, v. III.

Janzen, D.H., P.J. DeVries, M.L. Higgins & L.S. Kimsey. 1982. Seasonal and site variation in Costa Rican euglossine bees at chemical baits in lowland deciduous and evergreen forests. Ecology 63: 66-74.

Kimsey, L.S. 1987. Generic relationships within the Euglossini (Hymenoptera: Apidae). Syst. Entomol. 12: 63-72.

Köppen, W. 1948. Climatologia. Mexico, Fondo Cultura Economica, 478p.

Linsley, E.G. 1958. The ecology of solitary bees. Hilgardia 27: 541-599.

Michener, C.D. 1979. Biogeography of the bees. Ann. Mo. Bot. Gard. 66: 277-347.

Otero, J.T. & J.C. Sandino. 2003. Capture rates of male euglossine bees across a human intervention gradient, Chocó Region, Colombia. Biotropica 35: 520-529.

Pearsall, W.H. 1950. Mountains and Moorlands. Collins, London, 312p.

Peruquetti, R.C. & L.A.O. Campos. 1997. Aspectos da biologia de *Euplusia violacea* (Blanchard) (Hymenoptera, Apidae, Euglossini). Rev. Bras. Zool. 14: 91-97.

Peruquetti, R.C., L.A.O. Campos, C.D.P. Coelho, C.V.M. Abrantes & L.C.O. Lisboa. 1999. Abelhas Euglossini (Apidae) de áreas de Mata Atlântica: Abundância, riqueza e aspectos biológicos. Rev. Bras. Zool. 16 (Supl. 2): 101-118.

Peterson, M.A. 1997. Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. Ecology 78: 167-180.

Ramírez, S., R.L. Dressler & M. Ospina. 2002. Abejas euglosinas (Hymenoptera: Apidae) de la Región Neotropical: Listado de especies con notas sobre su biología. Biota Colombiana 3: 7–118.

Rathcke, B. & E.P Lacey. 1985. Phenological patterns of terrestrial plants. Ann. Rev. Ecol. Syst. 16: 179-214.

Rebêlo, J.M.M. & C.A. Garófalo. 1991. Diversidade e sazonalidade de machos de Euglossini (Hymenoptera, Apidae) e preferências por iscas-odores em um fragmento de floresta no sudeste do Brasil. Rev. Bras. Biol. 51:787-799.

Rebêlo, J.M.M. & C.A. Garófalo. 1997. Comunidades de machos de Euglossini (Hymenoptera: Apidae) em matas semidecíduas do Nordeste do estado de São Paulo. An. Soc. Entomol. Brasil 26: 243-255.

Roubik, D.W. & J.D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. Oecologia 73: 321-333.

Sofia, S.H. & K.M Suzuki. 2004. Comunidades de machos de abelhas Euglossina (Hymenoptera: Apidae) em fragmentos florestais no Sul do Brasil. Neotrop. Entomol. 33: 693-702

Tonhasca, A., Jr., J.L. Blackmer & G.S. Albuquerque. 2002a. Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic Forest. Biotropica 34: 416-422.

Tonhasca, A., J.L. Blackmer & G.S. Albuquerque. 2002b. Within-habitat heterogeneity of euglossine bee populations: A re-evaluation of the evidence. J. Trop. Ecol. 18: 929-933.

Whittaker, J.B. & N.P. Tribe. 1996. An altitudinal transect as an indicator of responses of a spittlebug (Auchenorrhyncha: Cercopidae) to climate change. Eur. J. Entomol. 93: 319-324.

Whitten, W.M., A.M. Young & D.L. Stern. 1993. Nonfloral sources of chemicals that attract male euglossine bees (Apidae, Euglossini). J. Chem. Ecol. 19: 3017-3027.

Wittmann, D., M. Hoffmann & E. Scholz. 1988. Southern distributional limits of euglossine bees in Brazil linked to habitats of the Atlantic and subtropical rain forest

(Hymenoptera: Apidae: Euglossini). Entomol. Gen. 14: 53-60.

Wittmann, D., R. Radtke, M. Hoffmann & B. Blochtein. 1989. Seasonality and seasonal changes in preferences for scent baits in *Euplusia violacea* in Rio Grande do Sul / Brazil (Hymenoptera: Apidae: Euglossini). Entomol. Gen. 14: 217-221.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. New Jersey, Prentice-Hall, 718p.

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