ECOLOGY, BEHAVIOR AND BIONOMICS

Forest Fragments with Larger Core Areas Better Sustain Diverse Orchid Bee Faunas (Hymenoptera: Apidae: Euglossina)

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Edited by Fernando Noll – UNESP


ABSTRACT - Male orchid bees were attracted to chemical baits and collected in nine Atlantic Forest fragments in southeastern Brazil. Fragments differed in size and shape. Three additional sites were also sampled in a nearby large fragment. Three hypothetical core areas of each fragment were measured as the total area minus an area of 50, 100, and 200-m-wide perimeter. Abundance and richness were not correlated with either fragment size or ratio area/perimeter, but were positively correlated with the size of core areas. These results suggest that orchid bee conservation requires the preservation of the fragments with the largest possible core areas. Neither size nor shape alone (area/perimeter ratio) seemed to be good indicators of the value of a given fragment for sustaining diverse and abundant faunas of orchid bees.

KEY WORDS: Atlantic Forest, conservation, Euglossine, habitat fragmentation

Deforestation almost always results in fragmentation of the original forest into isolated patches of tall trees embedded in a modified matrix (Tocher et al 1997). Species richness and population sizes of forest-dependent animals and plants usually decline as a result of forest loss and fragmentation (Franklin & Forman 1987, Collinge 1996, but see Cane 2001). Because there are no methods to determine the minimum areas of reserves with reference only to ecosystem properties (see Soulé & Simberloff 1986, Beier 1993), biologists have been forced to conduct viability analysis for a few “indicator” or “umbrella” species as an efficient way to address the viability of the whole system (Soulé 1987, Noss 1991). These analyses, however, have focused on large vertebrates, which require large areas (e.g. Picton 1979, Freemark & Merriam 1986, Dodd 1990, Laurance 1990, 1994, Beier 1993, Lankester et al 1991, Newmark 1991, Opdam 1991, Herkert 1994, Brooks et al 1999, Chiarello 1999) but little is known about the effects of fragmentation on faunas of invertebrates (see Hopkins & Webb 1984, Klein 1989, Daily & Ehrlich 1995).

The few studies involving fragmentation and orchid bees were carried out in recently fragmented landscape in the Amazon Basin (Biological Dynamics of Forest Fragments Project, Powell & Powell 1987, Becker et al 1991) or in Atlantic Forest areas in which fragmentation took place over a century ago (Bezerra & Martins 2001, Tonhasca Jr et al 2002, Souza et al 2005, Nemésio & Silveira 2007, Aguiar & Gaglianone 2008, Farias et al 2008). These studies involved few fragments and only related fragment size to bee diversity.

Although orchid bees are able to fly several kilometers each day in search for food and aromatic compounds (Janzen 1971), there are evidences that some species are unable to cross open spaces only a few dozen meters wide between two forest fragments (Powell & Powell 1987, Becker et al 1991). This suggests they are strongly dependent on forest environments.

Male orchid bees are the main (and frequently the only) pollinators of about 650 species of orchids (Ackerman 1989), as well as other plant species (reviewed by Dressler 1982). For this reason, their conservation is a matter of concern. Most euglossine species are only found in forest habitats (Roubik & Hanson 2004) which have been widely destroyed in the Neotropics. To effectively conserve orchid bees in remnant forests, it is necessary to understand all the effects of habitat fragmentation on these bees. The main goal of this paper was to assess the influence of size and shape of fragments on their orchid bee community structure.

Material and Methods

Study sites. Data were collected in nine forest fragments near the urban areas of the Belo Horizonte metropolitan region (state of Minas Gerais, Brazil), with more than three million inhabitants. Belo Horizonte (19°58’- 20°06’S, 43°55’- 44°04’W, elevation: 800-1,100 m) is at the border of two major Brazilian biomes, the Atlantic Forest and the “Cerrado” (Brazilian savanna). The dominant forest in the region is the semideciduous forest, called “low mountain rain forest” by Rizzini (1979), at elevations of 300-800 m. The forest canopy reaches 15-25 m and trunks vary from 40 cm to 60 cm in
diameter. There are relatively few epiphytes and lianas, but the understory is well developed. Denser stands of larger trees grow in the humid ravines. The forest gets sparser and shorter as the altitude increases, being substituted at the top of the tallest hills by patches of Cerrado or (above 1,000 m) by “campos rupestres” (rocky fields). The regional climate is the AW of Köppen (tropical with rainy summers and a dry winter with mean annual temperature of 18°C). These forest fragments are surrounded by areas with different degrees of anthropogenic disturbance. Locations, sizes, elevations and shape parameters of the nine sampled fragments are given in Table 1.

Besides the fragments above, three sites were also sampled at Reserva Particular do Patrimônio Natural da Serra do Caraça (RSC), a large (>10,000 ha) forest area situated in the municipality of Catas Altas, ca. 60 km from Belo Horizonte, with similar vegetation (Vasconcelos 2000). The first site (RSC-1; 20°02'37" S - 43°30'17"W) was situated at 850 m above sea level. The second one (RSC-2; 20°04'31" S - 43°30'37"W) at ca. 1,200 m and the third one (RSC-3; 20°05'44" S - 43°29'44"W) at ca. 1,350 m.

**Sampling.** Male orchid bees were captured monthly at a single fixed spot in each site, between 10:00h and 16:00h, during one year, between May 1999 and April 2000. Five chemicals (benzyl acetate, 1,8-cineole, eugenol, methyl trans-cinnamate, and vanillin) were used to attract the bees. They were imbued in cotton waddings hanging from branches at about 1.5 m above the soil surface and distant from each other at least 2.0 m. Monthly, the three sites at RSC were always sampled on the same day, as well as the three sites at Barreiro (Barreiro large, median, and small) and the two sites of Catarina (Catarina large and small). This practice was adopted to avoid bias due to influence of possible different climatic conditions if sampling in sites of the same area were taken in different days. All collected specimens were pinned, identified and deposited at the entomological collection of the Taxonomic Collections of the Universidade Federal de Minas Gerais. Taxonomy follows Nemésio (2009).

**Data analysis.** Sizes and “shapes” of forest fragments were correlated with the abundance and species richness of their orchid bee fauna through the Spearman rank correlation test, considering a 5% significance level. Shape of the forest fragment was calculated as: (i) the area/perimeter ratio and (ii) the core area size. The core area is that area resulting from the exclusion of a uniform border of a given width off the fragment. Three core areas were estimated for each fragment, excluding borders 50 m, 100 m, and 200 m wide (respectively, CA50, CA100 and CA200) measured from the forest edge. When, after excluding a given border, a fragment was split into two or more core areas, only the largest one was used for analysis. When no area was left after the exclusion of a border stripe of a given width, we tried two analyses: (i) this fragment was not considered in the correlation test for that category; (ii) the area of the fragment was considered to be zero and it was considered in the correlation test. The sites in RSC were not used for core area analyses, since they

<table>
<thead>
<tr>
<th>Fragments</th>
<th>SM</th>
<th>BS</th>
<th>BM</th>
<th>BL</th>
<th>CS</th>
<th>CL</th>
<th>FCH</th>
<th>PM</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Municipality</td>
<td>Brumadinho</td>
<td>Belo Horizonte</td>
<td>Belo Horizonte</td>
<td>Belo Horizonte</td>
<td>Brumadinho</td>
<td>Brumadinho</td>
<td>Nova Lima</td>
<td>Belo Horizonte</td>
<td>Ibirité</td>
</tr>
<tr>
<td>Elevation above sea level (m)</td>
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<td>1,100</td>
<td>1,100</td>
<td>1,100</td>
<td>900</td>
<td>900</td>
<td>1,350</td>
<td>1,100</td>
<td>950</td>
</tr>
<tr>
<td>Matrix (surrounding area)</td>
<td>Campo</td>
<td>Cerrado and campo</td>
<td>Cerrado and campo</td>
<td>Cerrado and campo</td>
<td>Cerrado and campo</td>
<td>Cerrado and campo</td>
<td>Cerrado and campo</td>
<td>Cerrado, campo, urban areas</td>
<td>Cerrado and campo</td>
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<td>2.0</td>
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<td>180.0</td>
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<td>93.0</td>
<td>100.0</td>
</tr>
<tr>
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<td>0.01</td>
<td>0.2</td>
<td>32.0</td>
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<td>68.0</td>
<td>292.2</td>
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<td>0.0</td>
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<td>0.0</td>
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<td>186.8</td>
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<tr>
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<td>28.7</td>
<td>36.7</td>
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</tr>
<tr>
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<td>1.4</td>
<td>6.3</td>
<td>4.9</td>
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<td>4.1</td>
<td>9.6</td>
<td>4.4</td>
<td>6.7</td>
</tr>
</tbody>
</table>

1Split into two areas of 149.2 ha and 143 ha, respectively; 2Split into four areas of 10.5 ha, 10.5 ha, 18.0 ha and 25 ha, respectively; 3Split into three areas of 3.0 ha, 124.6 ha and 123.4 ha, respectively; 4Split into four areas of 1.5 ha, 3.0 ha, 7.5 ha and 12.0 ha, respectively; 5Split into two areas of 10.0 ha, and 11.0 ha, respectively; 6Split into two areas of 91.1 ha and 95.7 ha, respectively.
are not fragments, but sites situated in the same continuous large area. For the same reason, they were considered as the largest fragments when effect of fragment size was analyzed. To avoid bias, when the nine fragments of the Belo Horizonte region were analyzed in respect to their core area, two sets of data were generated: the first including all nine fragments and the second excluding the two sites situated at the highest elevations (FCH and SM, Table 1), leaving only the seven sites situated at approximately the same elevation. Data and analyses focusing on elevation were published elsewhere (Nemésio 2008).

The similarity in faunistic composition among the twelve sites was estimated by the percent similarity index of Renkonen, recommended by Wolda (1981) for small samples. Based on those similarities, the areas were grouped using UPGMA (Sneath & Sokal 1973). The resulting similarity matrix was correlated to a matrix of geographic distance among the sites. Nevertheless, since the elements are not independent (Fortin & Gurevitch 1993), the Mantel permutation test was used for these correlations (Douglas & Endler 1982, Manly 1994, Sokal & Rohlf 1995). For calculating Z statistics, 1,000 permutations were used, as recommended by Fortin & Gurevitch (1993).

Results

A total of 2,381 male orchid bees belonging to at least 14 species were collected at the nine areas in Belo Horizonte and the three sites at RSC (Table 2). Abundance and species richness were not correlated with fragment size, independent of the data set employed.

No correlation was found between core area size and abundance or richness considering the nine fragments. Nonetheless, when the two sites situated at the highest elevations (Serra da Moeda and Fechos, both above 1,300 m) were excluded and only the seven fragments situated approximately at the same altitude (900-1,100 m) were considered, both abundance (CA$_{100}$ and CA$_{200}$; $r = 0.90$, $n = 5$, $P < 0.05$) and richness (CA$_{100}$ and CA$_{200}$; $r = 0.98$, $n = 5$, $P < 0.05$) were correlated with the core area of fragments for the widest perimeter categories (CA$_{100}$ and CA$_{200}$). This result was also achieved when the fragments with CA$_{100}$ = 0 were considered to have area zero and included in the analysis (for abundance CA$_{100}$ and CA$_{200}$; $r = 0.69$, $n = 7$, $P < 0.05$; for richness CA$_{100}$ and CA$_{200}$; $r = 0.72$, $n = 7$, $P < 0.05$). Abundance and species richness were not correlated with the area/perimeter ratio in any analysis.

The ordination of the sites according to their faunas (Fig 1) shows a great overall similarity among the sites, with the most distinctive of them (RSC-1) still sharing more than 40% similarity with the others. The seven sites at approximately the same altitude in Belo Horizonte region showed more similarity to each other than to the two other sites at the highest elevations or to the RSC sites.

When similarity was correlated to geographic distance through the Mantel test, a significant correlation was obtained ($r = -0.494$; $t = -2.68$; $n = 12$; $P = 0.004$), i.e., the shorter the distance, the greater the similarity among sites.

Discussion

Orchid bee species richness and composition. The species collected in the present study are essentially the same collected in a previous work carried out in the same region (Nemésio & Silveira 2007), although only the fragment Parque das Mangabeiras was sampled in both studies. The only species recorded in the present study and not collected by Nemésio & Silveira (2007) was Enfrisea violacea (Blanchard). Nonetheless, this species was collected at RSC and not in the Belo Horizonte region (see Table 2). The same is true for species composition; details on the currently known distribution of these species were also presented by Nemésio & Faria Jr (2004) and by Nemésio (2009). The high similarity among orchid bee faunas of all sampled sites may reflect the connections among the fragments and also their obvious common biogeographic history.

The correlation between geographic distance and similarity of faunas revealed by the Mantel test and clearly seen in Fig 1 should be pointed out. Besides, it is noticeable that fragments situated approximately at the same elevation grouped together (FCH and RSC-2; SM and RSC-3 and the seven fragments situated at approximately the same elevation in Belo Horizonte – [BS + (CL + CS)] + [(BL + BM) + TAB + PM]). Interestingly, BS grouped first with the two sites of Catarina reserve (CL + CS) instead of grouping with BL and BM, its neighbor sites. This is due to the strong influence of Eulaema nigrita Lepeletier (see Table 2), a species regarded as typical of open and/or disturbed areas (see Tonhasca Jr et al 2002 and Nemésio & Silveira 2006b; for alternative hypothesis, see Bezerra & Martins 2001 and Nemésio & Silveira 2006a). The four largest fragments of the Belo Horizonte area situated at similar elevations (BM, BL, TAB, and PM) grouped together (sites where the dominance of E. nigrita is weaker than in BS, CL and CS) (see Fig 1).

Fragment size. Nemésio & Silveira (2007) found a positive correlation between fragment size and abundance (but not to species richness, though it was suggested that fragment size could influence species richness). Nevertheless, the data presented here do not corroborate such correlation. The difference between those results may be due, primarily, to the areas sampled in each study. All four fragments sampled by Nemésio & Silveira (2007) are at similar elevations (850-1,100 m), whereas in this study fragments between 900 m and 1,400 m were sampled. Moreover, the four fragments of the first study were quite distant from each other (2.3-12.8 km) while, in the present study, different degrees of connection were selected.

Barreiro-small (2 ha) presented a high abundance and species richness, most probably because it is between two larger fragments (45-180 ha) and distant only a few tens of meters from both of them. Thus, many of the bees collected there may have been attracted from the larger fragments nearby. This, surely, contributed for the reduction of the correlations, since high values of abundance and richness were attributed to one of the smallest areas. It also should be noted that the orchid bee faunas of neighbor fragments tended to be the most similar to each other, when distance between fragments was smaller than 100 m (Barreiro large,
Table 2 Number (N) and relative abundance (%) of male orchid bees according to species collected in the twelve sampling sites: Barreiro-small (BS), Barreiro-median (BM), Barreiro-large (BL), Catarina-small (CS), Catarina-large (CL), Fechos (FCH), Serra da Moeda (SM), Taboões (TAB), Parque das Mangabeiras (PM), and the three sites at RSC (RSC-1, 2, and 3).

<table>
<thead>
<tr>
<th>Area</th>
<th>BS</th>
<th>BM</th>
<th>BL</th>
<th>CS</th>
<th>CL</th>
<th>FCH</th>
<th>SM</th>
<th>TAB</th>
<th>PM</th>
<th>RSC-1</th>
<th>RSC-2</th>
<th>RSC-3</th>
<th>T</th>
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</thead>
<tbody>
<tr>
<td>Species</td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>T</td>
</tr>
<tr>
<td>Eufriesea violacea (Blanchard)</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Ef. nigrohirta (Friese)</td>
<td>1</td>
<td>0.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>0</td>
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</tr>
<tr>
<td>Euglossa aratingae Nemésio</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Eg. fimбриata Rebêlo &amp; Moure</td>
<td>18</td>
<td>5</td>
<td>25</td>
<td>8</td>
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<td>7</td>
<td>4</td>
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<td>2</td>
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<td>4</td>
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<td>1</td>
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<td>1</td>
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<td>3</td>
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<td>7</td>
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<td>44</td>
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<td>2,381</td>
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median, and small; Catarina large and small; distances between all other fragments were larger than 1,000 m). This also suggests that some migration between close-by fragments does occur. Moreover, fragment sizes and shapes were more homogeneous among the forest patches studied by Nemésio & Silveira (2007), probably promoting similar environmental conditions among fragments.

**Fragment shape.** It is known that two patches of the same size but with different amount of edge may have different population dynamics (Fahrig & Merriam 1994) and it is common sense that, among fragments of the same size, the one with shape most closely approaching a circle should be preferred for conservation purposes, since it would best reduce the edge effects (*e.g.* Diamond 1975, Begon *et al.* 2006). Although Game (1980) argued that “in certain circumstances the optimal shape may be other than circular”, she recognizes that, if extinction rate is highly dependent on shape, then the optimal shape is circular (Game 1980:631). In relatively isolated fragments or sets of fragments, as in the present study, immersed in an urban matrix, the main challenge is to reduce the extinction rate and not to increase the immigration rate.

The area/perimeter ratio is suggested as a practical way to assess the “shape quality” of fragments. The higher its value, the more similar to a circle a fragment will be; the lower the value, the higher the edge effects will be. However, this ratio is of limited use when fragments of different sizes are compared, since the area/perimeter ratio of two areas of same shape but with different sizes are not equivalent, with the larger area also presenting a larger area/perimeter ratio.

Given that it is not shape itself that counts for organisms depending on deep-forest environments, but the actual area that is isolated from edge effects in the fragment, the use of core areas should be preferred as a tool to evaluate fragment quality for conservation. Moreover, the study of the correlation between core areas and population abundance and species richness is a practical tool for estimating the absolute distance below which edge effects are important for different kinds of organisms. Thus, our data, combined with those presented in a previous work (Nemésio & Silveira 2006b), suggest that at 50 m from the edge, the orchid bee community is still heavily affected by edge effects. Data on the orchid bee fauna of a large fragment of Atlantic Forest (36,000 ha) showed that the orchid bee faunas at 400 m and 500 m from the forest edge are more similar to those at 2,000 m and 4,000 m from the edge than to that at 50 m (Nemésio & Silveira 2006b).

The data presented here suggest that the orchid bee faunas of the fragments with the largest core areas at least 100 m far from the closest edge are richer and more abundant than those occurring in areas with limited core areas. Thus, large but narrowly linear reserves will not be effective in conserving orchid bees. Our data do not allow us to estimate the minimum area for effective conservation of euglossine species dependent on deep-forest environments. However, considering the fact that orchid bees are believed to fly a few to several thousands meters in search of the resources they need (Janzen 1971), it can be expected that those forest species demanding well preserved environments will need reserves of several hundreds to a few thousands hectares for long-term conservation. However, small fragments are important to conserve less restrictive species.

This study suggests that the best areas to be preserved in the Atlantic Forest domain, as far as orchid bee conservation is concerned, are those still holding well preserved core areas at least 100 m far from the closest edge. However, complementary studies involving larger number of fragments are necessary to define which the minimum size of such core areas would be for each species. The employment of core areas, thus, seems to be a useful tool for conservation policy, since areas to be preserved can be objectively selected. Since different organisms will respond differently to specific distances to the forest edge, combinations of minimum edge distances for core areas estimated for several taxa should be employed in selecting the best areas to be preserved.

**Acknowledgments**

We are indebted to James Cane, who kindly read the first
version of this manuscript and made valuable comments on it. Dr. Fernando Consoli, as the Chief Editor of Neotropical Entomology, and the anonymous referees also made important criticisms to previous versions of this manuscript. We also thank A. G. Damasceno and R. Scholte, who helped with fieldwork. We thank the Prefeitura Municipal de Belo Horizonte for allowing us to sample (through the Park’s administration) the Parque Municipal das Mangabeiras; the direction of the Reserva Particular do Patrimônio Natural da Serra do Caraça for allowing us to sample that area and the Companhia de Saneamento de Minas Gerais, COPASA-MG, for allowing us to sample their reserves at Fechos, Taboões, Barreiro and Catarina. This study was partly supported by the Ministério do Meio Ambiente and CNPq, through PROBIO (process #380678/1999-3), which also granted a fellowship to the first author. This paper is part of the first author’s M.Sc. Dissertation.

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Received 27/XI/08. Accepted 02/IV/09.