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**Original article**

# Seasonal changes in odour preferences by male euglossine bees (Hymenoptera: Apidae) and their ecological implications

Stefan Abrahamczyk[1], Peter Gottleuber[2], Michael Kessler[1]

[1]Institute for Systematic Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland
[2]Department of Systematic Botany, University of Goettingen, Untere Karspuele 2, 37073 Goettingen, Germany

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**Abstract –** Orchid bees are an important group of specialized insect pollinators in the Neotropics. Male orchid bees are attracted by a wide range of aromatic substances often produced by flowers. Previous studies found that in some species the males change their aromatic preferences between seasons. In our study we documented seasonal changes of aromatic preferences in five euglossine bee assemblages along a 380-km-long seasonality and precipitation gradient and related them to climatic factors. We found that the proportion of species per site showing changes in their aromatic preference between seasons increased with climatic seasonality towards the south. Those species mainly belong to the genus *Euglossa*, subgenus *Euglossa*. We conclude that climatic seasonality mainly affects the orchid bees via the turnover of the aromatic substances provided by the plants. Further, we suggest that the ability to change the aromatic preference between seasons could be interpreted as a phylogenetic pre-adaptation that enabled some species to colonize climatically strongly seasonal habitats.

**climatic gradient / precipitation / temperature / distribution / generalist**

## 1. INTRODUCTION

The about 200 species of euglossine orchid bees are an important group of insect pollinators in the Neotropics. A wide range of plant species from numerous families are visited by male and female orchid bees in order to feed on nectar or by males to collect aromatic substances (Ramírez et al. 2010a). Up to 650 orchid species exclusively produce fatty, aromatic substances as floral reward and exclusively rely on the pollination by male orchid bees (Whitten and Williams 1991). Male orchid bees collect aromatic substances mainly from floral sources and store them in pockets of their enlarged hind tibias where they mix a perfume to attract females for mating (Ramírez et al. 2010b).

Overall, orchid bees collect a wide range of different aromatic substances (Ackerman 1989). Some species are attracted by many substances, while others are specialized to one or a few. Eltz et al. (2005) showed that the composition of aromatic substances orchid bees collect is species specific and not influenced by locality or habitat on a local to regional scale. But it can change between seasons. In every orchid bee assemblage studied to date over a longer time period, some orchid bee species, usually those that are attracted by a large number of aromatic substances, change their aromatic preferences

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Corresponding author: S. Abrahamczyk, abraha@systbot.uzh.ch
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between seasons (Pearson and Dressler 1985; Ackerman 1989), but the reasons for these preference changes remain unknown. Ackerman (1989) and Ramírez et al. (2010b) further reported large-scale, geographical variations of preferences for aromatic substances between orchid bee populations of the same species, but the variations between populations were not related to environmental factors. Ackermann (1989) thus speculated that the environmental components involved are related to season, geography, fragrance availability, and population age. He included population age because Zimmermann and Madrinan (1988) showed that bee age may have a substantial influence on the fragrance foraging activity of male euglossine bees. Eltz et al. (1999, 2005) showed that especially older male orchid bees learn how much of a substance they have already collected and start to avoid it after a while. Additionally, the strength of climatic seasonality, in both temperature or precipitation, may also be expected to relate to seasonal shifts in foraging preferences among bees, but this factor has not yet been considered in detail.

In our study we focussed on the influence of climatic seasonality on the proportion of orchid bee species that change their aromatic preferences between seasons. We asked the following questions:

1. Which climatic factor is most closely related to the proportion of species in an assemblage that change their aromatic preferences between seasons?
2. What potential advantages might there be in the ability of orchid bee species to change their aromatic preference between seasons?

## 2. MATERIALS AND METHODS

### 2.1. Study sites

We sampled orchid bees between November 2007 and October 2008 at five sites along a 380-km-long latitudinal gradient from tropical, evergreen rainforests in central Bolivia (Villa Tunari: 16°57′59 S, 65°24′44 W; Sacta: 17°06′03 S, 64°47′02 W; Buena Vista: 17°30′49 S, 63°38′16 W) to subtropical, deciduous dry forests in southern Bolivia (Santa Cruz: 17°46′48 S, 63°04′02 W; Río Seco: 18°42′44 S, 63°11′35 W). Study sites were located in primary, lowland forests at 200–440 m a.s.l., which are part of a larger forest system extending from Amazonia to the Gran Chaco. At each locality, we established a 1-km transect inside the forest and a shorter 350-m transect at the forest edge. We visited each site twice, once in the rainy (November to April) and once in the dry (May to October) season. Sampling was conducted for 4 days per site and season. Climate data were extracted from WorldClim (Hijmans et al. 2005; Table I).

### 2.2. Census techniques

Euglossine bees were baited with the eight most powerful attractants following Ackerman (1983c): 1-8 cineole, benzyl acetate, methyl benzoate, eugenol, methyl salicylate, methyl cinnamate, vanillin, and additionally, the commercial drugs Olbas and Gelomyrtol as well as hydrogendiethylester and tea-tree oil. To catch the orchid bees, self-made modified McPhail traps were used (Steyskal 1977). All traps were placed about 15 paces apart and 1.7 m above ground in a straight line. Additionally, from 7:30 a.m.

**Table I.** Environmental data of the study sites as extracted from WorldClim (Hijmans et al. 2005); temperature seasonality (standard deviation *100), precipitation seasonality (coefficient of variation).

| | Mean temperature (°C) | Min. temperature (°C) | Temperature seasonality | Mean precipitation (mm) | Precipitation seasonality |
|---|---|---|---|---|---|
| Río Seco | 24.30 | 13.3 | 2,543.00 | 733 | 65 |
| Santa Cruz | 24.10 | 15.3 | 2,231.00 | 1,085 | 49 |
| Buena Vista | 24.10 | 14.6 | 2,182.00 | 2,101 | 55 |
| Sacta | 25.10 | 14.9 | 2,090.00 | 2,782 | 52 |
| Villa Tunari | 24.90 | 14.4 | 1,956.00 | 3,710 | 53 |

to 3:30 p.m., we patrolled these lines, netting all bees hovering at a trap. The bees were killed with acetic aether or formol. Specimens were dried on silica gel, put into paper bags for transport, and later pinned for identification. The species were identified following Dressler (1982a, b, c; 1985), Kimsey (1982), Bonilla-Gómez and Nates-Parra (1992), Bembé (2004), Roubik (2004), Anjos-Silva and Rebêlo (2006), Oliveira (2006), and Nemésio and Silveira (2009).

### 2.3. Data analyses

In the analyses we included all species of which more than 20 individuals had been collected. To test whether the number of aromatic substances used per species was related to the number of individuals per species, we conducted a linear regression. We used *g* tests to assess whether these species changed their aromatic preference between the rainy and the dry seasons. Further, we conducted paired *t* tests to assess whether one group of species (whole dataset; species with changes in their aromatic preferences between seasons) were more common during one season. To find out whether the number of aromatic substances used by the species that changed their aromatic preference between seasons was higher than the number of aromatic substances used by the other species, we conducted a *t* test. With another paired *t* test, we tested whether the number of aromatic substances that attracted the individual species differed between seasons. We tested this for the whole dataset and for the species that showed aromatic preferences between seasons. Then, by linear regression analyses, we related climatic factors (temperature and precipitation seasonality) to the proportion of species per site that showed significantly different preferences between seasons. The analyses were conducted in R (R Development Core Team 2007).

## 3. RESULTS

In total we collected 1,207 individuals of orchid bees belonging to 43 species (Supplementary Appendix 1). Of these, 11 species were recorded with more than 20 individuals and were included in further analyses (Table II). The number of aromatic substances that the individual species were attracted to ranged from five to ten with a mean of 8.3. The number of aromatic substances used per species was not significantly related to the individual number per species ($R$= 0.65, $P$=0.063). Six species showed significant changes in their aromatic preferences between seasons. There was no seasonal shift in the species richness of orchid bees in the whole dataset (paired *t* test: $t$=−0.75, $P$=0.472) nor among the species that showed changes in their aromatic preferences between seasons ($t$=−0.79,

**Table II.** Total number of aromatic substances (in brackets) used per species and number of orchid bee individuals per site.

| | Río Seco | Santa Cruz | Buena Vista | Sacta | Villa Tunari |
|---|---|---|---|---|---|
| *Euglossa amazonica** (10) | 0 | 10 | 52 | 64 | 33 |
| *Euglossa chalybeata* (5) | 0 | 0 | 2 | 7 | 17 |
| *Euglossa cordata* (10) | 0 | 76 | 20 | 2 | 2 |
| *Euglossa despecta** (7) | 4 | 4 | 30 | 26 | 19 |
| *Euglossa fimbriata** (10) | 30 | 47 | 9 | 1 | 0 |
| *Euglossa imperialis* (5) | 0 | 0 | 26 | 21 | 3 |
| *Euglossa magnipes* (9) | 0 | 4 | 29 | 18 | 16 |
| *Euglossa mixta* (10) | 0 | 3 | 77 | 53 | 35 |
| *Euglossa modestior** (6) | 0 | 1 | 3 | 47 | 56 |
| *Euglossa orellana** (10) | 0 | 0 | 22 | 66 | 104 |
| *Eulaema nigrita** (9) | 0 | 8 | 9 | 5 | 0 |

*$P \leq 0.05$, species with seasonally changing aromatic preferences

$P$=0.467). The number of attractants used by the species with changes in their aromatic preferences between seasons was not significantly higher than that used by the other species ($t$ test, $t$=0.66, $P$=0.525). We did not find significant differences for the number of aromatic substances that attracted the individual species between seasons for the whole dataset (paired $t$ test: $t$=−2.17, $P$=0.056) nor for the species that showed changes in their aromatic preferences between seasons ($t$=−1.88, $P$=0.119). When we related the proportion of species that did not show seasonal changes in their aromatic preferences per site to environmental characters, we found that temperature seasonality was the most powerful explanatory variable (Table III, Figure 1).

## 4. DISCUSSION

At all study sites, we found orchid bee species that changed their aromatic preferences between seasons. Importantly, the proportion of these species in the local assemblages increased from tropical evergreen rainforests to subtropical, deciduous dry forests. This pattern was best explained by increasing climatic seasonality, especially regarding temperatures.

Orchid bees are known to visit a wide array of plant species for nectar supply and to collect aromatic substances, although some species are very specific in the aromatic substances that they collect (Ackerman 1989). In Peru, Pearson and Dressler (1985) found that those specialized euglossine bee species that are only attracted by a few substances did not show changes in their aromatic preferences between seasons, whereas some of the generalistic species, using a large number of aromatic substances, differed in their preferences between seasons (see also Ackerman 1989). In our study, we found the same tendency, although the results were not quite significant. Probably, we mainly found generalists and only a few specialists, as suggested by the relatively high number of aromatic substances that the species were attracted to. In accordance to this, we found that the proportion of species that changed their aromatic preferences between seasons increased with increasing climatic seasonality towards the south. Unsurprisingly, it thus appears that only generalistic species using a wide range of aromatic substances are able show shifts in their preferences between seasons. However, not all generalistic species do so. We can conceive two non-exclusive interpretations of the causes of shifting aromatic preferences between seasons among orchid bees.

First, in extension to previous studies mainly conducted in climatically largely aseasonal evergreen rainforests (Pearson and Dressler 1985; Ackerman 1989), we were able to link the variation of aromatic preferences between seasons to climatic seasonality. It is likely that climatic seasonality mainly affects the orchid bees via the turnover of the aromatic substances provided by the plants. Plant phenology is well

**Table III.** Strength of relation ($R$ values) for regression analysis of the proportion (percent) of species without aromatic preferences per site against environmental parameters.

| | % Species without aromatic preferences |
|---|---|
| Mean temperature (°C) | −0.40 |
| Min. temperature (°C) | −0.73 |
| Temperature seasonality | 0.97* |
| Mean precipitation (mm) | −0.82 |
| Precipitation seasonality | 0.83 |

*$P \leq 0.01$

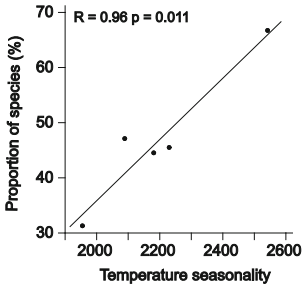


**Figure 1.** Proportion of species without aromatic preferences per site against temperature seasonality (extracted from WorldClim, Hijmans et al. 2005) in the different study sites.

known to be strongly determined by environmental factors, and plant species in climatically more seasonal sites tend to synchronise their phenology more strongly than in climatically non-seasonal sites (Günter et al. 2008). Furthermore, drier habitats are generally less species rich in plants than humid ones, also with respect to orchids in our study region (Linares-Palomino et al. 2009), which are the major source of aromatic substances for the bees (Whitten and Williams 1991). Therefore, in more seasonal habitats, orchid bees have to change their aromatic preferences between seasons because some aromatic substances are not available during parts of the year. The learning effect, as reported by Eltz et al. (2005), is not likely to explain our pattern of seasonal preference changes because we did not visit our study sites during the dry season in the same order as in the rainy season. The intervals between the visits varied between 3 and 5 months. Thus, bee populations at the different sites had different absolute ages, which strongly influence learning behaviour. It is much more likely that the change in odour preferences is a reaction to a changed availability of substances. Indeed, Eltz et al. (2005) and Ramírez et al. (2010b) showed not only that euglossine species have a species-specific odour composition but also that the composition of collected substances can change when only a subset of substances is available, for example on a small island or in areas where orchid bees were introduced. Accordingly, the shifts of aromatic preferences between seasons among orchid bee species at the southern sites may mainly be an opportunistic reaction to the seasonal turnover of a limited number of aromatic substances provided by the plants.

Second, it is striking that the species found in our study that show preferences of aromatic substances between seasons are not randomly distributed across the phylogenetic tree of orchid bees. Rather, most species belong to *Euglossa* subgenus *Euglossa*, which evolved and diversified rather recently (Ramírez et al. 2010a), with a single additional species belonging to *Eulaema*. No species from another clade occurred in the two climatically most seasonal study sites. It is therefore tempting to speculate that the generalistic and opportunistic behaviour, which also occurs in tropical sites, is a phylogenetically restricted pre-adaptation to seasonally shifting environmental conditions and enabled these species to colonize climatically strongly seasonal habitats. To support this statement, it would be necessary to show in a behavioural experiment that species from other groups are unable to react in the same flexible manner to chances of aromatic substance availability. Another approach might be to sample the content of the pockets of the hind tibia of different species in different seasons and check whether the composition is more variable in species belonging to the subgenus *Euglossa* compared to species of other subgenera in the same habitat.

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**Changements saisonniers dans les préférences olfactives des mâles d'abeilles Euglossine (Hymenoptera: Apidae) et leur implication écologique.**

**gradient climatique / précipitations / température / distribution / espèce généraliste**

**Jahreszeitliche Änderungen der Duftpräferenzen männlicher Prachtbienen (Euglossini, Hymenoptera: Apidae) und ihrer ökologischen Auswirkungen.**

**Klimatischer Gradient/ Niederschlag/ Temperatur/ Ausbreitung/ Generalist**

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