Chemoecology (2015) 25:193–199
DOI 10.1007/s00049-015-0190-9

CHEMOECOLOGY

RESEARCH PAPER

Correlates of perfume load in male orchid bees

T. Eltz · C. Bause · K. Hund · J. J. G. Quezada-Euan · T. Pokorny

Received: 12 May 2014 / Accepted: 8 July 2014 / Published online: 19 February 2015

Abstract Male neotropical orchid bees collect volatile substances from their environment and compose complex, species-specific odour blends in leg pouches. These perfumes are accumulated by the males over time and are exposed during pre-mating display. It has been hypothesized that perfumes are indicators of male genotypic quality and that females chose mates by the quality or intensity of their odour. Because direct experimental proof is lacking, we investigated whether the amount or complexity of male perfumes is related to male (1) size, (2) fluctuating (left–right) asymmetry, or (3) age, traits that are known to be sexually selected in other animals. We measured left and right forewings (cell node distances for 1 and 2, wing wear for 3) of *Euglossa dilemma* and *Euglossa viridissima* collected during dry and rainy seasons on the Yucatán peninsula, Mexico (total $N = 768$). Wing size was not related to the quantity or the complexity of perfume extracts in either species after excluding the effect of season, which positively affected both size and perfume load in *E. dilemma*. Wing asymmetry had also no effect, except in rainy season *E. viridissima*, where it was positively (not negatively) correlated with the quantity of perfume. Wing wear, an established age indicator of orchid bees, had the only consistent overall effect, being positively correlated with perfume amount and complexity in both species. This is in agreement with the idea that perfumes are an honest indicator of male survival capacity.

Keywords Fragrances · Fitness indicator · Age indicator · Sexual selection · Female choice · Male size · Fluctuating asymmetry · Wing wear

Introduction

Male mating success is often difficult to quantify accurately in studies of sexual selection, especially in non-model organisms for which copulation success is difficult to assess in the field or which require unrealistic efforts to be bred in captivity (Andersson 1994). Male mating success has eluded study in neotropical orchid bees (Apinae: Euglossini) [but see Eltz et al. (2003)] which have therefore retained one of the greatest enigmas in behavioural biology: why do male orchid bees collect environmental volatiles (odours) from a range of sources, including flowers of orchids, and store them in specialized pouches on their enlarged hind tibiae (Dressler 1982; Vogel 1966)? The behaviour has intrigued many naturalists, and a variety of ultimate causes for the behaviour have been proposed. Most authors assume that tibial perfumes are used in an intraspecific signalling context (Eltz et al. 1999; Schemske and Lande 1984; Vogel 1966), which is supported by two lines of circumstantial evidence. First, the individual perfumes are chemically species-specific, i.e., their individual composition is more similar within species than among species, potentially allowing species and mate recognition (Eltz et al. 2005a; Pokorny et al. 2013; Zimmermann et al. 2009). Also, males expose their perfumes actively during a characteristic pre-mating behaviour (‘display’) for which they perch at vertical structures in the forest understory,

---

Handling Editor: Michael Heethoff.

T. Eltz (✉) · C. Bause · K. Hund · T. Pokorny
Department of Animal Ecology, Evolution and Biodiversity,
Ruhr University Bochum, 44780 Bochum, Germany
e-mail: thomas.eltz@rub.de

J. J. G. Quezada-Euan
Departamento de Apicultura, Universidad Autónoma de
Yucatán, 97100 Merida, Yucatán, Mexico

where copulations occur (Eltz et al. 2005b). However, attraction of females to male perfumes has yet to be experimentally demonstrated, and it therefore remains unclear whether the signals are aimed at conspecific males or females or both. Assuming that females are the primary signal receivers, it is further unclear whether perfumes are short, medium, or long-range attractants, and whether their main function is recognition of the correct species or whether between-male discrimination and female choice are paramount.

In the present paper, we explore the notion that perfumes are sexually selected male traits that allow females to evaluate male genotypic quality before or during mating. Given the lack of direct evidence for female choice, we employ an indirect approach. We test whether aspects of perfume phenotypes, i.e., the quantity and complexity of individual perfume loads, are related to certain traits that are related to mating success or viability fitness in other organisms (Archer et al. 2012; Bonduriansky et al. 2008; Friedl and Klump 2005; Moller and Alatalo 1999), including other groups of bees (Alcock 1996; Amin et al. 2012; Jaffe and Moritz 2010; Stone et al. 1995; Villalobos and Shelly 1991). These traits are male size (related to competitive strength), fluctuating asymmetry (related to developmental stability), and wing wear (related to age, i.e., survival ability). We were able to derive all three traits from forewings of a large number of Mexican *Euglossa* for which we also have detailed perfume data (Pokorny et al. 2013). If perfume quantity or complexity evolves through sexual selection for good genes by female choice, positive (size, wing wear) or negative (fluctuating asymmetry) correlations with trait expression would be in support of such an idea.

Materials and methods

Bees and chemical analysis

Details on bee sampling and chemical analysis are given in Pokorny et al. (2013). Briefly, males of sympatric *Euglossa dilemma* and *Euglossa viridissima* were collected at 16 localities across the Yucatán peninsula, Mexico, during the dry (March/April) and the rainy season (September/October) of 2010. Each locality was sampled once per season using the following chemical baits: benzyl benzoate, 1,8-cineole, eugenol, methyl salicylate, *p*-dimethoxybenzene, and methyl cinnamate. The first 20 males of each species at each locality were collected in individual Eppendorf vials, frozen, and pairs of hind legs were extracted in 0.5 ml hexane p.a. (Sigma-Aldrich). Hexane extracts were analysed with coupled gas chromatography and mass spectrometry (GC/MS) using splitless injection and a DB-5MS column (30 m, 0.25-μm film thickness, 0.25 mm diameter) at Bochum. The total peak area (quantity) of exogenous perfume compounds was obtained by summing peak areas (integrated ion currents) of all individual peaks in a chromatogram excluding aliphatic cuticular hydrocarbons and lipids originating from the bees' labial glands (Eltz et al. 2007; Zimmermann et al. 2009). Total amounts of perfumes were corrected for variation in injection volume and detector sensitivity by dividing sums of areas through peak areas of known contaminants in the solvent. We also counted the number of chemical components contributing to each individual perfume extract (complexity).

Morphometry

Left and right forewings of each individual were cut off at the wing base and mounted in their natural orientation between glass slides (48 × 28 mm, 1.55-mm thickness; Knittel, Braunschweig, Gemany) fixed at wing bases by double-sided tape (four pairs per slide). Slides were scanned at 3600 dpi using an OpticFilm 7200 scanner (Plustek) and images were saved as high resolution .jpg files. Individual wings were cropped from these raw images, saved as individual files, and right wings were mirrored horizontally to allow standardized data acquisition using the software tpsdig2 by F. James Rohlf, Morphometrics Lab, Stony Brook University (http://life.bio.sunysb.edu/morph/). As an indicator of individual size, we measured the distance from the proximal end of the medial cell to the distal end of the radial cell, because endpoints were unambiguous and normally present even in wings with damaged margins. Distances in pixels were converted to mm following calibration measurements using a stereomicroscope. Fluctuating asymmetry was calculated as the absolute value (mm) of the difference between left and right measurements in an individual. We tested whether size measurements were of sufficient accuracy for evaluating individual differences by repeatedly measuring 30 randomly chosen individuals. Distances were highly predictable between repeated measurements of the same individual (linear regression: $N = 30$, $R^2 = 0.99$, $p < 0.0001$). Left–right size differences (fluctuating asymmetry) were also predictable, but with lower accuracy ($R^2 = 0.51$, $p < 0.0001$). For wing wear, we counted the number of discrete notches in the margins of both forewings while inspecting images at 1:1 zoom factor, excluding individuals that had obviously suffered wing damage during or after capturing (broken wings, wing ruptures). This measure of wing wear has previously been shown to correlate with time between recaptures, i.e., age, in Panamanian *Euglossa cognata* (Eltz et al. 1999).

Statistical procedures

All statistical tests were done using Statistica v10 by StatSoft. Non-parametric Spearman Rank correlations were used to test for effects of size, fluctuating asymmetry, and wing wear on perfume quantity and complexity. Perfume quantity and complexity are highly skewed to individuals with low values (see also Eltz et al. 1999; Zimmermann et al. 2009). Mann–Whitney *U* test was used to test for differences in variables between seasons in each species separately.

Results

Effects of season

Season had significant effects on some of the predictor variables as well as on perfume quantity and complexity (Table 1). Males of both species were significantly larger in the rainy season, and *E. dilemma* had also substantially larger and more complex perfume loads at that time (Fig. 1). In *E. viridissima,* the effect of season on perfume loads was absent (quantity) or marginal (complexity). This difference between species with respect to perfume load may have resulted from differences in population age structure. While wing wear (age) was not affected by season in *E. dilemma*, it showed a shift to less wing wear (younger males) in the rainy season in *E. viridissima*.

Correlates of perfume loads

Because season and size and season and wing wear were not independent, we ran our correlation analyses separately for each season, still based on substantial sample sizes (see Table 2). Within a given season, male size was not related to the quantity or complexity of its perfume extract in either species. Wing fluctuating asymmetry had also no effect except in rainy season *E. viridissima*, where it was marginally (and positively) correlated with the quantity of perfume. Wing wear, an established age indicator of orchid bees, had the only consistent overall effect, being positively correlated with perfume quantity and complexity in both species (Table 2; Fig. 1).

Discussion

A good theoretical argument can be made for male euglossine perfumes being indicators of the overall fitness of their bearer. Volatiles are scarce, scattered in space and time, difficult to locate in a highly complex three-dimensional habitat, potentially toxic when contacted with sensitive tissue, and they certainly require the collector to survive for sufficient amounts of time to accumulate the composite complexity that is found in hind tibial perfumes. Thus, it is plausible that aspects of perfumes (e.g., odour intensity, complexity) may function as condition-dependent sexual signals and are honest indicators of male fitness. However, very little to no evidence exists to support the argument, and the correlational findings of the present study are either negative (indicator of size or developmental stability) or have too little predictive power to make a good case on their own (indicator of age).

We found no support for the idea that perfumes are an indicator of male size, say competitive strength. This is concluded from the lack of correlations between male size and perfume quantity/complexity across large samples of individuals of two species of *Euglossa*. The negative results obtained for Mexican *E. viridissima* and *E. dilemma* of this study are backed by unpublished negative results for Panamanian *Euglossa tridentata* ($N = 51$; T. Eltz 1997). Generally, there is no indication that large size is an important trait for intra- or intersexual selection in male

Table 1 Effect of season (dry or rainy) on perfume and morphological variables in males of two species of Mexican *Euglossa* orchid bees

		Valid *N*	*Z*	*p*	+
E. dilemma	Perfume complexity	459	−6.86	**0.0000**	Rainy
E. dilemma	Perfume quantity	459	−8.61	**0.0000**	Rainy
E. dilemma	Size	458	−10.95	**0.0000**	Rainy
E. dilemma	Fluctuating asymmetry	453	1.45	0.1465	
E. dilemma	Wing wear	457	1.72	0.0861	
E. viridissima	Perfume complexity	310	−2.41	**0.0162**	Rainy
E. viridissima	Perfume quantity	310	0.55	0.5841	
E. viridissima	Size	310	−11.06	**0.0000**	Rainy
E. viridissima	Fluctuating asymmetry	308	−0.49	0.6228	
E. viridissima	Wing wear	308	4.61	**0.0000**	Dry

p values of significant Mann–Whitney *U* tests are in bold, and the season with the larger median (+) is indicated

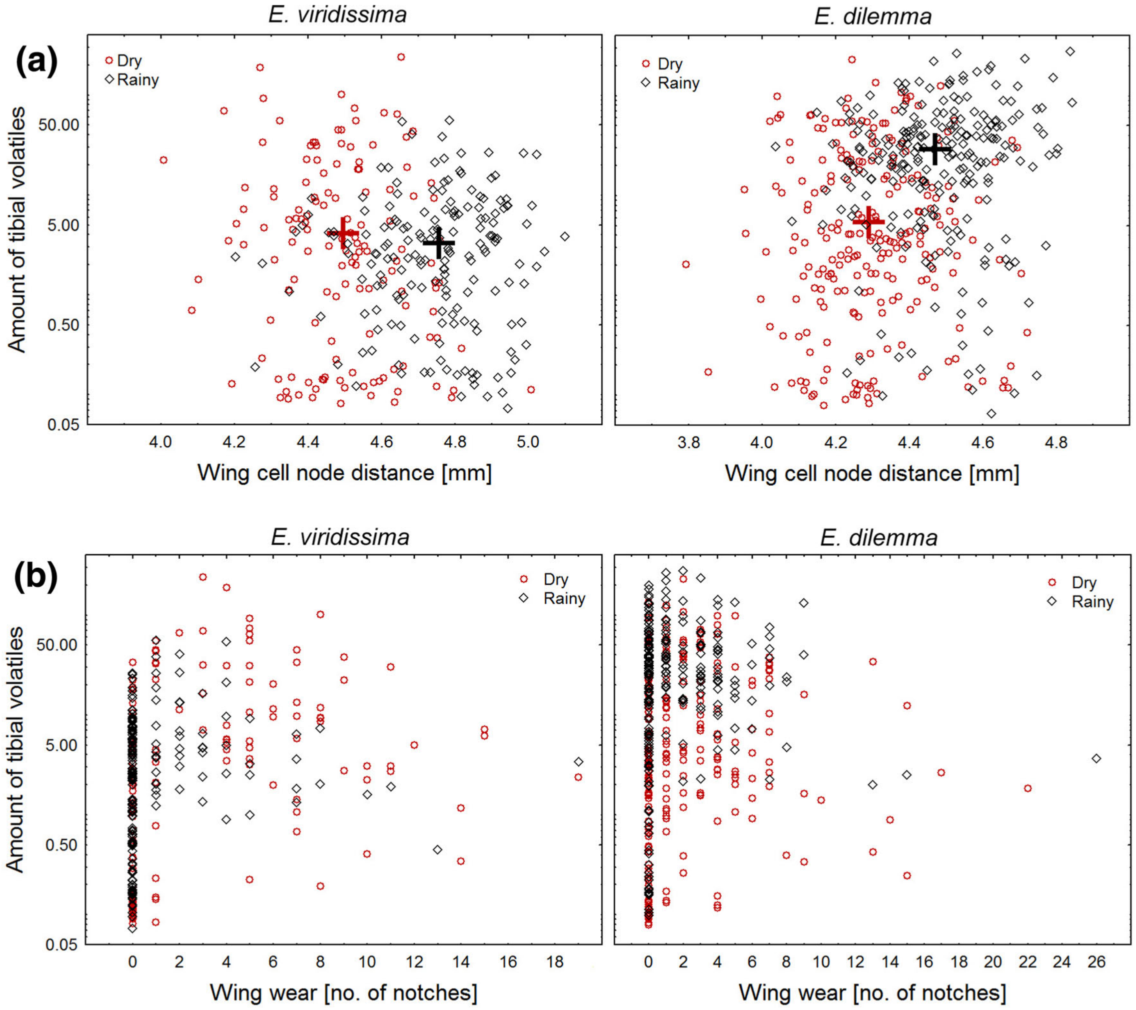

Fig. 1 Relationship between wing size (**a**) and wing wear (**b**) on the individual amount of tibial perfume in males of two species of Mexican orchid bees, *Euglossa viridissima* (*left*) and *Euglossa dilemma* (*right*), captured on the Yucatán peninsula in dry (*red circles*) and rainy (*black diamonds*) season. Amount of perfume (*Y*-axis) is plotted on a logarithmic scale. Correlation statistics are given in Table 2. Crosses mark medians of *x*/*y* variables in **a**. Perfume amount and size are confounded by season in *E. dilemma* (colour figure online)

orchid bees. Males are either equal-sized or minimally smaller than females (D. W. Roubik, pers. comm., T. Eltz, pers. obs.), which is in contrast to bee species with a pronounced large male mating advantage, e.g., wool-carder bees (Severinghaus et al. 1981; Villalobos and Shelly 1991). Also, large size seems to entail no strong advantages for accessing volatile resources in orchid bees. We have often seen males of small and large species collecting synchronously and peacefully at the same chemical bait or natural odour source, and while aggressive interactions do occasionally occur, individuals are not normally able to monopolize a source completely. Finally, size has evidently a strong environmental component in orchid bees that will reduce its value as an indicator of male genetic quality for females. Generally, adult size in mass-provisioning aculeate Hymenoptera (stinging wasps and bees) is influenced by the amount and quality of food available during the provisioning of the larval brood cell (Roulston and Cane 2000; Strohm 2000). In pollen-consuming bees, this is influenced by the phenology of flowering pollen plants (Kim and Thorp 2001). In the present study, males of both species of *Euglossa* were significantly larger in the mid rainy season (October/November) than in the dry season (March/April) which suggests that pollen of food plants [mostly Solanaceae and legumes, see Villanueva et al. (2013)] were in better supply at the time when the brood cells of rainy season bees were being provisioned. This would have been approximately in August/September (early rainy season) because it takes a larva about 6–10 weeks to develop from egg to adulthood. Good foraging conditions in the early rainy season are also indicated by *E. viridissima* trap nest occupancy in Xmatkuil, Merida, which peaks at about the same time as our rainy season samples were collected (May-Itzá et al. 2014).

Table 2 Results of Spearman Rank Correlation tests between perfume variables (quantity and complexity) and morphological predictor variables calculated for males of two species of Mexican *Euglossa* orchid bees captured in two different seasons

Variable A	Variable B	Species	Season	Valid *N*	Spearman *R*	$T(N-2)$	*P*
Quantity	Size	*E. dilemma*	Dry	226	0.06	0.83	0.4073
Quantity	Size	*E. dilemma*	Rainy	232	0.11	1.69	0.0924
Quantity	Size	*E. viridissima*	Dry	137	−0.14	−1.68	0.0953
Quantity	Size	*E. viridissima*	Rainy	173	0.04	0.49	0.6281
Quantity	FA	*E. dilemma*	Dry	223	0.03	0.46	0.6428
Quantity	FA	*E. dilemma*	Rainy	230	−0.06	−0.89	0.3750
Quantity	FA	*E. viridissima*	Dry	137	0.11	1.34	0.1827
Quantity	FA	*E. viridissima*	Rainy	**171**	**0.19**	**2.47**	**0.0146**
Quantity	Wing wear	*E. dilemma*	Dry	**227**	**0.24**	**3.70**	**0.0003**
Quantity	Wing wear	*E. dilemma*	Rainy	230	0.11	1.72	0.0877
Quantity	Wing wear	*E. viridissima*	Dry	**136**	**0.48**	**6.38**	**0.0000**
Quantity	Wing wear	*E. viridissima*	Rainy	**172**	**0.27**	**3.71**	**0.0003**
Complexity	Size	*E. dilemma*	Dry	226	0.05	0.80	0.4244
Complexity	Size	*E. dilemma*	Rainy	232	0.01	0.14	0.8921
Complexity	Size	*E. viridissima*	Dry	137	−0.11	−1.23	0.2215
Complexity	Size	*E. viridissima*	Rainy	173	−0.03	−0.36	0.7165
Complexity	FA	*E. dilemma*	Dry	223	0.02	0.34	0.7368
Complexity	FA	*E. dilemma*	Rainy	230	0.07	1.02	0.3079
Complexity	FA	*E. viridissima*	Dry	137	0.16	1.88	0.0617
Complexity	FA	*E. viridissima*	Rainy	171	0.13	1.66	0.0980
Complexity	Wing wear	*E. dilemma*	Dry	**227**	**0.27**	**4.23**	**0.0000**
Complexity	Wing wear	*E. dilemma*	Rainy	**230**	**0.21**	**3.24**	**0.0014**
Complexity	Wing wear	*E. viridissima*	Dry	**136**	**0.43**	**5.47**	**0.0000**
Complexity	Wing wear	*E. viridissima*	Rainy	**172**	**0.29**	**3.90**	**0.0001**

p values of significant correlations are given in bold. Wing wear has the only consistent (positive) effect on perfume loads across species and seasons

Seasonal effects on body size of euglossine bees were also found by studies in Brasil (Peruquetti 2003; Silva et al. 2009), where larger size was also attained in the rainy season. All this suggests that individual size of orchid bees varies strongly by environment and has little heritability [see Tepedino et al. (1984)]. It is interesting to note that perfume loads were also larger (*E. dilemma*) and more complex (both species) in the rainy season, which led to confounded correlations between size and perfume traits when individuals from both seasons were pooled. It appears that moist conditions do not only increase the availability of pollen resources but also that of volatile sources, which include both floral and microbial substrates (Whitten et al. 1993).

The measurement of fluctuating asymmetry allows researchers to evaluate developmental stability, i.e., the capacity of an individual to develop properly in the face of genetic and environmental stresses which upset development (Watson and Thornhill 1994). Developmental stability is a component of the viability of an individual genotype and thus likely related to its overall fitness. If the expression of a trait that is hypothesized to be a fitness indicator correlates negatively with fluctuating asymmetry, this would support its putative role as fitness indicator. There was no negative correlation between asymmetry and perfume loads in either species, with the accuracy of measurements being clearly sufficient to detect such a relationship. Not only was there no significant correlation, but there was not even a trend in support of the idea that more symmetric individuals may have been better in accumulating perfumes than their more asymmetric competitors. Possibly, the measured distance between wing vein junctions that we used in the analysis was not appropriate for evaluating overall developmental stability, i.e., left–right deviations in this trait did not reflect deviations in traits of greater functional importance. It remains to be stated that left–right differences in measurements were generally very small across individuals (a mean of 0.4 % and a maximum of 1.8 % of the average size of the measured distance), and possibly such small deviations can be easily compensated by physiological or behavioural means.

Wing wear was the only consistent (positive) correlate of perfume quantity and complexity in the two species, with the footnote that there was only a positive trend for *E. dilemma* in the rainy season. Wing wear, i.e., the number of notches in the margins of the forewings, has been found to correlate with the time interval between recaptures and thus with age of male *E. cognata* in Panama (Eltz et al. 1999). In the Panamanian study, the rate of wing wear accumulation varied strongly between individuals, limiting the predictive power of wing wear as an age indicator. The weaknesses of wing wear as an age indicator may also explain some of the (substantial) noise in its relationships with perfume quantity and complexity in the present study. Aside from stating that individuals with flawless wings often have empty leg pouches, very little further information can be deduced from the relationship. Judging from Fig. 1c, one might suspect that the relationship between wing wear and perfume load is hump-shaped, and that individuals with large numbers of notches also have little perfume. Such a relationship might mean that the oldest individuals have lost (or spent) some of their perfumes over their lives, but it is also possible that these are individuals that have accumulated wing wear more rapidly while also having deficiencies in volatile foraging. Future studies should attempt to find a more precise age indicator to correlate with perfume variables.

In any case, the detected correlations confirm that age/survival capacity is reflected to some extent by the tibial blends. In theory, old males are more likely to convey good genes to their offspring than young males simply because they have already proven their viability (Brooks and Kemp 2001; Manning 1985). However, the fitness of an individual is a function of both survival and mating success, and often these two fitness components cannot be maximized simultaneously. Conditionally expressed traits that enhance the likelihood of mating, such as ornaments and sexual displays, may do so at the expense of longevity (Brooks and Kemp 2001). The accumulation of rich perfume in male orchid bees is very likely condition-dependent, and equally likely to impose survival costs. Volatile collection directly increases the exposure to predators, some of which may even ambush at volatile sources like *Apiomerus* assassin bugs which have repeatedly been observed to prey on euglossines at chemical baits (T. Eltz, pers. obs.). A male that manages to put together an intense and complex perfume and lives to present it during display is therefore likely to be a good genetic father.

Acknowledgments Jorge Ramirez-Pech helped with sample collection. Funding was provided by the German Science Foundation (EL 249/6) to TE. and the PROALMEX program (120989) of the German Academic Exchange Service and the Consejo Nacional de Ciencia y Tecnologıa (103341) to TE and JQE.

References

Alcock J (1996) The relation between male body size, fighting, and mating success in Dawson's burrowing bee, *Amegilla dawsoni* (Apidae, Apinae, Anthophorini). J Zool 239:663–674

Amin MR, Bussiere LF, Goulson D (2012) Effects of male age and size on mating success in the bumblebee *Bombus terrestris*. J Insect Behav 25:362–374

Andersson M (1994) Sexual selection. Princeton University Press, New Jersey

Archer CR, Zajitschek F, Sakaluk SK, Royle NJ, Hunt J (2012) Sexual selection affects the evolution of lifespan and ageing in the decorated cricket *Gryllodes sigillatus*. Evolution 66: 3088–3100

Bonduriansky R, Maklakov A, Zajitschek F, Brooks R (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. Funct Ecol 22:443–453

Brooks R, Kemp DJ (2001) Can older males deliver the good genes? TREE 16:308–313

Dressler RL (1982) Biology of the orchid bees (*Euglossini*). Ann Rev Ecol Syst 13:373–394

Eltz T (1997) Zur Duftstoffbiologie neotropischer Prachtbienen (Apidae: Euglossini). Diplomarbeit, Universität Würzburg, Germany, pp 104

Eltz T, Whitten WM, Roubik DW, Linsenmair KE (1999) Fragrance collection, storage, and accumulation by individual male orchid bees. J Chem Ecol 25:157–176

Eltz T, Roubik DW, Whitten WM (2003) Fragrances, male display and mating behaviour of *Euglossa hemichlora*: a flight cage experiment. Phys Entomol 28:251–260

Eltz T, Roubik DW, Lunau K (2005a) Experience-dependent choices ensure species-specific fragrance accumulation in male orchid bees. Behav Ecol Sociobiol 59:149–156

Eltz T, Sager A, Lunau K (2005b) Juggling with volatiles: exposure of perfumes by displaying male orchid bees. J Comp Physiol A 191:575–581

Eltz T et al (2007) Enfleurage, lipid recycling and the origin of perfume collection in orchid bees. Proc Royal Soc B Biol Sci 274:2843–2848

Friedl TWP, Klump GM (2005) Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. Anim Behav 70:1141–1154

Jaffe R, Moritz RFA (2010) Mating flights select for symmetry in honeybee drones (*Apis mellifera*). Naturwissenschaften 97:337–343

Kim JY, Thorp RW (2001) Maternal investment and size-number trade-off in a bee, *Megachile apicalis*, in seasonal environments. Oecologia 126:451–456

Manning JT (1985) Choosy females and correlates of male age. J Theor Biol 116:349–354

May-Itzá WdJ, Medina Medina LA, Medina S, Paxton RJ, Quezada-Euán JJG (2014) Seasonal nest characteristics of a facultatively social orchid bee, *Euglossa viridissima*, in the Yucatan Peninsula, Mexico. Insectes Soc 61:183–190

Moller AP, Alatalo RV (1999) Good-genes effects in sexual selection. Proc Royal Soc B Biol Sci 266:85–91

Peruquetti RC (2003) Variação do tamanho corporal de machos de *Eulaema nigrita* Lepeletier (Hymenoptera, Apidae, Euglossini). Resposta materna à flutuação de recursos? [Body size variation in males of *Eulaema nigrita* Lepeletier (Hymenoptera, Apidae, Euglossini). Maternal response to resource fluctuation?]. Rev Bras Zool 20:207–212

Pokorny T et al (2013) Acquisition of species-specific perfume blends: influence of habitat-dependent compound availability on odour choices of male orchid bees (*Euglossa* spp.). Oecologia 172:417–425

Roulston TH, Cane JH (2000) The effect of diet breadth and nesting ecology on body size variation in bees (Apiformes). J Kansas Entomol Soc 73:129–142

Schemske DW, Lande R (1984) Fragrance collection and territorial display by male orchid bees. Anim Behav 32:935–937

Severinghaus LL, Kurtak BH, Eickwort GC (1981) The reproductive behavior of *Anthidium manicatum* (Hymenoptera: Megachilidae) and the significance of size for territorial males. Behav Ecol Sociobiol 9:51–58

Silva MC, Lomonaco C, Augusto SC, Kerr WE (2009) Climatic and anthropic influence on size and fluctuating asymmetry of *Euglossine* bees (Hymenoptera: Apidae) in a semideciduous seasonal forest reserve. Genet Mol Res 8:730–737

Stone GN, Loder PMJ, Blackburn TM (1995) Foraging and courtship behavior in males of the solitary bee *Anthophora plumipes* (Hymenoptera, Anthophoridae): thermal physiology and the roles of body-size. Ecol Entomol 20:169–183

Strohm E (2000) Factors affecting body size and fat content in a digger wasp. Oecologia 123:184–191

Tepedino VJ, Thompson R, Torchio PF (1984) Heritability for size in the *Megachilid* bee *Osmia lignaria propinqua* Cresson. Apidologie 15:83–87

Villalobos EM, Shelly TE (1991) Correlates of male mating success in two species of *Anthidium* bees (Hymenoptera: Megachilidae). Behav Ecol Sociobiol 29:47–53

Villanueva RA, Quezada-Euan JJG, Eltz T (2013) Pollen diets of two sibling orchid bee species, *Euglossa*, in Yucatán, southern Mexico. Apidologie 44:440–446

Vogel S (1966) Parfümsammelnde Bienen als Bestäuber von Orchidaceen und Gloxinia. Österr Bot Z 113:302–361

Watson PJ, Thornhill R (1994) Fluctuating asymmetry and sexual selection. TREE 9:21–25

Whitten WM, Young AM, Stern DL (1993) Nonfloral sources of chemicals that attract male euglossine bees (Apidae: Euglossini). J Chem Ecol 19:3017–3027

Zimmermann Y, Ramírez SR, Eltz T (2009) Chemical niche differentiation among sympatric species of orchid bees. Ecology 90:2994–3008