Research Article / Artículo de Investigación

Going up: new altitudinal records of orchid bees (Hymenoptera: Apidae) in the inter-Andean valleys of southern Ecuador and their potential dispersal route

Subiendo: nuevos registros altitudinales de abejas de las orquídeas (Hymenoptera: Apidae) en los valles interandinos del sur de Ecuador y su potencial ruta de dispersión

Pablo Sebastián Padrón[1*], Madeleine Campaña[1], Manuela Burbano[1], and Michelle Armijos[1]

[1]*Laboratorio de Entomología, Universidad del Azuay, Cuenca, Ecuador.* **sebastianpadronm@yahoo.com*

ZooBank: urn:lsid:zoobank.org:pub:5BF5F8F7-7F3E-4B0E-B2C7-F64801BFA08F
https://doi.org/10.35249/rche.49.4.23.13

Abstract. Orchid bees are a conspicuous and ecologically important group of insects, commonly distributed at medium and low altitudes in tropical ecosystems. Therefore, new recordings of orchid bees at higher altitudes are interesting. Here we report the presence of two species of orchid bees in urban and peri-urban environments within the inter-Andean valleys in the province of Azuay in southern Ecuador at more than 2,200 m. One male of *Eulaema* (*Apeulaema*) *polychroma* (Mocsáry, 1899) and a female of *Euglossa* (*Euglossa*) cf. *charapensis* Cockerell, 1917, were recorded in the city of Cuenca at 2,550 m, and several females of *Eg.* (*Eg.*) cf. *charapensis* in the surroundings of the city of Gualaceo at 2,264 m. These new altitude distribution records represent the highest for the genus *Euglossa* in Ecuador. Also, they show the great altitude dispersal capacity, and high adaptability of these insects to urban and peri-urban environments. Finally, we proposed the Jubones river basin as a potential migration route of these bees from lowland areas in the western foothills of the Andes to the inter Anden valleys of Cuenca and Gualaceo.

Key words: Andes; Euglossini; *Eulaema*; Jubones river; mountains.

Resumen. Las abejas de las orquídeas son un grupo de insectos conspicuos y ecológicamente importantes, comúnmente distribuidos a altitudes medias y bajas en ecosistemas tropicales. Por ello, son interesantes los nuevos reportes de abejas de las orquídeas en elevaciones más altas. Aquí se reporta la presencia de dos especies de abejas de las orquídeas en ambientes urbanos y periurbanos dentro de los valles interandinos en la provincia de Azuay en el sur de Ecuador a más de 2.200 m. Un macho de *Eulaema* (*Apeulaema*) *polychroma* (Mocsáry, 1899) y una hembra de *Euglossa* (*Euglossa*) cf. *charapensis* Cockerell, 1917, fueron registrados en la ciudad de Cuenca a 2.550 m, y varias hembras de *Eg.* (*Eg.*) cf. *charapensis* en los alrededores de la ciudad de Gualaceo a 2.264 m. Estos nuevos registros de distribución altitudinal representan los más altos para el género *Euglossa* en Ecuador. Además, muestran la gran capacidad de dispersión altitudinal, y alta adaptabilidad de estos insectos a ambientes urbanos y periurbanos. Finalmente, proponemos la cuenca del río Jubones como una ruta potencial de migración de estas abejas desde zonas bajas en las estribaciones occidentales de los Andes hasta los valles interandinos de Cuenca y Gualaceo.

Palabras clave: Andes; Euglossini; *Eulaema*; río Jubones, montañas.

Received 10 August 2023 / Accepted 15 November 2023 / Published online 30 November 2023
Responsible Editor: José Mondaca E.

Introduction

Orchid bees (tribe Euglosini) are a diverse, visually conspicuous, and ecologically important group of insects (Ramírez *et al.* 2002, 2010; Roubik and Hanson 2004). These insects were originally restricted to the Neotropics, but now can be found further north (Skov and Wiley 2005; Pemberton and Wheeler 2006). These bees are important pollinators of orchids and other plants in the Neotropics (Ramírez *et al.* 2011). Pollination of orchids is done by males, which actively search and collect floral fragrances that are used in elaborate reproductive courtships directed toward females (Eltz *et al*. 2003; Roubik and Hanson 2004). Most orchid bee species are restricted to medium and low elevations in tropical areas (Nemésio and Silveira 2007a). Orchid bee diversity is inversely related to the increase of altitude in the Andes (Ramírez *et al.* 2002). Therefore, new records of orchid bees at elevations above 2,000 m are scarce and rare (Ramírez *et al.* 2002; Dick *et al.* 2004; Gonzalez and Engel 2004; Perger 2015).

Padrón *et al*. (2018) published the first preliminary list of species in Ecuador, in which distribution data, including elevation, was presented for 115 species of orchid bees. Information of their geographic distribution in the country, especially for common and abundant species is known, but for species inhabiting poorly studied or isolated and little explored regions such as the mountainous regions of the Andes is poorly known. In recent years, several species of orchid bees have been recorded in urban environments in the Neotropics (Nemésio and Silveira 2007b; Perger 2015). These records highlight the importance of these new "landscapes", which are actively used by a wide variety of insects, including orchid bees.

In this publication we report the presence and potential establishment of orchid bees at more than 2,200 m in urban and peri-urban areas in the inter-Andean valleys of southern Ecuador. Finally, we propose a potential migratory route to these new high areas in the Andes.

Materials and Methods

Study area

The new altitude distribution records were made in three localities in urban and peri-urban environments located in inter-Andean valleys of southern Ecuador in the Azuay province (Fig. 1A). Two localities (-2.91872 -79.00153, -2.89902 -79.00413 at 2,530 m and 2,552 m respectively) are in the urban environment of the city of Cuenca where the vegetation cover is dominated by grass and ornamental species of trees and shrubs. An additional locality was in the peri-urban of Gualaceo (-2.90019 -78.75910 at 2,264 m). Vegetation at this site is composed of grass and ornamental plants, among which the wax bush *Clusia orthoneura* (Standl.) within the Clusiaceae family stand out. Also, in this place, there are orchids as ornamental plants. This location is near the San Francisco River, where there are small remnants of native forest on the banks.

In relation to the climate, these three localities experience seasonal changes, with the dry season being from June to September and the rainy season from October to May. During the day, the temperature and precipitation can vary greatly according to the season.

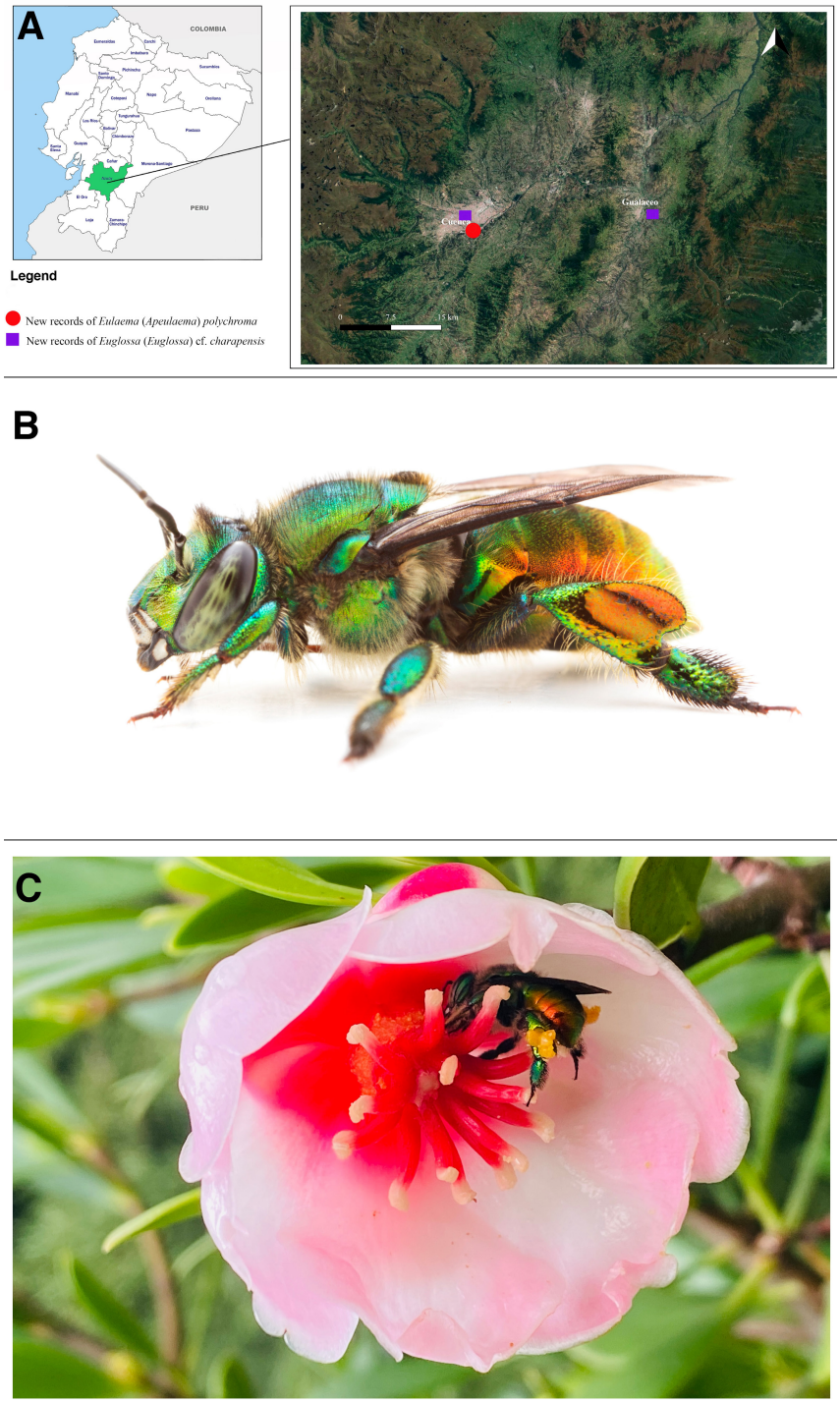

Figure 1. A. Map showing new localities for *Eulaema* (*Apeulaema*) *polychroma* and *Euglossa* (*Euglossa*) cf. *charapensis*, in Azuay province, Ecuador. **B.** Female of *Euglossa* (*Euglossa*) cf. *charapensis*. **C.** Female of *E.* cf. *charapensis* visiting a flower of *C. orthoneura* upon which yellow resin is observed in the rear expanded tibia. / Mapa que muestra nuevas localidades para *Eulaema* (*Apeulaema*) *polychroma* y *Euglossa* (*Euglossa*) cf. *charapensis*, en la provincia de Azuay, Ecuador. **B.** Hembra de *Euglossa* (*Euglossa*) cf. *charapensis*. **C.** Hembra de *Euglossa* (*Euglossa*) cf. *charapensis* visitando una flor de *C. orthoneura* sobre la cual se observa resina amarilla en la tibia trasera expandida.

Collection and taxonomic identification of orchid bees

Most of the orchid bees were collected using entomological nets and sacrificed; one specimen included in this study was found dead. All samples were preserved in 96% alcohol. Later, the specimens were dry mounted, labeled with information about their collection and incorporated into the entomology collection of the Zoology Museum of the University of Azuay in Cuenca, Ecuador. Their voucher numbers are MZUA-EN013889 - EN013895. The specimens were collected under the research permit issued by the Ministry of Environment, Water and Ecological Transition (181-2018-DPAA/MA).

Collected specimens were photographed using a Canon 5D Mark III camera with a Canon MPE 65 mm lens. Details of structures were photographed using a Mitotuyo 5X APO microscope lens attached. Detailed images were generated using a photo stacking technique with Zerene Stacker Software. The final images were created using Photoshop CS3. The map and landscape in Fig. 1 were generated using the QGIS 3.10 program.

For taxonomic identification, a Nikon SMZ745 stereo microscope was used and external morphological diagnostic characteristics were reviewed. These identifying characteristics were compared with taxonomic keys and original species descriptions. Also, lateral and dorsal photos of the holotype of *Euglossa charapensis* Cockerell, 1917 from Peru, Cajamarca, río Charape, collected by C.H.T. Townsend and deposited at the Smithsonian Institution, National Museum of Natural History in Washington DC. USNM 23142 and uploaded on the Taxonomía de las Euglosinas page at the Smithsonian Tropical Research Institute web page were revised and compared. Additionally, detailed photos of different parts of our specimens were checked for identification by Dr. David Roubik from the Smithsonian Institute, who is a specialist in Euglossini.

Results and Discussion

Knowing the altitudinal distribution of organisms is fundamental to define conservation strategies under a climate change scenario (Kharouba *et al.* 2019). This is even more necessary for sensitive and important species such as orchid bees (Roubik and Hanson 2004). In this publication we report the presence of two species of orchid bees identified as *Eulaema* (*Apeulaema*) *polychroma* (Mocsáry, 1899) and *Euglossa* (*Euglossa*) cf. *charapensis* Cockerell, 1917, at elevations above 2,264 m. Although there are sporadic records of orchid bees in the high Andes (Ramírez *et al.* 2002; Dick *et al.* 2004), and in recent years Perger (2015) found a community of orchid bees in a garden in San Joaquín, Salancachi Bolivia at an elevation of 2,640 m; distribution records at elevations above 2,200 m are rare (Ramírez *et al.* 2002).

A male of *El.* (*A.*) *polychroma* (Fig. 2) was found dead on the floor during early morning hours in the gardens at the University of Azuay in 2018 in the city of Cuenca. In relation to the taxonomic certainty of their identification, *El.* (*A.*) *polychroma* can be identified according to Roubik and Hanson (2004) by the combination of the following characters: the body is approximately 18-20 mm long; the unextended tongue barely reaches the metasoma and extends it reach; the male rostrum is black with color markings on the clypeus and eye margin; the metasoma tergite I is black, and tergites II-VII have orange hairs; there is marked pubescence at the edge of the tibia (Fig. 2D). Although this species can be confused with *Eulaema* (*Apaulaema*) *speciosa* (Mocsary, 1897), due to the similarity in its coloration, the latter has more metallic reflections in the integument of the metasoma and males lack markings on the face (Fig. 2C).

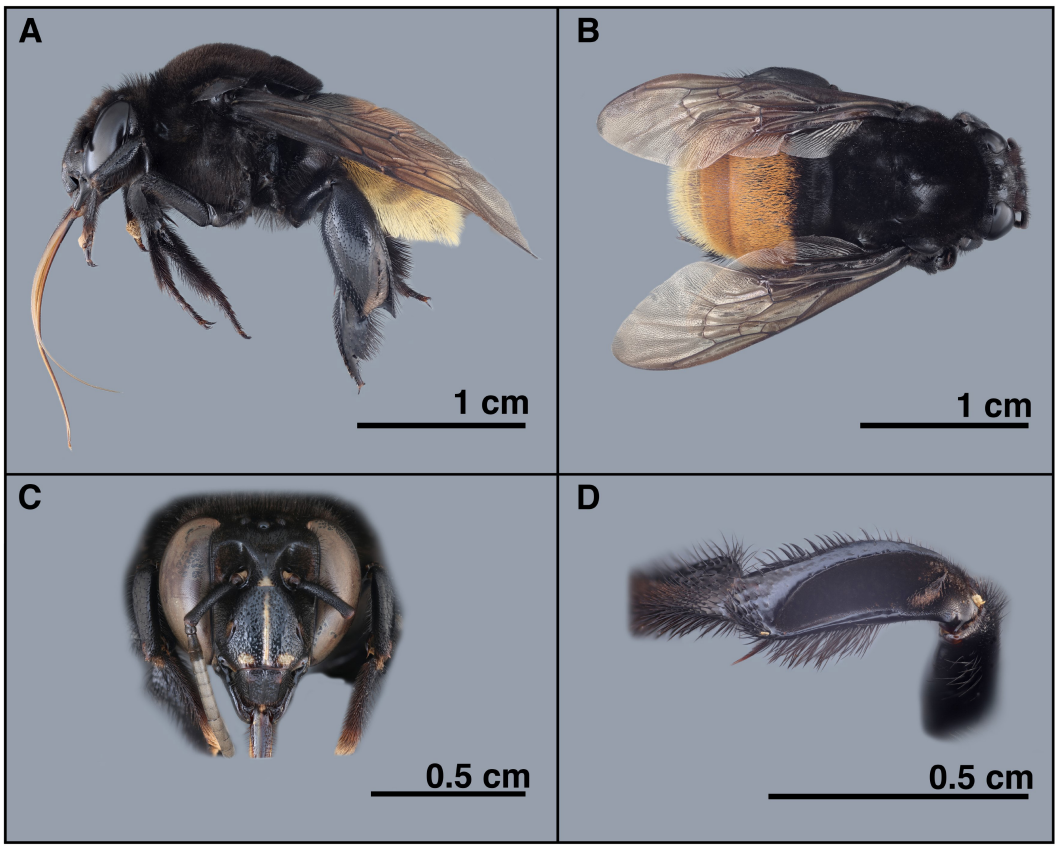

Figure 2. Male of *Eulaema* (*Apeulaema*) *polychroma* collected in Cuenca. **A.** Lateral view. **B.** Dorsal view. **C.** Face. **D.** Detail of tufts presents in the middle tibia. / Macho de *Eulaema* (*Apeulaema*) *polychroma* recolectado en Cuenca. **A.** Vista lateral. **B.** Vista dorsal. **C.** Cara. **D.** Detalle de mechones presentes en la tibia media.

The females collected in Gualaceo and in downtown Cuenca were identified as *Eg.* (*Eg.*) cf. *charapensis* (Figs. 1B, 3). First, a group of specimens were observed and later collected in a private garden in the peri-urban areas of Gualaceo (-2.90019 -78.75910) at 2264 m on March 02, 2018. Then successive visits in different months of the year at the same garden have been carried out from 2018 to 2023 in search of males. During all these visits several females have been observed actively flying and visiting flowers. Then, a second specimen of *Eg.* (*Eg.*) cf. *charapensis* was collected on October 22, 2021, in downtown Cuenca (-2.89902 -79.00413) at 2,552 m on a sunny day in the morning. Observations of *Eg.* (*Eg.*) cf. *charapensis* at this altitude exceed at least 663 m previous records for this species in Ecuador (1,601 m) (Padrón *et al.* 2018).

Euglossa (*Eg.*) *charapensis* was originally described from a female by Cockerell (1917). The diagnosis of the species was based on the combination of some external morphological characteristics, in the thorax, having a shorter scutellum in proportion to its width, and the apical area of the abdomen with a very strong reddish-coppery tints (Cockerell 1917). However, final confirmation of species identification could be made when the male is obtained or when funds and permits are available for additional molecular work (DNA Barcoding).

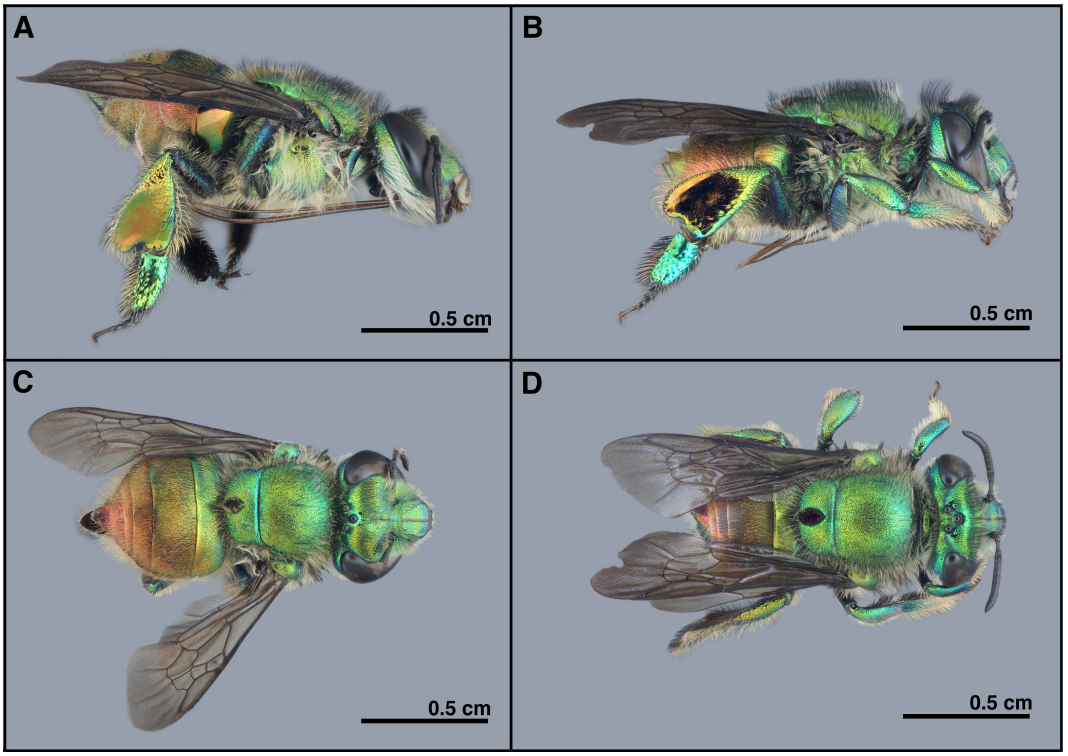

Figure 3. New collected females of *Euglossa* (*Euglossa*) cf. *charapensis*. **A.** Lateral view of specimen collected in Cuenca. **B.** Lateral view of specimen collected in Gualaceo. **C.** Dorsal view of specimen collected in Cuenca. **D.** Lateral view of specimen collected in Gualaceo. / Nuevas hembras recolectadas de *Euglossa* (*Euglossa*) cf. *charapensis*. **A.** Vista lateral de ejemplares recolectados en Cuenca. **B.** Vista lateral de ejemplares recolectados en Gualaceo. **C.** Vista dorsal de ejemplares recolectados en Cuenca. D. Vista lateral de ejemplares colectados en Gualaceo.

In the locality of Gualaceo, several females of *Eg.* (*Eg.*) cf. *charapensis* were observed actively visiting flowering plants of *Clusia orthoneura* Standl. (Clusiaceae), commonly known as the Wax Flower (Fig. 1C). This is a shrub native to Colombia that is currently marketed as an ornamental plant for gardens in Ecuador. It is characterized by abundant flowering, and resin production that is collected by females (Fig. 1C).

In relation to the potential dispersal route of these bees from the western foothills of the southern Andes to the internal valleys of Cuenca and Gualaceo, we hypothesize that this could be through the Jubones river valley to Portete de Tarqui and then disperse to Cuenca and Gualaceo through the Paute river basin that connects the latter two localities (Fig. 4).

The two new localities reported here (Cuenca and Gualaceo) are almost at the same elevations and are connected by the Paute river basin. The Paute river basin is limited in the South by the Jubones river basin, a desert ecosystem that, on its way to the west, creates a deep canyon that connects the high mountains of Azuay province with the coast of El Oro province, crossing several ecosystems at different heights until reaching the coastal lowlands. The highest pass that the bees would have had to overcome on their potential route from the Jubones river basin to the Inter Andean valleys is located in Portete de Tarqui at 2,750 m (Fig. 4). Once overcoming this altitude barrier, their way to Cuenca and Gualaceo would not be blocked by any other geographic barrier. Therefore, this route is quite likely the one that was used by the orchid bees to disperse from the west side of the Andes to the inter Andean valleys that include Gualaceo and Cuenca. This phenomenon of using river canyons as migration routes has been reported before for other flying insects

(Williams 1975) and especially for short altitude migrations of bees using rivers (Robinson 2021), as may be the case reported here. Finally, our hypothesis is reinforced by observations showing that both *El.* (*A.*) *polychroma* and *Eg.* (*Eg.*) cf. *charapensis* have been collected in the Jubones river basin, and both species are common in lowland west coastal areas of Ecuador (Padrón *et al.* 2018).

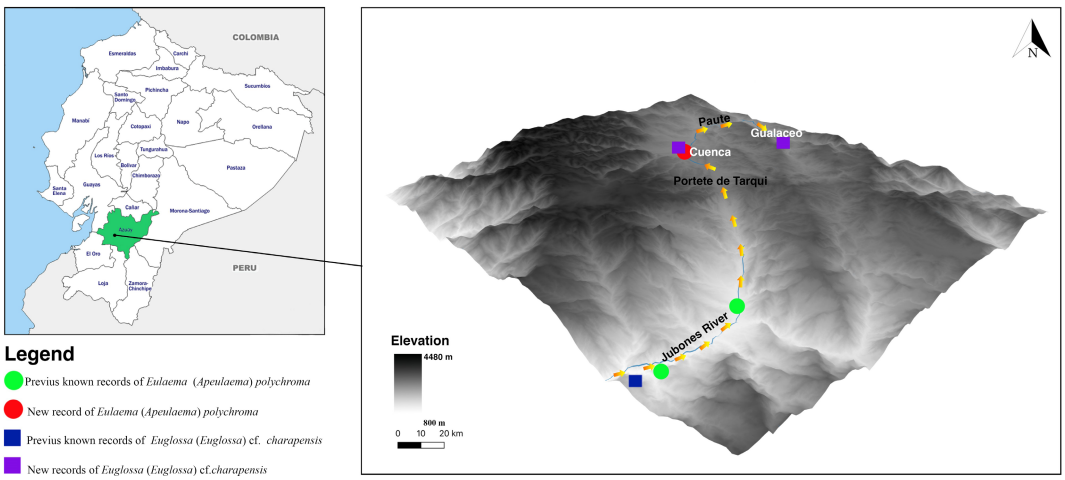

Figure 4. Potential dispersal route from the west lowlands of the Andes in Azuay province to the inter-Andean valleys of southern Ecuador. / Posible ruta de dispersión desde las tierras bajas occidentales de los Andes en la provincia de Azuay hasta los valles interandinos del sur de Ecuador.

It is also well known that their migration and establishment in places outside their original distribution range can be facilitated by several factors, such as the availability of resources and dispersal routes (Wikelski *et al.* 2010). But other aspects such as anthropic degradation or climatic variability seem to be less important at the time of establishment at least for *El.* (*A.*) *polychroma* (Damon *et al.* 2012).

Additionally, we consider that the females of *Eg.* (*Eg.*) cf. *charapensis* observed in Cuenca and Gualaceo are an established population, since females of this species were observed actively visiting flowers, and several female bees were observed entering cracks in stone walls (Gualaceo locality) (personal observation), where nests are presumably located. Although females also actively seek resources to build and maintain their nests, they tend to move less (in comparison to males), within their foraging territories (López-Uribe *et al.* 2008). They are constantly around their nesting sites (Dressler 1982), flying to and from their nests (Kroodsma 1975), unlike males, which can move several kilometers in search of courtship essences (Roubik and Hanson 2004; William and Dodson 1972). This can also be evidenced in the condition of the wings; females have nearly perfect wings when they are likely to nest nearby as the ones shown on the figures. Males, unlike females, "wander" more in search of chemical compounds and therefore generally have more wing wear.

These observations suggest that in Cuenca and Gualaceo there is at least one population of orchid bees that have managed to become established. This conclusion is strengthened by the fact that females in the Gualaceo location have been observed since 2018 to the present time and at different months of the year.

Regarding the presence of a male of *El.* (*A.*) *polychroma* found dead in Cuenca, this could be an anomalous and isolated case of distribution since it is known that the ability to move vertically to higher elevations seems to be related to body size (Dick *et al.* 2004). The bees in the genus *Eulaema* Lepeletier, 1841 are large and robust and, therefore, can move great

distances daily (Dressler 1982; Gonzalez and Engel 2004). Males of this genus in capture and marking experiments have been recaptured at very far distances from where they were originally marked (Pokorny *et al.* 2015). Also, Hinojosa-Díaz (2010), reported an anomalous distribution record of a male of *El.* (*A.*) *polychroma* in Arizona, USA, which was the result of the bee moving too far from its original distribution range, or it may have been accidentally introduced. These observations suggest that the male we found may have moved in search of resources but got too far away from its original habitat. One may speculate that this bee's death was caused by the large fluctuations in temperatures between day and night, which are common in places above 2,500 m in the Andes. A study carried out by Armbruster and Berg (1994), determined that the activity in bees of the *Eulaema* Lepeletier, 1841 genus is negatively affected by the time of day and environmental temperature. However, it cannot be ruled out that this could be the initial steps of migrations to a new place, and that in the future, new specimens may be found in these inter Andean valleys.

Morphological aspects of orchid bees, such as their coloration and generally shiny or metallic appearance along with their contrasting and striking colors of black green and orange give them a striking appearance. Also, most orchid bees are medium to large in size, and their behavior includes active flower visitation (Roubik and Hanson 2004), which makes these bees conspicuous; therefore, easy to observe and record. Thus, their migration and especially their potential establishment in these new localities in the inter-Andean valleys could be recent events since they have not been observed and reported until now.

Another interesting aspect of the new observations of orchid bee species at high altitude is that they were made in urban and peri-urban environments in populated and environmentally degraded areas. This has important implications for their conservation by demonstrating their great adaptability and capacity to settle into these ecosystems, reinforcing the already known importance of urban areas and forest fragments in maintaining orchid bee communities (Storck-Tonon *et al.* 2013; Perger 2015). There are several reports of significant expansion of orchid bee species distribution to urban areas (Skov and Wiley 2005; Anjos-Silva *et al.* 2006; Silva and Rebêlo 2009). Also, in these urban ecosystems, the availability and abundance of resources such as nectar, pollen, nesting sites and floral resins, along with fewer natural enemies can favor the migration and establishment of orchid bees (Skov and Wiley 2005). In addition, the incorporation of new species of ornamental plants in gardens such as orchids (which are widely cultivated in urban gardens in this part of Ecuador) or the wax tree, *C. orthoneura*, can provide the essences that males collect and use in courtship. The wax tree may also provide wax or resin for nest construction by female orchid bees. In the Gualaceo location, we have observed that females visit the flowers of *C. orthoneura* in search of resins. This behavior has been reported before in females of Euglossini bees which collect resins from species in the genus *Clusia* L. (Clusiaceae) (Bittrich and Amaral 1997; Roubik and Hanson 2004). In addition, the ability to adapt and use exotic plants has been reported by Perger (2015) in Bolivia where bees used *Hibiscus rosasinensis* L. (Malvaceae) and *Agapanthus praecox* Willd. (Amaryllidaceae) which are exotic plants from China and South Africa respectively. Pemberton and Wheeler (2006), determined tha*t Euglossa* (*Euglossa*) *viridissima* (Friese, 1899) established in Florida, USA, can be abundant in the absence of their mutualistic orchids, which suggests that this mutualism can be flexible, thus facilitating adaptation to new sites (Genaro *et al.* 2020). Climate change can also modify the distribution ranges of orchid bees and affect interactions with other species (Silva *et al.* 2015), but for the species reported here, this hypothesis needs to be tested with more field and laboratory work.

Finally, the study of the entomofauna in urban environments, especially in the tropical Andes, is necessary and urgent. These areas can be refuges for a great diversity of insects (Padrón 2020), including orchid bees (Otero and Sandino 2003; Pemberton and Wheeler 2006; Nemésio and Silveira 2007b; López-Uribe *et al.* 2008). Orchid bees are solitary and nest in cracks along with being polygolectic, which allows them to adapt to urban environments

(López-Uribe *et al*. 2008). Therefore, these "new" landscapes at high altitude should be considered in conservation programs, not only for ecosystem services but also for the possibility of incorporating them into conservation programs by allowing a more direct approach and empowerment of citizens with the conservation of the urban biodiversity that surrounds them.

Acknowledgment

We are very grateful to Dr. David Roubik of the Smithsonian Institute for sharing with us the photos of the holotype of *E. charapesnis*, which helped us in the identification of the species, also for his comments and suggestions that allowed us to greatly improve the quality of the manuscript. We thank Dr. Wayne Hanson and his wife Estée for alerting us of the presence of orchid bees in their garden, and for kindly allowing us to visit his home to study the bees. P.S. Padrón thanks the University of Azuay and its Research Program (2023-2024) and the Ministry of the Environment, Water and Ecological Transition for the research permits (181-2018-DPAA/MA).

Literature Cited

Anjos-Silva D., E.J., Camillo, E. and Garófalo, C.A. (2006) Occurrence of *Aglae caerulea* Lepeletier & Serville (Hymenoptera: Apidae: Euglossini) in the Parque Nacional da Chapada dos Guimarães, Mato Grosso State, Brazil. *Neotropical Entomology*, *35*: 868-870. https://doi.org/10.1590/S1519-566X2006000600024

Armbruster, W.S. and Berg, E.E. (1994) Thermal ecology of male euglossine bees in a tropical wet forest: fragrance foraging in relation to operative temperature. *Biotropica*, *26*(1): 50-60.

Bittrich, V. and Amaral, M.C.E. (1997) Floral biology of some *Clusia* species from Central Amazonia. *Kew Bulletin*, *52*(3): 617-635.

Cockerell, T.D.A. (1917) Some euglossine bees. *The Canadian Entomologist*, *49*(4): 144-146.

Damon, A., Hernández-Ramírez, F., Riggi, L., Verspoor, R., Bertolini, V., Lennartz-Walker, M., Wiles, A. and Burns, A. (2012) Pollination of euglossinophylic epiphytic orchids in agroecosystems and forest fragments in southeast Mexico. *European Journal of Environmental Sciences*, *2*(1): 5-14. https://doi.org/10.14712/23361964.2015.34

Dick, C.W., Roubik, D.W., Gruber, K.F. and Bermingham, E. (2004) Long-distance gene flow and cross-Andean dispersal of lowland rainforest bees (Apidae: Euglossini) revealed by comparative mitochondrial DNA phylogeography. *Molecular Ecology*, *13*(12): 3775-3785. https://doi.org/ 10.1111/j.1365-294X.2004.02374.x. PMID: 15548290

Dressler, R.L. (1982) Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics*, *13*(1): 373-394.

Eltz, T., Roubik, D.W. and Whitten, M.W. (2003) Fragrances, male display and mating behaviour of *Euglossa hemichlora*: a flight cage experiment. *Physiological Entomology*, *28*(4): 251-260. https://doi.org/10.1111/j.1365-3032.2003.00340.x

Genaro, J.A., Hinojosa-Díaz, I.A. and McDowell Johnson, L. (2020) First record of the orchid bee *Euglossa dilemma* (Hymenoptera: Apidae) in Hispaniola, the Antilles. *Insecta Mundi*, *0779*: 1-5.

Gonzalez, V.H. and Engel, M.S. (2004) The tropical Andean bee fauna (Insecta: Hymenoptera: Apoidea), with examples from Colombia. *Entomologische Abhandlungen*, *62*(1): 65-75.

Hinojosa-Díaz, I.A. (2010) Comparative genital morphology, phylogeny, and classification of the orchid bee genus *Euglossa* Latreille (Hymenoptera: Apidae), with distributional modeling of adventive Euglossines [dissertation]. Kansa (KS): University of Kansas. 211 pp.

Kharouba, H.M., Lewthwaite, J.M., Guralnick, R., Kerr, J.T. and Vellend, M. (2019) Using insect natural history collections to study global change impacts: challenges and opportunities. *Philosophical Transactions of the Royal Society B*, *374*(1763): 1-10. https://doi.org/10.1098/rstb.2017.0405

Kroodsma, D.E. (1975) Flight distances of male euglossine bees in orchid pollination. *Biotropica*, *7*(1): 71-72.

López-Uribe, M.M., Oi, C.A. and Del Lama, M.A. (2008) Nectar-foraging behavior of euglossine bees (Hymenoptera: Apidae) in urban areas. *Apidologie*, *39*(4): 410-418. https://doi.org/10.1051/apido:2008023

Nemésio, A. and Silveira, F.A. (2007a) Diversity and distribution of orchid bees (Hymenoptera: Apidae) with a revised checklist of species. *Neotropical Entomology*, *36*: 874-888.

Nemésio, A. and Silveira, F.A. (2007b) Orchid bee fauna (Hymenoptera: Apidae: Euglossina) of Atlantic Forest fragments inside an urban area in southeastern Brazil. *Neotropical Entomology*, *36*: 186-191. https://doi.org/10.1590/S1519-566X2007000200003

Otero, J.T. and Sandino, J.C. (2003) Capture rates of male Euglossine bees across a human intervention gradient, Chocó region, Colombia. *Biotropica*, *35*(4): 520-529. https://doi.org/10.1111/j.1744-7429.2003.tb00608.x

Padrón, P.S. (2020) Primer reporte para el Ecuador de la avispa endoparasitoide *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae). *Revista Chilena de Entomología*, *46*(2): 291-297. https://doi.org/10.35249/rche.46.2.20.19

Padrón, P.S., Roubik, D.W. and Picón, R.P. (2018) A preliminary checklist of the orchid bees (Hymenoptera: Apidae: Euglossini) of Ecuador. *Psyche: A Journal of Entomology*, *2018*: 1-14. https://doi.org/10.1155/2018/2678632

Pemberton, R.W. and Wheeler, G.S. (2006) Orchid bees don't need orchids: evidence from the naturalization of an orchid bee in Florida. *Ecology*, *87*(8): 1995-2001. https://doi.org/10.1890/0012-9658(2006)87[1995:obdnoe]2.0.co;2

Perger, R. (2015) The highest known euglossine bee community from a garden in the Bolivian Andes (Hymenoptera, Apidae, Euglossini). *Journal of Hymenoptera Research*, *45*: 65-73. https://doi.org/10.3897/JHR.45.5003

Pokorny, T., Loose, D., Dyker, G., Quezada-Euán, J.J.G. and Eltz, T. (2015) Dispersal ability of male orchid bees and direct evidence for long-range flights. *Apidologie*, *46*: 224-237. https://doi.org/ 10.1007/s13592-014-0317-y

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

Ramírez, S.R., Roubik, D.W., Skov, C. and Pierce, N.E. (2010) Phylogeny, diversification patterns and historical biogeography of euglossine orchid bees (Hymenoptera: Apidae). *Biological Journal of the Linnean Society*, *100*(3): 552-572. https://doi.org/10.1111/j.1095-8312.2010.01440.x

Ramírez, S.R., Eltz, T., Fujiwara, M.K., Gerlach, G., Goldman-Huertas, B., Tsutsui, N.D. and Pierce, N.E. (2011) Asynchronous diversification in a specialized plant-pollinator mutualism. *Science*, *333*: 1742-1746. https://doi.org/10.1126/science.1209175

Robinson, W.S. (2021) Surfing the sweet wave: Migrating giant honey bees (Hymenoptera: Apidae: *Apis dorsata*) display spatial and temporal fidelity to annual stopover site in Thailand. *Journal of Insect Science*, *21*(6): 1-12. https://doi.org/10.1093/jisesa/ieab037

Roubik, D.W. and Hanson, P.E. (2004) Abejas de orquídeas de la América tropical: Biología y guía de campo / Orchid bees of tropical America: Biology and field guide. 1 ed. Costa Rica: Instituto Nacional de Biodiversidad, INBio. 370 pp.

Silva, O. and Rebêlo, J.M. (2009) Primeiro registro de *Euglossa stilbonota* Dressler (Apidae: Euglossini) fora da Floresta Amazônica: implicações biogeográficas. *Neotropical Entomology*, *38*: 880-882. https://doi.org/10.1590/S1519-566X2009000600027

Silva, D.P., Macêdo, A.C., Ascher, J.S. and De Marco, P. (2015) Range increase of a Neotropical orchid bee under future scenarios of climate change. *Journal of Insect Conservation, 19*: 901-910. https://doi.org/10.1007/s10841-015-9807-0

Storck-Tonon, D., Morato, E.F., Melo, A.W.F.D. and Oliveira, M.L.D. (2013) Orchid bees of forest fragments in southwestern Amazonia. *Biota Neotropica, 13*: 133-141. https://doi.org/10.1590/S1676-06032013000100015

Skov, C. and Wiley, J. (2005) Establishment of the neotropical orchid bee *Euglossa viridissima* (Hymenoptera: Apidae) in Florida. *The Florida Entomologist, 88*(2): 225-227. https://doi.org/10.1653/0015-4040(2005)088[0225:EOTNOB]2.0.CO;2

Wikelski, M., Moxley, J., Eaton-Mordas, A., López-Uribe, M.M., Holland, R., Moskowitz, D., Roubik, D.W. and Kays, R. (2010) Large-range movements of neotropical orchid bees observed via radio telemetry. *PLoS ONE, 5*(5): 1-6. https://doi.org/10.1371/journal.pone.0010738

Williams, C.B. (1957) Insect migration. *Annual Review of Entomology, 2*(1): 163-180.

Williams, N.H. and Dodson, C.H. (1972) Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution, 26*: 84-95.