A note on *Bombus (Fervidobombus) digressus* (Hymenoptera: Apidae) in Costa Rica, with a description of the queen

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Abstract: Field research was carried out on *Bombus digressus* and *Bombus ephippiatus ephippiatus* in Costa Rica. In combination with data on *B. digressus* males and workers from the collection of INBio, this resulted in new information on the distribution of *B. digressus.* The queen of *B. digressus*, which was hitherto unknown, is described. The colour pattern of the queen of *B. digressus* differs from that of the workers and males. Caste dimorphism is pronounced and comparable with that of *B. ephippiatus ephippiatus,* which is very similar to *B. digressus.* At Volcan Barva *B. ephippiatus ephippiatus* and *B. digressus* coexist, which could indicate Müllerian mimicry. It seems that *B. digressus* and *B. ephippiatus ephippiatus* are largely sympatric, which raises interesting questions on the distribution of *B. digressus.* The relatively long hairs of the pile of *B. digressus* is consistent with the idea that this species occurs only at higher altitudes. The greater tongue length of *B. digressus,* in comparison with *B. ephippiatus ephippiatus*, explains the preference of *B. digressus* for long corolla flowers. Although individuals of *B. digressus* have been found all year round in Costa Rica, the duration of their colony cycle remains unknown.

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Introduction

Bumblebees are much more common and diverse in temperate than in subtropical and tropical regions. Most of the estimated 239 (P. H. Williams, personal communication) species of bumblebees inhabit cool, north-temperate regions, but about 39 species are known from the neo-tropics (Williams, 1998). Until now six species have been reported to occur in Costa Rica (Hanson & Gauld, 1995; Labougle, 1990): *Bombus weisi / nigrodorsalis* Friese / Franklin, *Bombus mexicanus* Cresson, *Bombus digressus* (Milliron), *Bombus pullatus* Franklin, *Bombus ephippiatus ephippiatus* Say and *Bombus volucelloides* Gribodo.

In temperate and arctic areas seasonal constraints on food resources impose limits on the colony life cycle of *Bombus* species and the active season of most temperate species (all annual) lasts four to six months (Laverty & Plowright, 1985). For tropical species the course of the colony life cycle is still unknown. In the tropics, due to the absence of an unfavourable winter, the active season can be prolonged, and it is probable that the establishment of new colonies does not follow the synchronised pattern of temperate areas (Laverty & Plowright, 1985; Zucchi, 1973). Some species, e.g. *Bombus atratus* Franklin in Brazil, are recorded to be active all year long (Zucchi, 1973).

Until now, *Bombus digressus* has only been reported from Guatemala (Volcan de Fuego, Dept. of Escuintla) and Costa Rica (Rio Sucio, Prov. de Limon; Villa Mills, Prov. de Cartago) (Milliron, 1962; Laverty, Plowright & Williams, 1984). All specimens with known collecting dates were taken in June,

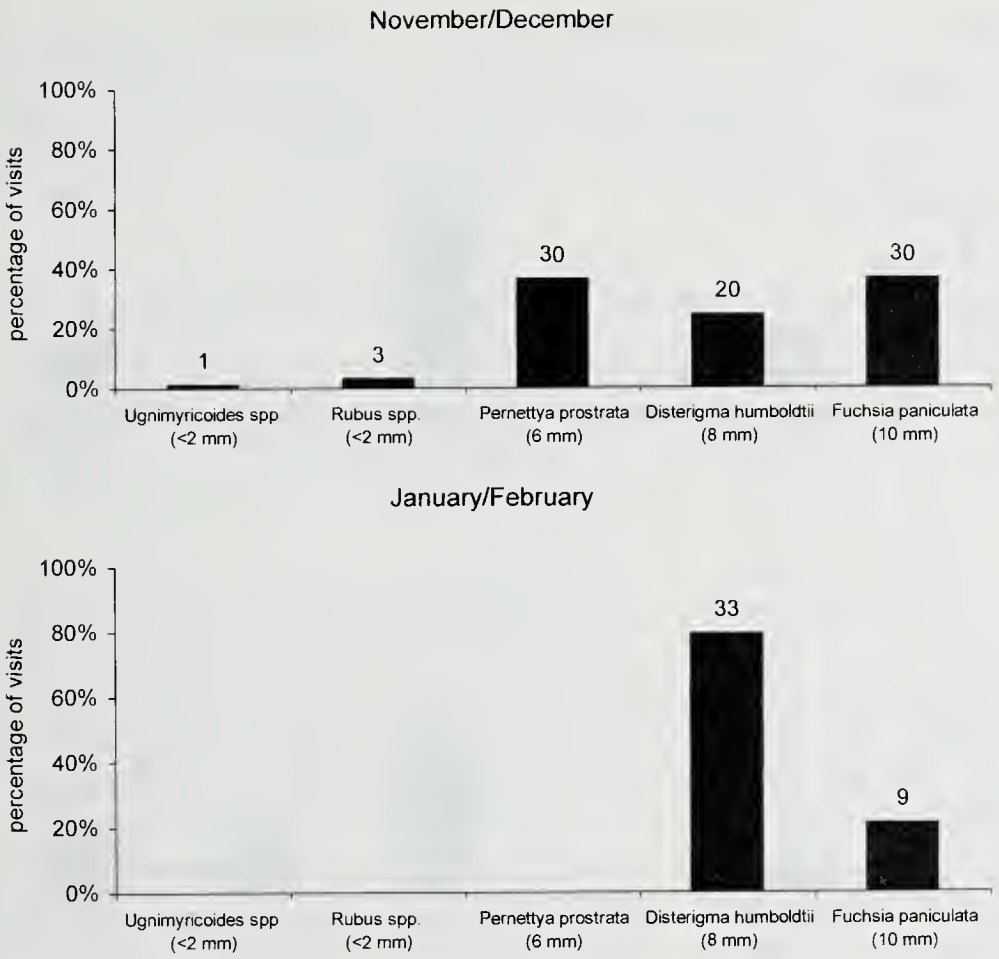

Figure 1a: Frequency of plant species (with corolla length) visited by *Bombus digressus* workers on walking transect at Volcan Barva in November/December and January/February.

and the only record with altitudinal information is from Villa Mills (Costa Rica) at 3300 m (Labougle, 1990).

Milliron (1962) was the first who recognised and described *Bombus digressus* as a distinct species and placed this species in his *Megabombus* (subgenus *Megabombus*) on the basis of two worker specimens. Laverty, Plowright & Williams (1984) described the male of *B. digressus* on the basis of one specimen and used three additional worker specimens to establish a new subgenus, *Digressobombus*. Williams (1985, 1995, 1998), from cladistic analysis, turned *B. digressus* to *Fervidobombus* Skorikov. Until now, the queen remained unknown (Laverty, Plowright & Williams, 1984; Labougle, 1990).

Our field study was carried out to obtain data on the distribution and foraging behaviour of miscellaneous *Bombus* species in Costa Rica. This, in combination with data on *Bombus digressus* material in the collection of INBio (National Institute of Biodiversity, Costa Rica), supplies information on the behavioural ecology of *B. digressus*. The queen of *B. digressus* is described here for the first time.

Methods

During our research in November/December 1998 and January/February 1999 in Costa Rica most recordings of *Bombus digressus* were made at Volcan Barva (2600 m, Heredia province).

The research site at Volcan Barva was visited during two periods of three weeks. During these periods, observations on bumblebee activity were made every day. Transects were walked, along which five species of flowering plants (fig. 1) were recorded as being visited by *Bombus* species. All *Bombus digressus* specimens used for quantitative measures were captured alive, marked and released after determination (66 workers, 8 males and 11 queens). A small number of specimens were collected for the reference collection (18 workers, 5 males and 6 queens plus an additional queen from San Gerardo de Dota, 2200 m, San José province).

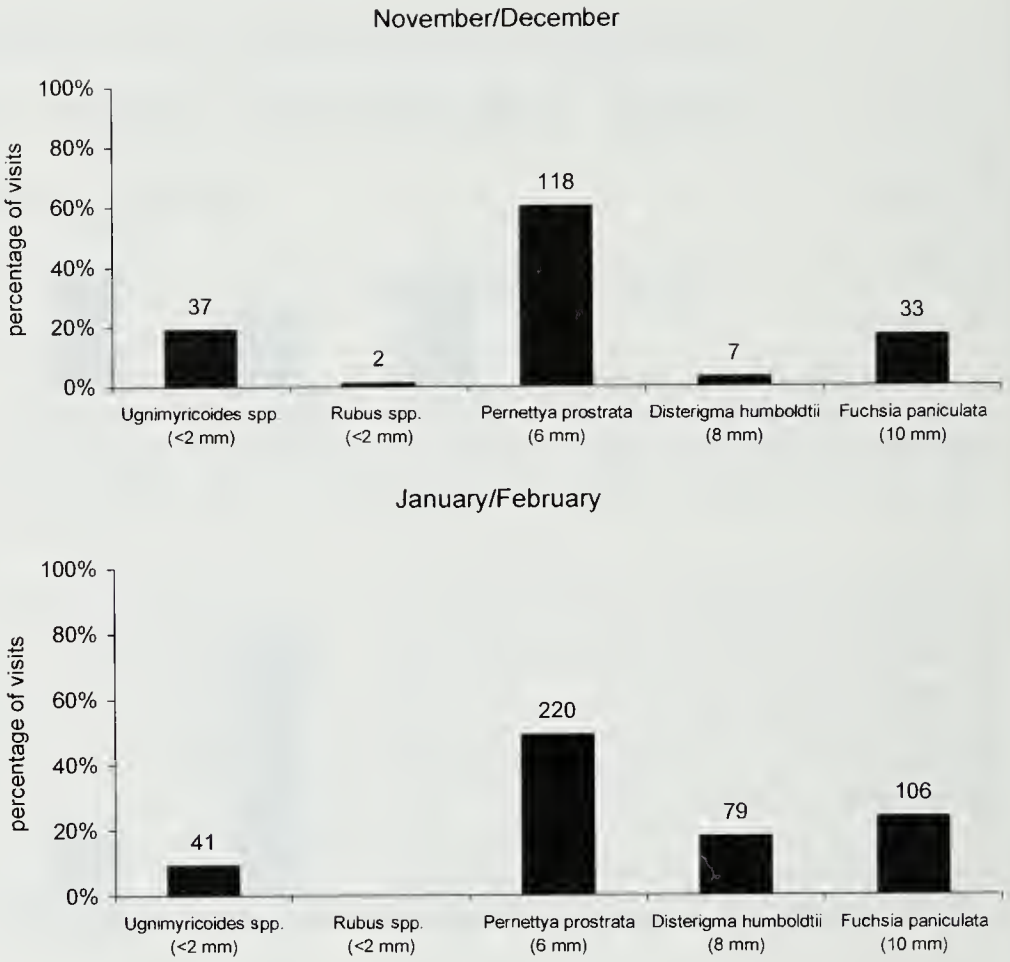

Figure 1 b: Frequency of plant species (with corolla length) visited by *Bombus ephippiatus ephippiatus* workers on walking transect at Volcan Barva in November/December and January/February.

In addition to our own records, data on 13 males and 7 workers from the INBio collection were used in this study.

Bombus digressus

Material

All material was collected at Volcan Barva, 2600 m, except for one queen from San Gerardo de Dota, 2200 m.
Queens: 3: 2.xii.1998, 4.xii.1998 and 3.ii.1999, *Fuchsia paniculata* Lindl.; 1: 14.xii.1998, *Pernettya prostrata* (Cav.) DC.; 2: 14.xii.1998 and 15.xii.1998, flying; 1: San Gerardo de Dota, 21.ii.1999, *Malus domesticus* Borkh.
Males: 1: 2.xii.1998-15.xii.1998, *Disterigma humboldtii* (Klotzsch) Nied.; 4: 2.xii.1998-15.xii.1998, *F. paniculata*.
Workers: 5: 2.xii.1998-15.xii.1998 and 19.i.1999-4.iii.1999, *D. humboldtii*; 7: 2.xii.1998-15.xii.1998 and 19.i.1999-4.iii.1999, *F. paniculata*; 6: 2.xii.1998-15.xii.1998 and 19.i.1999-4.iii.1999, *P. prostrata*.

The specimens are deposited in the collection of the Department of Ethology and Socio-ecology, Utrecht University, except for one specimen of each caste, which are kept in the Zoological Museum, Section Entomology, Amsterdam and one queen which is kept in the Natural History Museum, Department of Entomology, London.

Description of the queen

Queen: Length approximately 23 mm, interalar width (table 1b) on average 8.3 mm, range 7.0 mm - 9.0 mm.
Head: little higher than wide. Ocular-malar distance (malar space) equal to the breadth of the mandible at its base (distal width), twice the length of the first flagellomere. Lateral ocelli touching supra-orbital line. Clypeus weakly convex and densely covered with small and some medium punctures. Labral furrow shallow and about 1/4 of labral breadth. Labral tubercles raised.
Flat triangular indentation on the sixth metasomal tergum (T6) of which the lower 1/3 makes an angle of circa 140 degrees with the upper part.
Pubescence: medium in length, less uneven than in worker and male, moderately fine.
Colour: Head: frons and occiput with a mixture of long blackish and short pale yellowish hairs. Thorax pale orange-yellow, pleura pale yellow. T1 laterally pale yellow, medial 1/3 brown orange; T2 laterally pale yellow,

Table 1a: Mean tongue length in cm of all castes of *B. digressus* in comparison with mean tongue length of *B. ephippiatus ephippiatus*.

	Males	Workers	Queens
B. digressus	0.62 (0.6-0.65) n=5	0.77 (0.7-0.81) n=18	0.98 (0.95-1.05) n=7
B. ephippiatus	0.55 (0.52-0.60) n=7	0.57 (0.46-0.70) n=128	0.78 (0.67-0.83) n=49

Table 1b: mean interaler width in cm of all castes of *B. digressus* in comparison with mean interaler width of *B. ephippiatus ephippiatus*.

	Males	Workers	Queens
B. digressus	0.56 (0.50-0.60) n=5	0.50 (0.40-0.60) n=18	0.83 (0.70-0.90) n=7
B. ephippiatus	0.48 (0.40-0.55) n=7	0.45 (0.35-0.60) n=128	0.71 (0.60-0.80) n=49

medial 1/2 brown orange or black tipped with brown-orange; T3 laterally pale yellow, medial 1/3 brown-orange, distally yellow; T4 and T5 brownish with lighter distal fringes; T6 brownish. Legs: integument dark brownish-black; hairs, including hairs of femora, blackish. Metasomal sterna brownish-black.

The colouration of the pile of *Bombus digressus* resembles the colouration of the pile of *Bombus ephippiatus ephippiatus*, which occurs in the same area. Both species show pronounced caste dimorphism.

The differences between queens and workers show some similarity across taxa, in that the queens of both *Bombus digressus* and *B. ephippiatus ephippiatus* are orange-yellow, with red-orange on the abdomen of the latter. The workers and males of both taxa are predominantly black with yellow.

Queens of the two species differ in that *Bombus digressus* queens are larger than those of *B. ephippiatus ephippiatus*, and have a longer tongue and a longer malar space. The labral furrow is deeper and less wide in *B. ephippiatus ephippiatus*. On T6 there is a triangularly bent indentation in *Bombus digressus,* whereas it is semicircular and only slightly indented in *B. ephippiatus ephippiatus* queens. In *B. ephippiatus ephippiatus* the pubescence on the frons and occiput is entirely black, the orange on the abdomen is much brighter, and only T4 and T5 show some darker hairs in the middle, while the pubescence is much shorter. The medial zone of brown-orange in *B. digressus* queens echoes the medial black zone in workers and males where on T1 it is 1/3 and on T2 1/2.

Distribution and phenology

Bombus digressus specimens of the collection at INBio have been collected in five different provinces of Costa Rica: Heredia, San Jose, Puntarenas, Cartago and Limon. These records of *B. digressus* show an altitudinal range from 1150m to 2700m. The only record with altitudinal information so far was from Villa Mills (Costa Rica) at 3300 m (Labougle, 1990).

At Volcan Barva queens of *Bombus digressus* were found during our entire research period (November-February). Males and workers of this species have been reported almost all year round throughout Costa Rica (males: January, March-April, July, August, October-December; workers: January, February, April-June, November-December).

It is notable that at Volcan Barva we found males, workers and queens of *Bombus digressus* in November/December, but only queens and workers of this species in January/February.

Co-occurrence with other species

At Volcan Barva *Bombus digressus* was found together with *B. ephippiatus ephippiatus* (all castes) and *B. volucelloides* (it is notable that at Volcan Barva only *B. volucelloides* queens were found, while at San Gerardo de Dota specimens of all castes of this species were

obtained). During both research periods *B. ephippiatus ephippiatus* seemed to be the most abundant species (numbers of *B. ephippiatus ephippiatus*: *B. digressus* in November/ December = 179: 62; January/February = 274: 12, in total only 16 queens of *B. volucelloides* were observed).

Flower visiting behaviour

Bombus digressus and *Bombus ephippiatus ephippiatus* showed distinct differences in their food plant use (fig. 1). In general, *B. digressus* workers were found more frequently on the long corolla flowers compared to *B. ephippiatus ephippiatus* workers ((chi-square test): $\chi^2 = 10.3$; df = 1; p = 0.001). This is probably related to the difference in tongue length (table 1a), which is significant ((One Way- ANOVA): queens: F = 160.88; p = 0.00: workers: F = 209.1; p = 0.00).

Discussion

Like *Bombus ephippiatus ephippiatus*, *B. digressus* shows pronounced caste dimorphism. There are only a few examples of bumblebee species in which the colour pattern of the queens differs markedly from those of workers and males, the most outstanding being *B. festivus* Smith from the eastern Himalayas and *B. rufofasciatus* Smith, *B. simillimus* Smith and *B. pyrosoma* Morawitz from the western Himalayas (Williams 1991).

The strong similarity of *Bombus digressus* queens to *B. ephippiatus ephippiatus* queens may explain why the queen of *B. digressus* has not been described until now. In the field it was possible to distinguish between the two queens because *B. digressus* queens have a pronounced yellow-orange abdomen, while *B. ephippiatus ephippiatus* queens have a primarily red-orange abdomen. Our field method (collecting all specimens, then releasing most of them) allowed for easy determination of all specimens. Another explanation for the absence of a description of the *B. digressus* queen can be the altitude at which this species occurs. Until now *B. digressus* has been found within an altitudinal range from 1150 to 3300 m (own data in combination with INBio, Labougle, 1990, and Hanson & Gauld, 1995). The relatively long hairs of the pile of *B. digressus* is consistent with the observation that *B. digressus* occurs only at higher altitudes. Hanson & Gauld (1995) indicated that *B. digressus* is rare in Costa Rica, but we conclude that this species is not rare at higher altitudes, at least at Volcan Barva.

Although individuals of *Bombus digressus* have been found in almost every month of the year throughout Costa Rica, no conclusion on the colony cycle can be drawn because it can not be excluded that colony cycles may differ among areas, or even among years.

The fact that the co-existing species *Bombus digressus* and *B. ephippiatus ephippiatus* are similar in colouration could indicate Müllerian mimicry, as proposed by Plowright & Owen (1980). It seems that these two taxa are also largely sympatric. *B. ephippiatus ephippiatus*, which is restricted to Costa Rica and West Panama (Quiriqui) (Labougle, 1990), is the only of the three *B. ephippiatus* subspecies that shows pronounced caste dimorphism. Most specimens of *B. digressus* have been found in Costa Rica. So far no specimens of *B. digressus* were collected in Quiriqui. The lower altitude may explain the absence of *B. digressus* in this area, where *B. ephippiatus ephippiatus* does occur.

The holotype of *Bombus digressus* was described by Smith in 1879 as a variety of his *B. lateralis*. This specimen is labelled as being from "Val de Fuego" (first label: 'Val/de/ Fuego/Guatem/ala', no date) and was thus supposed to originate from Guatemala (Milliron, 1962). However, no other *B. digressus* specimens have ever been reported from Guatemala (Labougle, 1990) or were observed by the third author during three collecting trips to that country. This raises an interesting question. As Labougle's (1990) distribution map for *B. ephippiatus* shows, this species is not known from Nicaragua, but only from Costa Rica, Panama and areas north of Nicaragua. While *B. ephippiatus ephippiatus* has been found in Costa Rica and Panama,

north of Nicaragua two other subspecies of *B. ephippiatus* (*B. ephippiatus vauflavus* Cockerell and *B. ephippiatus formosus* Smith) occur (Milliron, 1962 and 1971). It is possible that the lake of Nicaragua and the lower areas north of Costa Rica formed a barrier that caused the origin of these subspecies (Panfilov, 1957). Did *B. digressus*, which until now has only been found at high altitudes, cross this border or has the holotype been mislabelled?

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