

# Is the caste-ratio of the oligolectic bumblebee *Bombus gerstaeckeri* Morawitz (Hymenoptera: Apidae) biased to queens?

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**Abstract.** Three bumblebee species, foraging on *Aconitum* spp. have been commonly observed in Eyne (France, East Pyrénées): *Bombus gerstaeckeri*, *B. hortorum* and *B. wurflenii*. We estimated the population of these three species. For *B. hortorum* and *B. wurflenii*, the total workers populations foraging on *Aconitum* spp. ranged from 101 to 523 and 156 to 270, respectively. These two species also forage on other plants while *B. gerstaeckeri* visits only *Aconitum* spp. The population of *B. gerstaeckeri* observed was extremely small, founded by 33 queens only in 2001. With a total number of workers estimated from 40 to 102, the observed workers/queens ratio, 1 to 3 workers for each queen, is very unusual for a eusocial species. Also we observed queens foraging during the whole life of the colony. This kind of social organisation is similar to that of some high arctic species. It could be interpreted as the result of an insularity syndrome.

**Résumé.** Trois espèces de bourdons butineurs d'*Aconitum* spp. sont communément observés à Eyne (France, Pyrénées-Orientales) : *Bombus gerstaeckeri*, *B. hortorum* and *B. wurflenii*. Nous avons estimé la population de ces trois espèces. Pour *B. hortorum* et *B. wurflenii*, la population totale des ouvrières butineuses d'*Aconitum* spp. était dans les intervalles, respectivement, 101-523 et 156-270. Ces deux espèces butinent aussi d'autres plantes tandis que *B. gerstaeckeri* visitait uniquement *Aconitum* spp. La population de *B. gerstaeckeri* était extrêmement petite, seulement 33 reines fondatrices en 2001. Avec un nombre total d'ouvrières de cette espèce compris entre 40 et 102, le rapport ouvrières/reines est très inhabituel pour une espèce eusociale : 1 à 3 ouvrières par reine. Nous avons aussi observé des reines qui continuaient à butiner durant toute la durée de vie de la colonie. Ce type d'organisation sociale est proche de celui qu'on trouve chez certaines espèces arctiques. Cela peut être interprété comme le résultat d'un syndrome d'insularité.

**Keywords:** *Bombus*, *Aconitum*, insularity, oligolecty, Pyrénées.

*Bombus gerstaeckeri* Morawitz is one of the least common subalpine bumblebee species in Europe (Rasmont 1988, 1999; Amiet 1996). It may be locally abundant but most of the collected specimens come from a very few places (fig. 1). Rasmont (1999) showed that more than half of the observations in France are concentrated on only two places in the Pyrénées-Orientales (Eyne and Nohèdes). In the Pyrénées-Orientales, the specimens are found between 1560 and 2180 m (Rasmont 1999).

*Bombus gerstaeckeri* feeds exclusively on monkshoods (*Aconitum* spp.) (Pittioni 1937; Delmas 1976; Rasmont 1988; Bosch *et al.*, 1997). These Ranunculaceae grow near the banks of mountains rivers and on screes. They do not depend on *Bombus gerstaeckeri* (fig. 2) only for their pollination (Bosch *et al.*, 1997; Utelli

& Roy 2000). *Bombus hortorum* (L.) (fig. 3) and *Bombus wurflenii* Radoszkowski (fig. 4) are two other bumblebees species that feed on monkshoods. *Bombus gerstaeckeri*, however, with its very long tongue is the fastest species foraging on monkshoods (Utelli & Roy 2000).

Bumblebees are primitive eusocial Hymenoptera. The queen hibernates solitarily at the end of the summer. In spring she starts a colony by laying her first eggs, leading to the emergence of the workers about three weeks later. Dependent on the species a colony includes 10 to 1000 workers. At the end of the season, males and young queens are produced. Some species lack a worker caste and are inquilines (Alford 1975; Goulson 2003).

In this study we want to estimate the *B. gerstaeckeri* population size in the Eyne Valley and its foraging caste-ratio. We want to verify the floral choice of the species and which bumblebees species are likely competitors.

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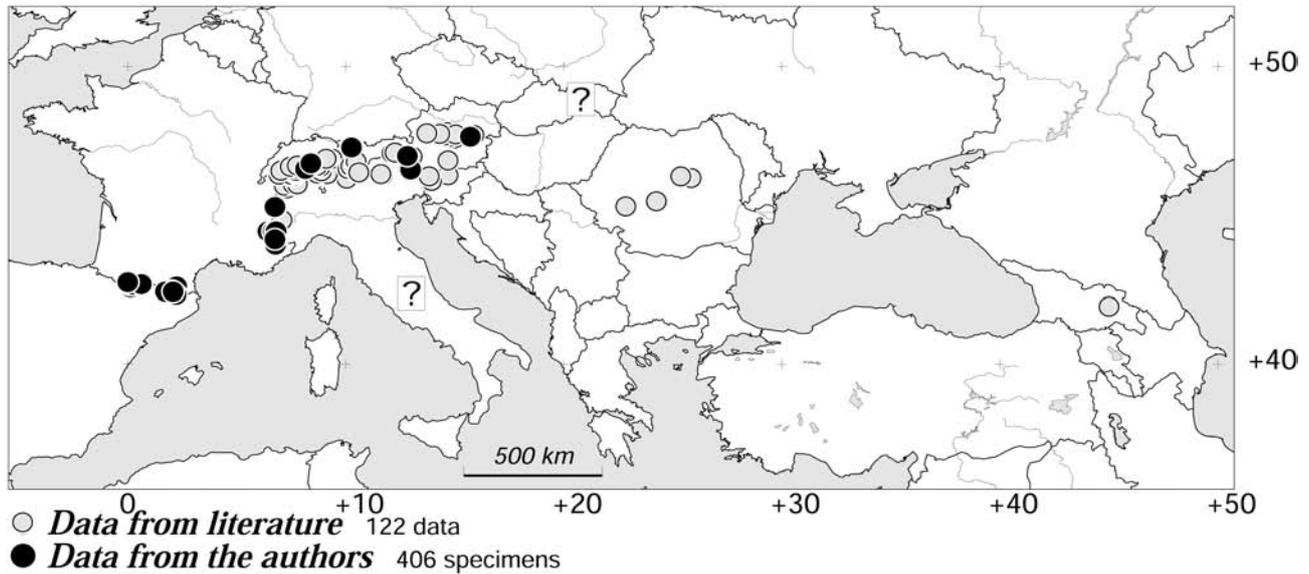


Figure 1

**Distribution of *Bombus gerstaeckeri* Morawitz.**

Open circles: data from literature (Gerstaecker 1869, Morawitz 1882, Hoffer 1883 1888, Handlirsch 1888, Moczar 1897, Pérez 1904, Frey-Gessner 1912, Pittioni 1937 1938, Moczar 1953a b, Stoeckert 1954, Løken 1973, Ornos 1984, Rasmont 1988, Intoppa *et al.* 1995, Amiet 1996, Gogala 1999). Solid circles: data from the authors (original observations and collections from NHM, ENAM, MNHNP, UB, UMH, ZSM). Data from Apennine mountains (Grandi, 1957) and Slovakia (May 1959) have never been confirmed, they are marked “?”.

**Material and Methods**

A comprehensive survey of the bumblebees of the Eyne valley has been completed in 1993, 1998, 1999 and 2000 (Rasmont *et al.* 2000). During this operation, we recorded the insects foraging on flowers at 227 locations in the valley (fig. 6). With the help of the Nature reserve staff, all the Monkshoods have been mapped : 72 locations, among wich 5340 *Aconitum lycoctonum* L. subsp. *vulparia* (Reichenb.) plants. The other species: *Aconitum napellus* L. subsp. *vulgare* Rouy et Fouc. and *Aconitum anthora* L. are much less common and have not been counted. In the valley, *Bombus gerstaeckeri* has been recorded in 15 locations only (fig. 6).

Probosces were measured by the method of Heinrich (1979) on specimens collected since 1978 in Eyne and in the nearby places Egat and Nohèdes.

The foraging speeds were measured in Eyne and Nohèdes in 1993. For each individual bumblebee, the number of flowers visited in one minute was recorded. The bumblebee can change inflorescence during this measurement

The population density of *B. gerstaeckeri* has been estimated in the Eyne valley, probably the most densely populated place in France for this species (Rasmont 1999). The area of the valley is 20.18 km<sup>2</sup>. Each location has been visited as often as possible, for 45 days from July 10th to August 31st 2001. The duration of these visits were 10 minutes (area < 50m<sup>2</sup>), 15 minutes (area from 50 to 100m<sup>2</sup>) or 20 minutes (area > 100m<sup>2</sup>), in this manner all the stations are visited in one day. During the visits all other foraging bumblebees were recorded. All the bees foraging on Monkshoods were individually tagged with numbered labels fixed onto their mesothorax with cyanoacrilic glue and the caste of the bee noted. The difference between a queen and a worker is mainly the size, queen is one and half

time bigger than worker. With regard for the extreme rarity of *Bombus gerstaeckeri*, great care was taken to sacrifice as few specimens as possible.

The number of untagged queens decreased to zero during the observations, indicating that they had all been tagged. Therefore, the census of the queens was best estimated as the number of tagged individuals. The population density of the workers were estimated by Capture-Marking-Recapture methods (CMR ): the Petersen method, the Schnabel method, the Schumaker et Eschmeyer method (Krebs 1989) and by “removal collection” (Southwood 1978). This last method was modified in that each tagged bee was considered as “removed”. A graph was drawn with the abscissa representing the cumulative total number of tagged specimens at day (i-1) and the ordinate the number of specimens tagged each day. The intersection between the regression line and the abscissa gives the estimate of the total number of specimens living on the site.

Distribution and phenology data are from literature completed by data from the authors. Data from the following collections have been examined: NHM: Natural History Museum, ENAM: Ecole Nationale d’Agronomie de Montpellier, UB: Universität Bern, UMH: Université de Mons-Hainaut, MHHNP: Muséum National d’Histoire Naturelle de Paris, ZSM: Zoologisches Staatssammlung München. These data were processed and mapped with Data Fauna Flora (Barbier *et al.*, 2000) and Carto Fauna Flora 2.0 (Barbier & Rasmont 1999).

**Results**

Distribution and phenology data are summarized in the fig. 1 and 7.



Figures 2-5

2, *Bombus gerstaeckeri* Morawitz queen foraging on *Aconitum anthora* L., Eyne, August 2001, photo P. Rasmont; 3, *Bombus hortorum* (L.) worker foraging on *Aconitum napellus* L., Nohèdes, August 1994, photo P. Rasmont; 4, *Bombus wurflenii* Radoszkowski worker foraging for nectar through holes in corollae on *Aconitum lycoctonum* L. subsp. *vulparia* (Reichenb.), Nohèdes, August 1994, photo P. Rasmont; 5, nest of *Bombus gerstaeckeri* Morawitz; this nest was obtained by the Dr. R. De Jonghe (Westerlo, Belgium) from a queen collected in the wild; it harboured 4 workers only, photo P. Rasmont.

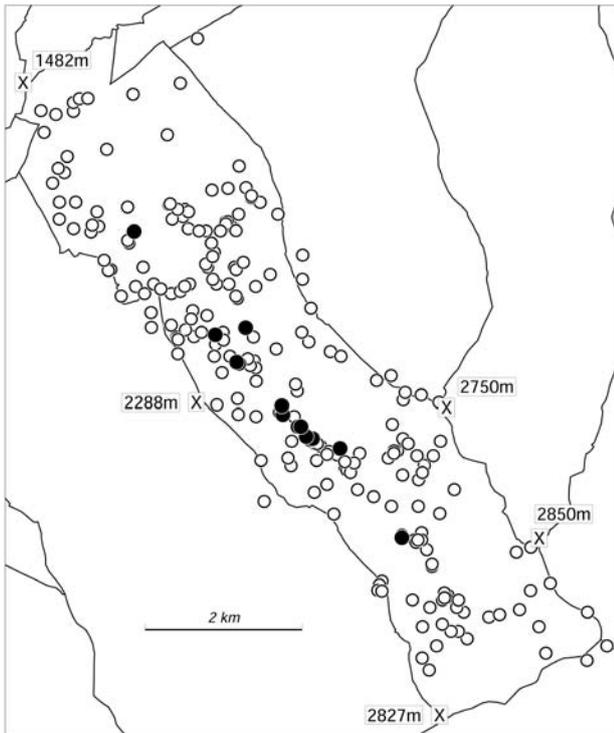
A total of 89 *Bombus gerstaeckeri* were tagged on *Aconitum lycoctonum* L., *A. napellus* L. and *A. anthora* L. (Tab. 1), 33 queens, 40 workers and 16 males. During July, only queens were foraging (fig. 8). The first workers appeared the last day of July. During August, the daily number of workers never exceeded 3 times the number of queens (with the exception of two days : August 1<sup>st</sup> and 26<sup>th</sup>). Most of the queens were collecting pollen. The first male has been tagged on August 28th.

The lengths of the queens probosces were 18.7,

16.6 and 12.0 mm for *B. gerstaeckeri*, *B. hortorum* and *B. wurflenii*, respectively (Tab. 2). For the workers, there measurements were 13.3, 12.4 and 9.9 mm and for the males, 14.5, 14.6 and 10.5 mm, respectively.

The foraging speeds (queens and workers pooled) were 25.3, 14.3 and 12.1 flowers visited per minute for *B. gerstaeckeri*, *B. hortorum* and *B. wurflenii*, respectively (Tab. 3).

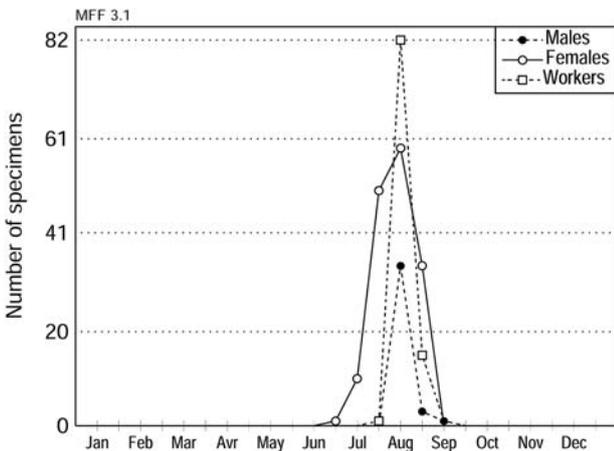
For the population density of *B. gestaeckeri* workers, the CMR methods gave confidence intervals (95%) ranging from 29 to 59 (Schnabel method) and 34



○ *Bombus* spp., 227 locations  
● *Bombus gerstaeckeri*, 15 locations

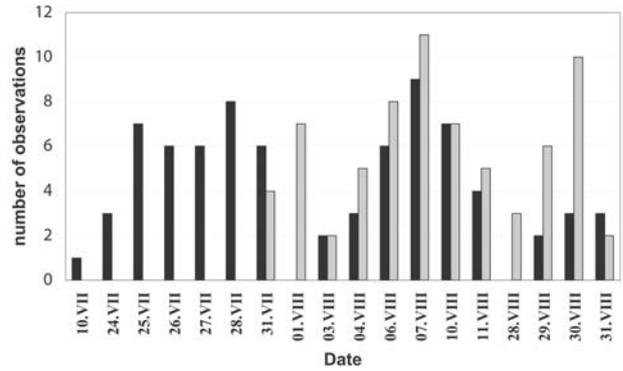
**Figure 6**

Locations of the observations in the Eyne valley. Open circles: all bumblebees (227 locations). Solid circles: *Bombus gerstaeckeri* (15 locations). The altitude of the village is 1574m, the commune extending from 1482 m to 2850 m.



**Figure 7**

Phenology of *Bombus gerstaeckeri* Morawitz in France (Alpes, Pyrenees). Data from the authors (field observations and collections from ENAM, UMH, MNHNP).



**Figure 8**

Daily numbers of observations of queens and workers of *Bombus gerstaeckeri*. X-axis: dates; Y-axis: daily observations. Black: number of queens; hatched: number of workers.

**Table 1.** Numbers of *B. gerstaeckeri* tagged on the three species of Monkshoods.

Q = queens; W = workers; M = males.

Caste	<i>Aconitum lycoctonum</i>	<i>Aconitum napellus</i>	<i>Aconitum anthora</i>	Total
Q	27	1	5	33
W	26	1	13	40
M	0	0	16	16

**Table 2.** Length of the proboscis of the main foragers of *Aconitum lycoctonum*.

Q= Queens; W= workers; M= males; n: number of specimens.

Species	Caste	Length of the proboscis (mean ± sd; mm)
<i>B. gerstaeckeri</i>	Q	18.7 ± 1.7 (n=21)
	W	13.3 ± 1.8 (n=18)
	M	14.5 ± 0.8 (n=11)
<i>B. hortorum</i>	Q	16.6 ± 0.7 (n=13)
	W	12.4 ± 1.4 (n=58)
	M	14.6 (n=2)
<i>B. wurflenii</i>	Q	12.0 (n=2)
	W	9.9 ± 0.7 (n=24)
	M	10.5 ± 0.5 (n=10)

**Table 3.** Foraging speed of the main visitors of *Aconitum lycoctonum* in East-Pyrenees.

Species	Speed flowers/min m ± s (n) (Utelli & Roy 2000)	Speed lowers/min m ± s (n) (Original data)
<i>B. gerstaeckeri</i>	17.63 ± 0.23 (n=15)	25.3 ± 3.9 (n=15)
<i>B. hortorum</i>	10.42 ± 0.35 (n=9)	14.3 ± 3.0 (n=18)
<i>B. wurflenii</i>	no data	12.1 ± 3.4 (n=11)

to 102 individuals (Schumacher method) (Tab. 4). The minimal number of workers was 40 which is the number of tagged specimens, while the maximal value was 102, as given by the most extreme estimator (Tab. 4). The removal collection gave a similar result (fig. 9). In the last days, all the observed queens had been marked. The estimated number was therefore equal to the total number of the 33 tagged queens. Only 16 males were tagged at the end of the observation period.

The numbers of *B. hortorum* and *B. wurflenii* workers observed in the same period on *Aconitum lycoctonum* were estimated by the same methods. The range of the *B. hortorum* worker populations ranged from 101 to 523 and for *B. wurflenii* from 156 to 270 individuals (Tab. 4). 145 queens and 106 males of *B. hortorum* were tagged. 5 queens and 30 males of *B. wurflenii* were tagged. It is noteworthy that contrary to *B. gerstaeckeri*, these two species are not confined to *Aconitum* spp. for foraging (Rasmont 1988).

### Discussion

Although it is present in the Pyrenean, Alpine, Carpathian and Caucasian regions, the distribution of *Bombus gerstaeckeri* is mainly patchy (fig. 1). The known populations are isolated from one another and could be compared to insular populations (Frankham *et al.* 2002). The phenology of this species is narrow as well. In the Pyrénées, it is the latest species to appear, as the queens are only observed from July. It disappears by mid September. Museum data show that some queens appear in July while workers and males appear together in August (fig. 7). Our own observations show that the founding queens appear from July 10<sup>th</sup> and the workers from July 31<sup>st</sup> (fig. 8). During August queens and workers were foraging together. As the first male was seen on August 28<sup>th</sup>, it is likely that we missed the offspring of new queens while we stopped the observations the day after.

In the Eyne valley, *B. gerstaeckeri* forages exclusively on *Aconitum lycoctonum*, *A. napellus* and *A. anthora*. *A. lycoctonum* is the first of these species to bloom and it was clearly the preferred of *B. gerstaeckeri* as it is well known from literature (Pittioni 1937; Delmas 1976; Rasmont 1988).

The size of the population of *B. gerstaeckeri* in the Eyne valley is extremely small : 33 queens only (for the whole valley). Moreover, its narrow altitudinal range in Pyrénées-Orientales (1560-2180 m, data from Rasmont 1999) confines it between the crests and the plains limiting the Eyne valley. Despite these limitations, this population does survive and this location is even one of the most represented in collections (Rasmont 1999).

**Table 4.** Estimated populations of the three castes of *Bombus gerstaeckeri*, *B. hortorum* and *B. wurflenii* on monkshoods in the Eyne valley.

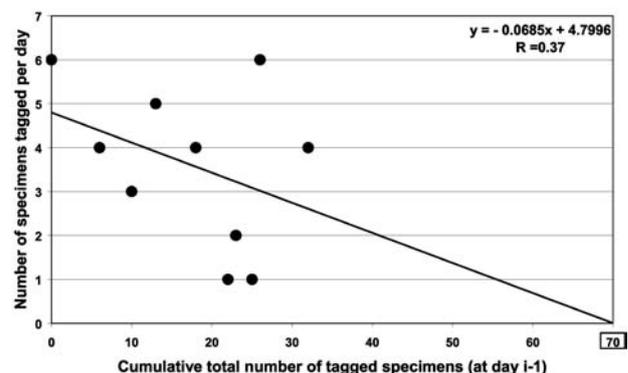
For the workers, numbers of individuals estimated by the Schnabel and the Schumacher methods (Krebs 1989). Numbers in parentheses are the minimum-maximum intervals.

Species	Queens	Males	Workers		
	Tagged	Tagged	Tagged	Schnabel (I 95%)	Schumacher (I 95%)
<i>B. gerstaeckeri</i>	33	16	40	40 (29 - 59)	51 (34 - 102)
<i>B. hortorum</i>	145	106	101	152 (109-225)	181 (109-523)
<i>B. wurflenii</i>	5	30	156	170 (143-213)	192 (149-270)

A careful research in the surrounding areas showed that the nearest numerous populations of *B. gerstaeckeri* live in Egat and Nohèdes, 8 and 22 km from Eyne, respectively and well separated from this location by unsuitable habitats.

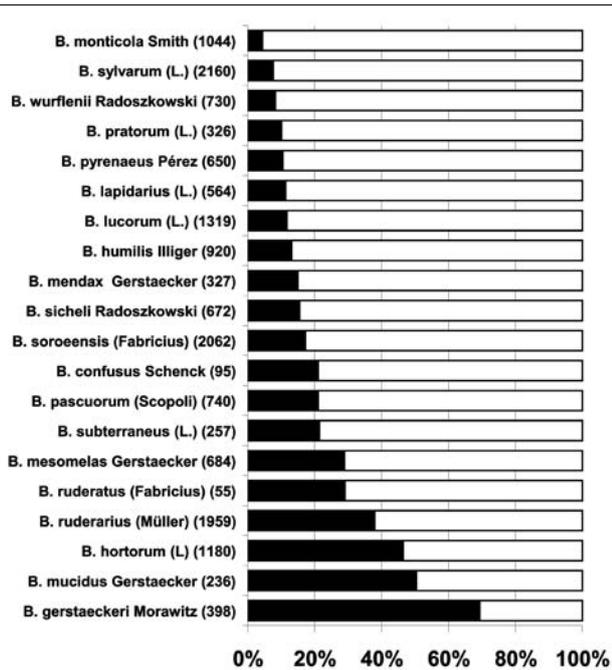
Such very small insect populations have been described for scattered species in patchy areas, e.g. for butterflies like *Plebejus argus* (L.) (Lewis *et al.* 1997), *Proclissiana eunomia* Esper (Schtickzelle *et al.* 2002; Mennechez *et al.* 2004) and *Bolloria aquilonaris* (Stichel) (Baguette & Schtickzelle 2003). However, these butterfly populations are more dense by at least one order of magnitude, compared to *Bombus gerstaeckeri* in the Eyne valley.

One extreme situation is that of *Cicadetta montana* (Scopoli) in England, for which only 100 males have been counted in New Forest in 1962 (Anonymus 1999). In the case of this cicada, it is obviously the



**Figure 9**

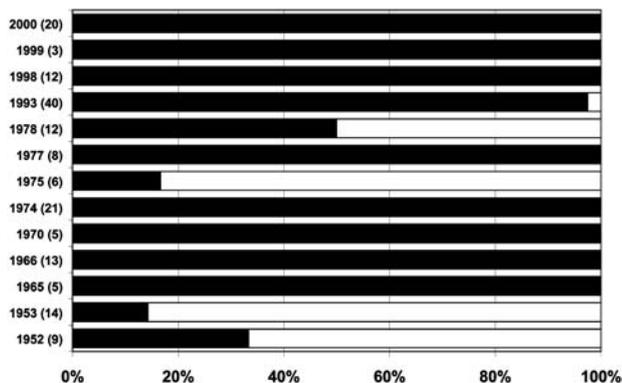
Assessment of worker population density. One can estimate population size by extrapolating the linear regression to the X-axis. In this case N is about 70 specimens.



**Figure 10**  
Caste ratio q/w of the mountain bumblebees of East-Pyrenees. Data from Rasmont (1988, 1999) and Rasmont *et al.* (2000). The total numbers of observations for founding females of each species are given between parentheses. Workers in white, queens in black.

result of a strong recent decline, which does not seem to be the case for *Bombus gerstaeckeri*.

The special constraints of the *Bombus gerstaeckeri* population in the Eyne valley could result in an insularity syndrome. The features of this syndrome could be discussed as follows.



**Figure 11**  
Caste ratio q/w of East-Pyrenean *Bombus gerstaeckeri* in museum collections. Total number of specimens is given between parentheses. Years with less than 3 specimens are not figured.

## 1. A restricted working force

The total number of *Bombus gerstaeckeri* is very small, the tagged-queen-to-tagged-workers ratio being  $33/40 = 1,2$  (Tab. 1). This should be compared with the caste ratio in the other mountain bumblebees of the Pyrénées-Orientales as shown in fig. 10 (data set from Rasmont 1988, 1999 and Rasmont *et al.* 2000). *B. gerstaeckeri* is the only species for which queens outnumber the workers (caste ratio  $q/w = 276/122 = 2.26$ ) (fig. 10). For most other species from Pyrénées-Orientales, this ratio lies below 0.2 (same data set). During some years, despite that the region were comprehensively sampled for bumblebees, only queens have been recorded, without a single worker (fig. 11). While most bumblebee nests contain from ten to several hundreds workers, the case of *B. gerstaeckeri* is clearly special.

Unfortunately, we did not succeed in finding a single nest of *B. gerstaeckeri* in the Pyrénées and the species is that uncommon that such a discovery remains quite unlikely. The nest with 4 workers in fig. 5 was reared by Dr. R. De Jonghe (Biobest, Westerlo, Belgium). It was founded by a queen from the Alps.

This low number of workers may be an adaptation to the short blooming period and the scarcity of the Monkshoods. With the scanty resources of this insular situation, the very small size of the colonies allows to multiply the nests and the reproducers productivity and, in this way, to lower the risk of stochastic extinction. The situation may be less exacting and the insularity syndrome less strict in the Alps, where von Hagen (1994: 252) reported *Bombus gerstaeckeri* nests with 40-100 specimens. This could be also very different for the other specialised bumblebee *Bombus consobrinus* Dahlbom in Northern Europe (Løken 1950, 1961; Mjelde 1983). Its food-plant, *Aconitum septentrionale* Koelle, is very widespread and abundant. In this special case, the extreme specialisation of *Bombus consobrinus* could be an optimal foraging solution (William 1989).

## 2. Foraging queens

Some years, no workers have been observed in the Pyrénées-Orientales (fig. 11). This is consistent with our observations made in Eyne. As far as we could see, most queens continued to forage for the whole nesting season. Without an opportunity to study the nests, it was not possible to know whether the queens continued to forage while some workers had already emerged in the nest or if some nests did not produce any workers at all. Such a behaviour is exceptional in bumblebees: the only other known species acting in the same way are Arctic species like *Bombus polaris* Curtis and *B.*

*hyperboreus* Schönherr observed on Ellesmere island by Richards (1973) or *Bombus glacialis* Friese on Wrangel island (Berezin 1990, 1994, 1995). It seems that the oligolecty of *B. gerstaeckeri* in a mountain environment could involve a strategy, the constraints of which bear some similarity with the arctic conditions.

The anatomy of *B. gerstaeckeri* is adapted to these constraints. Indeed, its proboscis is much longer than in *B. hortorum* and *B. wurflenii* (Tab. 2). This long tongue could allow *B. gerstaeckeri* to access to the very last nectar drop, even after the flower has been visited by the two other species.

*Bombus gerstaeckeri* is two times faster at foraging as either *B. hortorum* or *B. wurflenii* (Tab.3). This allows *gerstaeckeri* to make better use of the best foraging periods, such as sunrise or dry spells on rainy days.

However, the foraging strategy of *B. gerstaeckeri* is adaptive only in as far as the species is not preyed upon. Its populations are that scarce that the destruction of few nests by rodents would jeopardise the species in the Eyne valley.

For Wasser *et al.* (1996), the generalization in pollination system is the most widespread and efficient foraging strategy. In comparison, the strategy of *B. gerstaeckeri* is risky but it seems effective. We can thus reasonably predict that as long as the Monkshoods populations remain stable, *B. gerstaeckeri* should not be endangered. The only risk is stochastic extinction, as it may occur in any small population.

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