

Male Parentage in a bumblebee : *Bombus terrestris* (LINNAEUS, 1758) (Hymenoptera : Apoidea)

by

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Abstract. By crossing two races of bumblebees (*Bombus terrestris terrestris* (LINNAEUS, 1758) and *Bombus terrestris xanthopus* KRIECHBAUMER, 1870), it was possible to determine male parentage, either of the queen or of ovipositing workers. During the queen's life all males descend from her. As long as she is dominant, all worker-laid eggs are destroyed. Considering the short survival period of free living colonies after the production of sexual imagines the contribution of workers to the gene pool seems to be negligible.

Samenvatting. Door het kruisen van twee hommelryassen (*Bombus terrestris terrestris* (LINNAEUS, 1758) en *Bombus terrestris xanthopus* KRIECHBAUMER, 1870) was het mogelijk de afkomst van de mannetjes vast te stellen, hetzij van de koningin, hetzij van eierleggende werksters. Gedurende het leven van de koningin stammen alle mannetjes van haar af. Zolang ze haar dominantie behoudt, worden alle door werksters gelegde eieren vernietigd. Door de korte levensduur van vrij levende kolonies na het produceren van seksuele imagines is de bijdrage van de werksters tot het genepotentiaal blijkbaar te verwaarlozen.

Résumé. Par hybridation de deux races de bourdon (*Bombus terrestris terrestris* (LINNAEUS, 1758) et *Bombus terrestris xanthopus* KRIECHBAUMER, 1870) il m'a été possible de déterminer si les mâles provenaient des reines fondatrices ou des ouvrières pondueuses. Au moment où la reine est encore vivante, tous les mâles sont produits par elle. Durant la période où la reine est dominante, tous les oeufs des ouvrières sont détruits. Vu la courte durée de survie des colonies dans la nature après la production des adultes sexués, la contribution des ouvrières au capital génétique semble être négligeable.

Introduction

In some circumstances, e.g. in the sexual producing stage of the colony, the worker caste in bumblebees is able to lay eggs (SLADEN, 1912). These eggs are not fertilised, so only males are produced. Consequently, the production of males is not a monopoly of the queen. The males originating from the queen and the workers are phenotypically similar, what makes it difficult if not impossible to determine the male parentage. A considerable oophagy by the queen and the workers (FREE et al., 1969) is a complicating factor.

So it is not surprising that several authors made widely differing estimations of the queen and worker share. VAN HONK et al. (1981) estimated that up to 82% of the males originated from the workers. On the other hand, ROESLER (1967) stated that as long as the queens were alive and dominant, all males descended from them. OWEN & PLOWRIGHT (1980) using the pile colour dimorphism in *Bombus melanopygus* NYLANDER could determine that 37% of the males resulted from worker-laid eggs. This was the first reliable study made on this subject.

In 1983 and 1984 (DE JONGHE, 1986), the author made crossing experiments with *Bombus terrestris terrestris* (LINNAEUS, 1758) from the European mainland and *Bombus terrestris xanthopus* KRIECHBAUMER, 1870 from the isle of Corsica. The phenotypical difference between pure, queen-produced and hybrid, worker-produced males made it possible to determine the male

parentage.

Material and Methods

Crossings were achieved between *terrestris* females and *xanthopus* males and vice versa (DE JONGHE, 1986). For rearing and hibernation see DE JONGHE (1982) and DE JONGHE & RASMONT (1983). In this way 7 colonies, founded by a queen mated with a male of another race, were obtained. Some colonies were started artificially (by providing a few pupae and/or a few workers to a broody queen) or in a natural way by allowing a queen to start her own nest in a nestbox provided with upholsterers cotton in a flying cage. After the emergence of the first workers the colony was placed in a porous concrete Pomeroy/Plowright hive (POMEROY & PLOWRIGHT, 1980) either in a climate room (29°C) or in a thermostatically controlled box connected with the outside world by a tube. The artificially kept colonies were fed with a sucrose/water solution (40/60 vol.%) medicated with Fumidil B, and fresh or deep frozen pollen. The naturally kept colonies had to forage themselves for pollen and nectar. Sucrose solution was fed only at very bad weather and at the decline of the colony. In this way the colony life was prolonged in order to facilitate the production of more males (in casu hybrid males). As can be seen below most colonies would have been finished before the eclosion of hybrid males, if they were left alone after the death of the old queen and the production of young queens.

This distinction in naturally and artificially kept colonies is useful in order to see if artificial factors (as abundance of food, high constant temperature, presence of large numbers of workers in the brood nest) would affect the results. A survey of the colonies is given in table 1.

colony number	type of crossing	type of colony foundation and maintenance
84-2	<i>xanthopus</i> ♀ x <i>terrestris</i> ♂	artificially founded colony without free flight
84-19		naturally founded colony with free flight
84-20		naturally founded colony with free flight
84-24		naturally founded colony with free flight
84-30		artificially founded colony without free flight
84-31	<i>terrestris</i> ♀ x <i>xanthopus</i> ♂	naturally founded colony with free flight
84-32		artificially founded colony with free flight

Table 1 : Type of colony foundation and maintenance of 7 hybrid *terrestris* colonies.

Data of eclosion of young queens, pure and hybrid males and of dominance losing and death of the foundress queen were recorded. The males were picked out of the nest nearly every day and divided in 2 groups with respectively mature and immature coat colour. The greyish looking immature males coloured out in 2 or 3 days. This procedure was necessary as males tend to hide under the brood clump and can be overlooked. Males with adult coat colour can be several days old. Also it is not impossible that males of a strange colony enter another nest. In this way the exact day of eclosion could be determined as males with immature colour were aged less than 24 hours.

Results and Discussion

Before the death of the foundress queen male production occurred in 3 of the 7 colonies. Without exception all these males were queen-produced. After the queen had died, all colonies produced at first only racial pure males, i.e. originating from queen-laid eggs. After a certain, often considerable time, hybrid worker-produced males appeared. This time was for colony 84-2 : 10 days; 84-19 : 26 days; 84-20 : 25 days; 84-30 : 33 days; 84-31 : 20 days and 84-32 : 30 days.

The development of a male from egg to adult takes approximately 25 days (HASSELROT, 1960; ROESLER, 1967). If we compare this space of time with the time between the queen's death and the apparition of the first worker-produced males (Table 2), it is clear that while the queen is still alive, she laid the vast majority of male-producing eggs. This is even more true if we omit colony 84-2. In this colony the queen had left hibernation before 58 days, when she was laying her first egg. Consequently she was already very weakened at the time of production of sexual imagines. We can not consider this as a normal colony development.

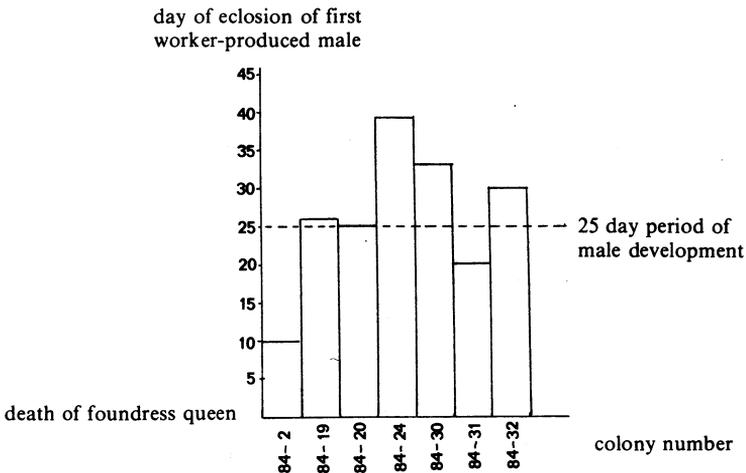


Table 2 : Time between death of foundress queen and eclosion of first worker produced male, compared with 25 day period of male development in 7 *Bombus terrestris/xanthopus* hybrid colonies.

In most colonies the queen loses dominance over the workers some time before her death. I recorded the moment when she started sitting on the side of her comb or even in the nest entrance or feeding compartment. In table 3 this time is compared with the date of eclosion of the first worker-produced male and with the duration of 25 days of male development. Excluding colony 84-2 (for reasons already mentioned) it is obvious that as long as the queen is dominant, she is monopolising the production of males. As a number of

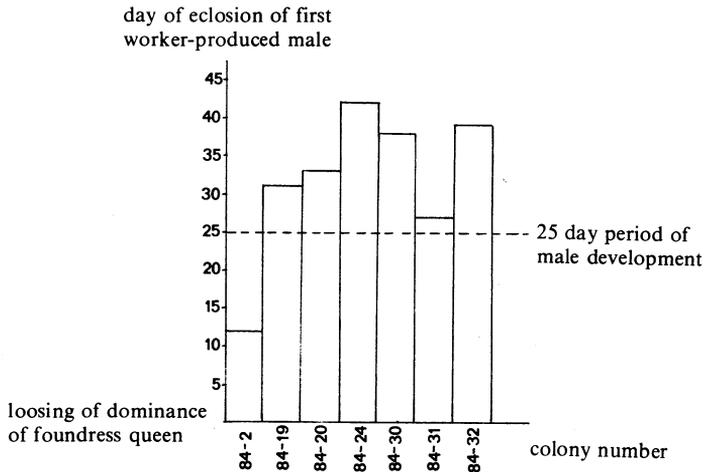


Table 3 : Time between dominance loosing of foundress queen and eclosion of first worker-produced male, compared with 25 day period of male development in 7 *Bombus terrestris/xanthopus* hybrid colonies.

workers frequently can be seen ovipositing at an age of approximately 70 days (VAN HONCK, 1981), the queen is capable to detect and destroy every egg laid by the workers. A considerable part of this oophagy is done by the workers themselves.

Worker-produced males are born not only 25 days after the queen's death, as can be expected, but even as late as 33 days after that moment. After the old queen's death, much oophagy is carried out by the workers in their competition to gain dominance. Another explanation is the position of the colony in the post-sexual producing stage (period of decline, HASSELROT, 1960), with instable temperatures, less care and prolonged development of the (male) brood.

In these experiments the colony's life is prolonged by adding energy by means of heath or food or both. It is questionable of these colonies would have been able to produce any worker-produced offspring at all, if they were not given support to survive. HASSELROT (1960) recorded the time between the apparition of the first young queens and the end of the colony in 9 natural successfull (male and queen producing) nests. The results were : 34, 35, 13, 20, 34, 31, 15, 13 and 30 days (mean = 25 days).

In 4 colonies the time of eclosion of the first young queen is recorded (colony 84-2 is omitted, and colony 84-31 and 84-32 did not produce queens). In table 4 these dates and those of apparition of the first worker-produced males are compared with the expected end of the colony. We see that none of the 4 colonies under consideration would have been living long enough to produce also worker-originating males. Thus the production of males depends exclu-

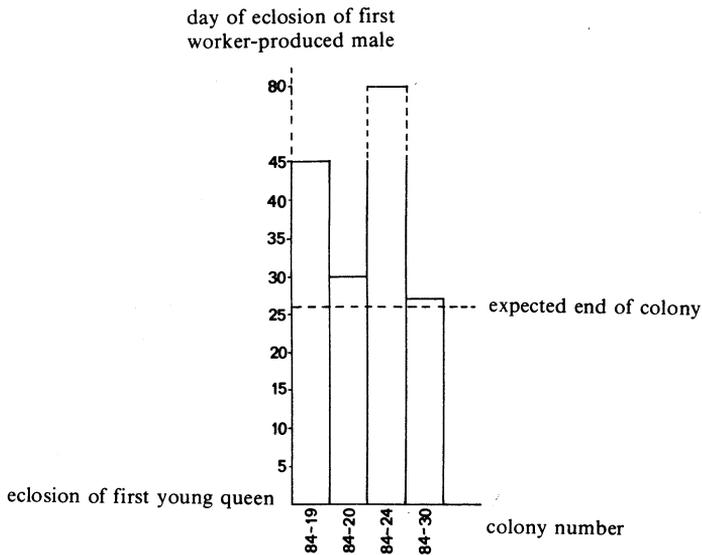


Table 4 : Time between eclosion of first young queen and eclosing of first worker produced male, compared with expected end of colony in 4 *Bombus terrestris/xanthopus* hybrid colonies.

sively on the foundress queen and the worker caste does not add anything directly to the gene pool.

I am aware that these results are contradictory to records or opinions of most other authors, except ROESLER (1967) who stated that as long as the foundress queen is dominant, all males descend from her. OWEN (1982), using a colour dimorphism as a genetic marker, estimated that in *Bombus melanopygus* 19% of the males originated from the workers, while the queens were still alive and that in total 39% of the males were worker-produced. As *B. melanopygus* belongs to the subgenus *Pyrobombus* and *B. terrestris* to *Bombus sensu stricto*, it is possible that subgeneric differences are involved.

On the other hand VAN HONK et al. (1981) estimated that in their *B. terrestris* colonies up to 82% of the males originated from workers. The way they come to this estimation is not clear to me in their paper. Probably they based their conclusions on the high frequency of worker ovipositions and took too less account of the queens ability to destroy worker eggs. Also they did not consider the artificial longevity of their colonies. OWEN (1982) stated that in artificially kept colonies the number of worker-produced males after the queen's death is possibly exaggerated, because the life expectancy of workers belonging to temperate species is very short (13,2 days) (RODD et al., 1980).

ZUCCHI (1973) estimated that in *Bombus atratus* FRANKLIN workers produce about 90% of the males. Unfortunately his work is not accessible to me and I do not know what his estimation is based upon. Conclusively we can say that

in colonies of *B. terrestris* with a normal development, the eventual production of a small number of worker-originating males after the queen's death does not increase the variability of the gene pool. Because when these males are flying, the young queens have already disappeared in their hibernacula. Similar experiences with bumblebees belonging to other subgenera can reveal the existence of subgeneric differences.

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References

- Free, J.B., Weinburg, I. & A. Whiten, 1969. The egg-eating behaviour of *Bombus lapidarius* L. *Behaviour* 35 : 313-317.
- Hasselrot, T.B., 1960. Studies on Swedish bumblebees (genus *Bombus* LATR.) : their domestication and biology. *Opusc.ent., Suppl.* 17 : 1-192.
- Honk, C.G.J. van, Röseler, P.F., Velthuis, H.H.W. & J.C. Hoogeveen, 1981. Factors influencing the egg laying of workers in a captive *Bombus terrestris* colony. *Behav.Ecol.Sociobiol.* 9 : 9-14.
- Jonghe, R. De, 1982. Copulations interspécifiques en captivité d'espèces du genre *Bombus* LATREILLE (sensu stricto) (Hymenoptera, Apidae, Bombinae). *Bull.Annls.Soc.R.ent.Belg.* 118 : 171-175.
- Jonghe, R. De, 1986. Crossing experiments with *Bombus terrestris terrestris* (LINNAEUS, 1758) and *Bombus terrestris xanthopus* KRIECHBAUMER, 1870 and some notes on diapause and nosemose (Hymenoptera : Apoidea). *Phegea* 14(1) : 19-23.
- Jonghe, R. De, & P. Rasmont, 1983. Kreuzungsexperiment mit Hummeln des Genus *Bombus* LATREILLE sensu stricto (Hymenoptera, Apidae). *Phegea* 11(1) : 7-10.
- Owen, R.E. & R.C. Plowright, 1982. Worker-queen conflict and male parentage in bumblebees. *Behav.Ecol.Sociobiol.* 11 : 91-99.
- Pomeroy, N. & R.C. Plowright, 1980. Maintenance of bumblebee colonies in observation hives (Hymenoptera : Apidae). *Can.Entomol.* 112 : 321-326.
- Rodd, F.H., Plowright, R.C. & R.E. Owen, 1980. Mortality rates of adult bumblebee workers (Hymenoptera : Apidae). *Can.J.Zool.* 58 : 1718-1721.
- Röseler, P.F., 1967. Untersuchungen über das Auftreten der 3 Formen im Hummelstaat. *Zool.Jb. Physiol.* 74 : 178-197.
- Sladen, F.W.L., 1912. The bumble bee, its life history and how to domesticate it. Macmillan, London.
- Zucchi, B., 1973. Aspectos bionomicos de *Exomalopsis aureopilosa* e *Bombus atratus* incluindo consideracoes sobre e evolucao do compartimento social (Hymenoptera : Apidae). Ph.D. Dissertation, Ciências e letras de Ribeirão Preto (S.P.).

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