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THE HISTORICAL BACKGROUND OF THE DOMESTICATION OF THE BUMBLE-BEE, *BOMBUS TERRESTRIS*, AND ITS INTRODUCTION IN AGRICULTURE

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ABSTRACT

The history of breeding bumble bees, including the application of *Bombus terrestris* as a pollinator in greenhouse crops, is briefly reviewed. Much knowledge had to be accumulated before large-scale breeding became possible. In the case of *B. terrestris* , a bottleneck for commercial breeding has been the production of young queens in sufficient numbers to meet the demands of a rapidly increasing market for colonies. The example shows that the successful exploitation of an as yet unutilised resource may have all the characteristics of a gold-rush, including devastating consequences for natural environments.

INTRODUCTION

In the discussions on sustainable development it is generally agreed that nature still harbours large numbers of organisms potentially and directly important for mankind. Their profitable use is only awaiting the discovery of their value, or the formulation of the way they should be multiplied. Concerning the more than 20,000 species of bees, there is the recognition that almost all have a certain role in pollination, leading to the production of seeds and fruits, and that the various morphological differences among these species (such as in their body size, the absolute and relative tongue length) are related to a certain degree of specialization for the rather varied flower types.

In the design of agricultural systems this diversity of bees does not play any role. Except for a few species, these bees are not cultivated, their natural nesting sites are not protected nor respected and in fact, pollination by such "wild" species is taken for granted as long as sufficient pollination occurs. If pollination is unsatisfactory, a generalist pollinator, most often the honeybee, kept in managed colonies, is brought to the site, and if pollination then occurs to the desired degree, this measure is considered to solve the problem. Why pollination was or became unsatisfactory seems to have been and continues to be an unimportant question.

The future use of the many undiscovered pollinators depends on the establishment of methods to breed them in the necessary quantities. The time needed for such a development is generally underestimated. Furthermore, breeding is only part of the way towards the successful use of such a new pollinator. In this regard I like to illustrate this using the bumble bee, *Bombus terrestris*, as an example. This species has become a valuable pollinator in intensive farming since 1988, when it was introduced in the greenhouse production of tomatoes in The Netherlands and Belgium, but it had already been studied and reared in laboratory settings for some decades.

I distinguish the following four aspects of the process: 1. learning how to breed the bee; 2. the search for an application; 3. towards application and wide acceptance of the new method; 4. international aspects of the dissemination of the new technology.

Early rearing attempts

The first accumulation of knowledge about breeding necessarily involves hobbyists, who, by sheer interest, devote their time to naturalistic observations. A prominent person with respect to the breeding of bumble bees in general was F.W.L. Sladen, who published his experiences in 1912. He collected incipient colonies or solitary queens after their hibernation, and put them in nest boxes of various designs. He observed that interactions among queens, or of workers placed in the box together with a queen prior to the start of her egg laying, increased the probability of success. He used workers of those species that start a colony early in spring to stimulate the queens of species that end their hibernation later in the season. He considered the major problems for the domestication of the bumble bees to be the control of their mating and of their hibernation. It is of interest, that by the word domestication he did not think of any practical application.

Sladen's recommendations were followed by others, who added their own techniques. Among them were H.-H. von Hagen (1975) and E. von Hagen (1986), who described their 30 years of experiences of breeding more than 15 species of Central European bumble bees. A brief summary of the earlier applied studies was given by Bornus (1975); and also Free and Butler (1959) mention the earlier breeding experiments. Part of these concerned the dimensions and design, the contents and the localities of nest boxes placed in the field to attract young queens in their search for a suitable nesting site. Extensive studies along these lines were also made at the Polish Research Institute, Pulawi. Here caged plots of 1 m^2 were provided with a nest box. Each cage contained flowering *Lamium album*, a noted food plant for various bumble bee species. On suitable days in spring, young queens of various species, and which just had emerged fom their hibernation sites, were captured and placed in the cages. The presence of abundant food resources and the carefully selected nest box, differing according to the species, made the queens start breeding (Bilinski 1976). The method was rather successful, but quite labour-intensive. In this case breeding was undertaken to rear colonies for the pollination of alfalfa and red clover, and a major problem was the production of mature colonies synchronised with the blooming period of these plants.

Laboratory breeding technology

The next step was the breeding of bumble bees under laboratory conditions, which involved the development of appropriate feeding methods. This was most successful in pollen storing species, such as *B. terrestris, B. lucorum, B. hypnorum*, and some of the American species (see Plowright and Jay 1966). Pollen harvested from honeybee colonies, using pollen traps at the entrance, proved to be excellent, provided the pollen was not dried (Ribeiro *et al.* 1996). The pollen could be stored in a freezer, and could be given in small quantities or even in bulk, without losing its attractivity or its nutritive value. Sugar water, in concentrations of about 50% w/w, proved to be an excellent substitute for nectar.

However, under laboratory conditions, queens apparently need to be stimulated in order to start breeding. Species that naturally start breeding under the ambient temperatures characteristic of early spring, needed to be placed in climate rooms with temperatures of 28 ^{o}C, and, in addition, needed to be placed in pairs. Much of the present-day techniques have been developed or combined by P.-F. Röseler, who only in 1985 published in full the results of his 20 years of experience. He developed the technique of having the queens mated, initially by letting them fly at the appropriate age in his rearing room together with a few drones. From this the mating cages of today were developed. After mating, he placed each queen in a small vial, together with a piece of humidified filter paper, and stored them in a refrigerator at about 5 ^{o}C, to simulate hibernating conditions.

While Röseler followed Sladen in placing two queens together, Ptacek (1985, see his 1990 paper) used worker honeybees to stimulate the onset of egg laying. In a sense, his method also goes back to Sladen, who used workers of another bumble bee species for the purpose. Ptacek also followed Zapletal (1966, see Ptacek 1990), who gave a piece of honeycomb to queens in which he offered them a sugar solution. Ptacek noted the queens, as long as they were alone, to be rather restless on this honeycomb, but they became quieter if accompanied by honeybee workers. As a consequence, they started breeding. For queens emerging early in spring, honeybee workers are more readily available than bumble bee workers, which made the method attractive for occasional breeding attempts. Furthermore, if two queens of the same species are placed together, they generally will become aggressive towards each other, with the consequence that often one of them will be killed. The use of honeybees, therefore, had certainly advantages at that stage of the technical developments.

In our own laboratory the attempts at breeding bumble bees started in 1974, and initially we adopted the techniques of Röseler, beginning in early spring with field-caught queens of *B. terrestris*, placing two queens together in the nest box. However, once continuous breeding became possible, we changed to adding young, adult bumble bee workers or male cocoons to a single queen. This had the same activating effect on the queen, and the advantage that more cages could be put up when a few queens were available.

Another important discovery made by Röseler was that the obligatory hibernation period of queens could be circumvented by giving them, after a successful mating, a CO2 narcosis. This allowed breeding throughout the year. The method has been widely used in the commercial breeding that developed soon after.

In our laboratory, however, we preferred a more natural hibernation. Already Zapletal (1961) had placed mated queens in boxes partly filled with loose, moist peat, and Ptacek (1985 in 1990) tried to imitate the natural hibernaculum by drilling holes in a piece of wood, in which queens could be placed after they were deactivated by cooling them in a refrigerator. Pouvreau (1970) offered to queens, flying in a greenhouse, a heap of moist peat dust, and these queens dug themselves into it. Under natural conditions, a few days after mating, queens had already sought a hiding place for the winter. In our own system we borrowed from these methods. Plastic boxes, containing a layer of 10-15 cm of peat dust, are placed underneath the mating cages. Most queens dig themselves a hole in this substrate, and become inactive. A few days later the box, covered with a plastic foil, can be placed in a cold room (Duchateau 1985). Within two months the queens can be reactivated, but longer periods of hibernation are equally well possible.

There are several advantages of this hibernation method over the CO2 narcosis method. In the first place, after CO_2 narcosis, queens may produce males among their first and second brood. Such early investment in males is a lost one, because males do not help the further development of the colony. This irregularity may also influence the pattern of colony development. Second, queens stored in the cold room can be used at a time most suitable for the breeder or experimenter. It needs to be said, however, that there is still a difference with natural conditions, in that in nature queens hibernate for periods of up to 8 months, a length of time most of them do not survive in the cold room. Mortality rates in relation to natural hibernation conditions are not known.

The application and wide acceptance

The importance of bumble bees, especially the long-tonged ones, has been recognised for more than a century, especially for the pollination of red clover and alfalfa. For this reason in the 19th century some species were introduced into New Zealand, and in Europe Hasselrot (1960) and Holm (1960, 1966) studied the attraction of several species to nest boxes, partly for the same purpose. Long-tonged bees are pocket making species, which are more difficult to breed (Griffin et al, 1990) than the pollen storers; it is to the latter group that *B. terrestris* belongs. In pollen storers, the foragers deposit the collected pollen and nectar in special receptacles, or in old cocoons, from which the nurse bees take it to feed the larvae. In pocket makers, however, the collected pollen is brought directly to a pocket at the base of the cell containing the larvae. These bumble bees do not transport to the larvae the pollen which the breeder provided somewhere near the brood. Unfortunately, *B. terrestris* has a relatively short tongue, and is not a pollinator for deep flowers like red clover and alfalfa.

In my imagination, our *B. terrestris* cultures were promising for applications in agriculture. I discussed these possibilities with a number of colleagues, some of whom were less optimistic (e.g. Röseler, 1979) than I was. With the help of the Directors of the Ambrosiushoeve, the Dutch research Institute for Beekeeping (Ir. Mommers, and later his successors Ir. Pettinga and Dr. van Heemert), I tried to find a greenhouse crop that was hand-pollinated, and where the relatively high costs of breeding bumble bees could compete with high labour costs. In 1982 this led to a study of pollination in Primula, where, apart from the expenses of hand pollination in the production of hybrid seeds, the strong tendency of the development of allergy among the workers made such a study rather attractive (Velthuis and Cobb, 1990).

Around 1985 Dr. R. de Jonghe, a Belgian veterinarian with interest in bumble bee taxonomy and an experienced breeder, made his first observations on the value of *B. terrestris* for the pollination of tomatoes. He placed bumble bees in a greenhouse in the southern part of Holland. The grower trusted him, to the later great delight of both of them. The grower got record prices for his produce in the market. Soon after, tomato growers in that area became aware of the value of insect pollination. The next year we received a busload of growers in our laboratory, where they hoped to see how easy it was to breed bumble bees. Many queens were collected by them, placed in nest boxes and treated carefully; probably none of the queens ever laid an egg. Also beekeepers, supposing breeding bumble bees would not be very different from rearing honeybees, attempted to take part in the rapidly developing breeding industry. Dr. de Jonghe started his company Biobest; in The Netherlands it were Bunting Brinkman, Koppert Biological Systems, and several smaller companies that initiated activities. Within a few years in the Low Countries there was hardly a tomato grower left that still used pollination through artificial vibration.

Why was it that the first attempt to pollinate tomatoes through the help of this bumble bee led to such a rapid change? I see three main factors. Firstly, there was much competition in the market, and only the better quality tomatoes fetched a satisfactory price. Bumble bee pollinated tomatoes were of distinctly better quality compared with fruits obtained through artificial vibration, and, during the first years, the grower that used bumble bees got away with the best prices. Secondly, bumble bees did their work at a much lower price compared to the labour costs of artificial vibration. Furthermore, the technology for biological control of insect pests on greenhouse tomatoes was already fully developed by Koppert.

Using bumble bees for pollination implies refraining from insecticide treatments. The availability of biological control agents made it easier for the growers to make the change. Up to the introduction of bumble bees in the greenhouse, this biological control system was only used by a few growers, because checking the crop regularly for developing insect pests needs more attention than following a strict scheme for preventive spraying.

After the tomatoes, other greenhouse products followed. Most prevalent is the use of bumble bees in sweet pepper production, where an upper quality category of product had to be added as a a result of insect pollination.

Why was it, that our questioning of agricultural specialists for hand-pollinated crops that could profit from bumble bee pollination never led to the idea that tomatoes could be worth testing? I think the answer lies in the fact that there was already a method that did lead to a satisfactory fruit set, and that there was a surplus production, leading to often low prices for the growers. There was no need to produce more, and quality aspects of natural pollination were never thought of. The differences in taste of field-grown tomatoes and those from the greenhouse were attributed to differences in the amount of sunshine, leading to a more juicy product with higher sugar contents in those summer-grown tomatoes coming from open fields. Juiciness and sugar concentration are also dependent on fruit physiology, and, in turn, this physiology is influenced by the degree of seed set, which was not considered before.

Problems at the start of commercial breeding

It probably needs no explanation that with the rapidly increasing demand for bumble bee colonies, the commercial breeders had difficulties in producing the large amount of colonies requested. In the laboratory, where answers to specific biological questions concerning the development of colonies, or of individuals within the colony, are sought, the failure of a number of queens to produce a colony is not very much a matter of concern. In commercial breeding, however, this success rate is a very important matter, and needed to be improved. The larger companies, therefore, invested in the finer details of the activation of queens, and each company developed its own improvements, which, up to the present, are carefully kept secret from the competitors on the market.

A second problem was in the fact that bumble bee colonies appear to produce males in much larger numbers than they do young queens (Duchateau and Velthuis 1988; Bourke 1997). Many colonies do not produce queens at all, and therefore, obtaining home-bred sexuals for a new generation of colonies often posed problems. To compensate, the southern parts of Europe became favorite places to collect queens. Especially from populations that produce colonies in winter, such as *B. terrestris sassaricus*, queens were collected in great numbers. This mass collection grew to such an extent that public reactions in these countries followed, and some countries prohibited the activity.

Why this male-biased reproduction occurs is still unexplained, but a recent analysis of our laboratory breeding of the last years, in which several hundred of colonies are included, indicates that it might be a consequence of a number of environmental factors (Duchateau *et al.* unpublished). In many breeding situations these environmental conditions might not be optimal for obtaining equality in the investments in the two sexes.

Furthermore, initially colonies from self-bred queens appeared to be weaker than those from field-collected queens. One explanation for this could be that it is an effect of inbreeding. We therefore started a study on inbreeding, and could demonstrate that sex is regulated in the same way as in many other Hymenoptera (Duchateau *et al.* 1994), i.e. through a series of alleles at a sex locus, and that homozygosity for this gene leads to diploid males instead of diploid workers. This indicated that, in the mating phase, care should be taken to select queens and males from different colonies, to avoid such rapid inbreeding effects. Fortunately, diploid males are almost unfertile (Duchateau and Mariën, 1995), and in case they should occur in the breeding system, their low reproductive success would eliminate any consequence of their appearance.

From the point of view of nature conservation, it is most enjoyable that also the commercial breeders nowadays rely largely on their own production of queens and males for the next generations. This circumvents the escalation of the conflict concerning mass collection of mated queens in the field. At the same time, the possibility of such conflicts might be a warning for future introductions of new pollinators: if there would be an economic success without a sufficiently developed breeding technique, the balance of the invention would soon skip to the negative side.

International aspects

The success of bumble bee pollination did not remain a secret of the Low Countries. Large scale exportation of colonies to other countries, within and outside Europe, soon took place. This brought a new kind of problem. Ideally, each country should breed the colonies it needs, using local populations to start with. This would avoid spreading bumble bees from one area to others. Geographic populations probably are genetically different, and mixing them would probably lead to unwanted local hybridization. Furthermore, moving bumble bees would have the possible consequence of the introduction of bumble bee parasites and diseases in places where they do not occur naturally. Governmental strictness stimulated the breeding companies to start breeding locally, like in Irael, where *B. terrestris* is native; in N. America species from that continent*, B. impatiens* and *B. occidentalis* (for use at the eastern or western side of the Rocky Mountains respectively) were selected as alternatives. In Turkey, however, a country that once provided the breeders with large numbers of very early queens, governmental restrictions so far made it impossible to revolutionise its tomato industry.

However, there are several reasons why the local production of colonies is not an ideal situation from the point of view of the breeding industry, as long as it concerns relatively small geographic areas, such as in Europe. In the first place because tomatoes and sweet pepper are not cultivated year-round in any country, and a local breeding centre therefore would face unemployment for part of the year. Producing colonies centrally, in combination with transportation to countries where the growing season for the plant to be pollinated is different, has big economic advantages. It allows the bumble bee breeder to invest in specialization of his personnel. Production costs become lower, as the breeding becomes more efficient.

The international market for the agricultural product demands for equal chances, and therefore growers in countries where bumble bees are not naturally available, seek importation of this pollinator. This is the case in Australia and some Latin American countries. In Japan the government stimulates the development of breeding techniques for local bumble bee species, but in the meantime allows importation of *B. terrestris* from Europe. In Australia the government prevented importation of bumble bee colonies. Pollination by large carpenter bees of the genus *Xylocopa* was proposed (Hogendoorn, personal communication), but in the meantime *B. terrestris* has already accidentally reached Tasmania (Semmens *et al.* 1993).

CONCLUSIONS

The example of the introduction of *Bombus terrestris* in greenhouses demonstrates, that the breeding technology necessarily has to be developed sufficiently before the application can be made. Otherwise, the use of a new pollinator will lead to permanent, excessive robbing of natural populations.

If one of the arguments for nature conservation is that in this way potential benefits can be safeguarded, then there should also be the possibility for scientific and hobbyist researchers to study the biology of the organisms occurring in that reserve, without asking any argumentation concerning utility. Only in that way the body of knowledge can be built on which future applications depend.

Improvements in production technology are measured in economic values only. New technologies, therefore, are only accepted by farmers if there is already such an economic perspective. Without such perspective, experiments on the biological possibilities of the use of a new pollinator are difficult to arrange, and meet skepticism. Even in the case of the Dutch tomatoes, it took years before they were advertised using the bumble bee as a symbol for low pesticide loads. Apparently, such a quality aspect did not belong to the aims of the industry.

Finally, the bumble bee example has shown that there were considerable problems in communication, between scientists, policy makers, and farmers, because most probably each group had, and still has, a different set of goals.

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