SOCIO-ECONOMIC EFFECTS ON COLONY SIZE IN THE BUMBLE BEE *BOMBUS TERRESTRIS*. (HYMENOPTERA: APIDAE)

BY

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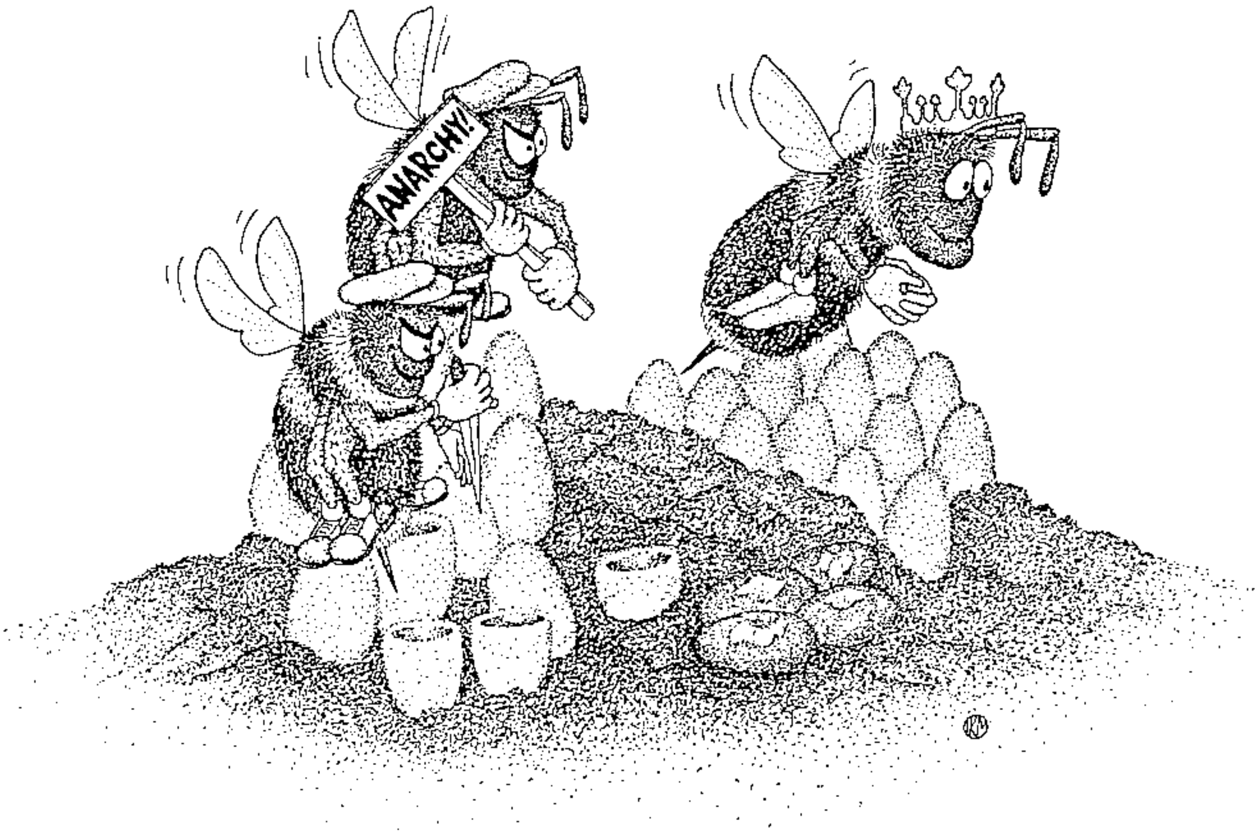
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ABSTRACT

This study examined factors related to the development and eventual size of bumble bee colonies (Bombus terrestris (L.). Experiments were conducted over two seasons in both the laboratory and the field. In the first season the effect of supplementary feeding of sugar solution upon colony growth was examined. In the second season the effect of sugar feeding on worker dominance was studied.

The feeding of sugar syrup to bumble bee colonies resulted in a reduced colony size and (at the 56th day from colony initiation) greater mean ovarian development in workers. In laboratory colonies that were sugar-fed foundress queen longevity was reduced. These results were interpreted as suggesting that sugar feeding influenced colony size via an effect on the social structure of the colony. Conflict between workers and the foundress queen near the peak of colony development has been widely reported in bumble bees and my results suggested sugar feeding increased worker dominance over the queen and that this curtailed colony growth. The relationship between worker dominance and colony development was studied, using the assumption that the dominance of workers increases with there age. Colonies were manipulated by selective removal of either the oldest or youngest workers, to produce a difference in the average age of the worker populations. In colonies with a higher mean worker age there was an earlier change to sexual production and fewer workers were produced. Earlier sexual production also occured where the number of workers in a nest was artificially increased. The small size of sugar-fed colonies was attributed to the early appearance of reproductives due to a premature rise in the numbers of dominant workers. It was concluded that worker dominance was affected by trophic/economic effects such as the effort required to procure nectar, and that the provision of sugar solution in hives seems inadvisable in commercial management of bumble bees.

CHAPTER 1

INTRODUCTION

Bumble bees are widely recognised as effective pollinators of commercial crops (Free 1970a, 1970b), specifically forage legumes of which the most important are red clover and alfalfa (Bohart 1957, 1958, 1960; Akerberg and Stapel 1966; Peterson *et al* 1960). Bumble bees are considered to be especially tolerant of adverse weather conditions and are seen foraging at times when honey bees are not active (Heinrich 1972, 1979a, 1979b; Heinrich *et al* 1977; Pyke 1978; Wilson 1929). The failure to set seed of the first red clover (*Trifolium pratense* L.) crops in New Zealand was a result of the lack of any native or introduced bumble bees (Tillyard 1926). A dramatic increase in seed yield resulted from the introduction of bumble bees to the South Island in 1885 (Hopkins 1914). Bumble bees quickly became established and spread to the North Island (Thomson 1922). A second release was made in 1906. After a survey in 1953 Gurr described the presence and distribution of four species (Gurr 1957a, 1964, 1972). These four species were *B. ruderatus* (Fab.), *B. hortorum* (L.), *B. subterraneus* (L.) subsp *latreillellus* (Kirby) and *B. terrestris* (L.).

Seed yields began to decline again after a number of years. This was possibly because the increased acreage of red clover which was enthusiastically planted could not all be pollinated by a limited bumble bee population (Gurr 1975). As such there have been continual demands from farmers for the introduction of new species of bumble bees. This has instigated much research into the commercial management of bumble bees.

B. terrestris was the only short tongued species introduced to New Zealand. The workers of this species cannot reach the nectaries of red clover. They therefore resort to "robbing" the flowers by biting holes through the base of the corolla tube and collecting nectar without pollinating the plant. In New Zealand honey bees may become secondary "robbers" by the use of the holes made by the primary robbers, though in other contries many other bee species may fill this role (Holm 1966). Contrary to the opinion of many authors there is no evidence that robbing is detrimental to red clover seed yield (Hawkins 1961; Morrison 1961)

Nevertheless *B. terrestris* has been found to be an ideal pollinator of many fruit and berry crops, including kiwifruit. A research project is currently being undertaken at Massey University to discover methods by which *B. terrestris* colonies can be commercially produced primarily for Kiwifruit pollination. This species was therefore chosen as the object of this study.

Although bumble bee colonies are known to range in size from 50 to 500 and sometimes 1000 workers (personal observations), researchers attempting to raise colonies by allowing them to free forage have found that a surprisingly large percentage produce very small colonies. Initially the major purpose of this study was to investigate methods by which bumble bee colony size could be increased. As small colony size is a handicap to commercialisation, this would enable artificial colonies of a reasonable size to be produced for crop pollination.

1.1 BUMBLE BEE NATURAL HISTORY

Inseminated queen bumble bees hibernate over the winter period for, in the British Isles, "anything from six to eight or even nine months" (Alford, 1975). In the mild climate of Palmerston North, N.Z. this period can be substantially shorter (Pomeroy personal communication). They hibernate individually in small cavities at some 10cm or less below the surface in well drained soil (Sladen 1912; Bols 1937, 1939; Alford 1969). On emerging from hibernation in the spring the queens spend two or more weeks actively flying, foraging or sunning themselves (Heinrich 1979a). Once the queen's ovaries have begun to develop she begins to search for nest sites (Cumber 1949a; Miyamoto 1960).

After selecting a suitable site, usually an abandoned rodent hole, the queen will manipulate the available nest material to form a cavity in the centre in which she keeps her brood warm. At this point the presence of good thermally insulating material is important as a comb temperature of 28 to 30 degrees Celsius is to be maintained through the season (Hasselrot 1960; Wojtowski 1963).

The queen then collects pollen which forms a "clump" on the floor of the nest cavity. A batch of 8-14 eggs (Pomeroy 1979) is then laid into a cup shaped depression lined with wax (egg cell) which is then closed over with wax. After hatching, about 4 days after oviposition, the larvae grow rapidly, feeding upon the pollen lump below them and from regurgitated pollen/nectar mix from the queen through holes in their wax canopy. The larvae ultimately spin cocoons of silk and pupate inside them.

Based on my own observations of *B. terrestris* the first workers emerge 19-21 days after the eggs are laid. During the first 12 - 24 hours young bees (termed callows) perform no "duties" within the nest, during this stage they are still developing coat colouration and wing hardness (Pomeroy 1977). The first workers eventually take over all the foraging and most nest duties from the queen. Batches of 6 to 20 eggs are laid in egg cells on top of newly spun cocoons. Cumber (1949a) and Brian (1951) calculated that for *B. agrorum* less than 50% of eggs laid survived to adulthood. The edges of empty cocoons are extended with wax collars and reutilised as honey pots and pollen storage pots (Heinrich 1979a).

The comb develops upwards and outwards becoming roughly hemispherical, though this may differ in some species, and also depends on the shape of the hole in which the nest is located. The number of workers increases exponentially (Plowright 1966, Röseler 1967a) until there is a change to the production of males and queens. It is not uncommon that some colonies produce no queens at all, if male production is started at an early stage when the colony is small. Once the production of males starts it is rarely reversed, and the production of workers diminishes.

A division of labour among the workers often develops in relation to size and age. The youngest (1-2 days old) and smallest bees often stay within the nest while the larger workers do most of the foraging. After some time many of the "house-bees" may begin to develop their ovaries, the possible causes for which form the major part of this study. Much antagonism begins to occur within the nest between workers with enlarged ovaries, and between these workers and the queen. The queen starts laying male eggs and soon after the workers also start laying eggs (Owen and Plowright 1980) (all worker eggs are unfertilised and therefore males). A large proportion of all the males may be worker produced. Owen and Plowright (1982) estimated 39% of males in 17 laboratory colonies of B. melanopygus to be produced by workers, and van Honk et al (1981) calculated that 80% of the males from a B. terrestris colony originated from worker laid eggs. At the start of male production any remaining female larvae are fed at an elevated rate and become new queens. Antagonism within the nest continues for some time and may increase to the point where the queen is killed or pushed off the comb by the most dominant workers. It should be pointed out that not all nests lose their queens in this way. Wild nests have been found in advanced stages of male and queen production in which the foundress queens seem to have retained their dominant position (personal observations).

After a young queen has emerged, in about mid summer, she stays within the nest for about 5 days before going on a mating flight (Cumber 1953a). She then returns to the colony and spends a period of time building up her fat bodies from the nest pollen and nectar store before going in search of a suitable hibernation area. During this time her ovaries would normally remain undeveloped (Cumber 1949b). Though in the few tropical Bombus species, eg. B. atratus, the young queens may not go into hibernation at all, but (after fertilization) will replace the old queen on the comb and start egg production (Sakagami et al 1967).

Males leave their nest when they are between two and four days old and normally never return. They generally live for three to four weeks spending their time foraging for their day to day food requirements from flowers, and inseminating young queens (Alford 1975).

1.2 BUMBLE BEE DOMESTICATION

As mentioned above, bumble bees are ideal pollinators of many crops. The pollination of these crops is ultimately dependent on the number of bees in the area (Jamieson 1950; Bird 1944), but the natural population is often too sparse and fluctuates from year to year. Many investigators have attempted to alleviate the problem of fluctuating numbers of bumble bees through propagation of the natural population (Frison 1926; Fye and Medler 1954 and Hobbs et al 1960). These and other authors have placed artificial domiciles of various designs in the field for attracting wild queens to initiate colonies. The most recent work in this area has been undertaken by Macfarlane et al (1983) and Donovan and Wier (1978) who had occupation rates of between 20 and 30 % (this is similar to the queen occupation rates of earlier researchers), and Pomeroy (1981a) who found that of 45 underground hives 93% were occupied by queens.

Laboratory initiation of colonies using wild-caught queens is another means by which researchers have attempted to raise bumble bees. Factors found to affect the success of this method were the physical design of the starter-boxes (Hasselrot 1952; Plath 1923), the food requirements and the way in which it is presented (Plowright and Jay 1966; Pomeroy personal communication.), heating requirements (early researchers used various types of insulation material, but it was later found that this was not required if the temperature within the nest box was raised (Hasselrot 1960)) and social factors (both Medler 1957 and Plowright and Jay 1966 found that some social stimulation from other queens or workers produced better colony initiation than did single queen confinement). Current work in this field is being undertaken by Pomeroy (unpublished) in which large numbers of colonies are being started in small, two chambered, plastic moulded starter boxes maintained at an elevated temperature. This is the method of colony initiation used in this investigation.

1.3 OBJECTIVES OF THE PRESENT STUDY

The original aim of this project was to study the factors affecting the size of bumble bee colonies and to determine means by which final colony size could be artificially, and economically increased. The 1984-85 summer season was spent on an experiment attempting to increase the size of colonies by feeding them excess sugar syrup. As many authors have suggested that food is limiting (Cumber 1949a, 1953b; Medler 1958) the expectation was that they would increase in size. The results were contrary to this expectation and in fact showed that feeding sugar syrup had a debilitating effect upon the colonies. They also indicated that this might be due to social factors (specifically the presence of dominant workers) within the nest. Work by Free (1955a), Röseler (1967b) and van Honk and Hogweg (1981) has shown that the presence of dominant workers can have a disrupting effect upon the colony and that these workers may affect the timing of male production. As the final colony size is to some extent dependent on the timing of male production (Pomeroy 1979) subsequent work was therefore directed towards determining the effect of sugar feeding on factors within the nest, particularly the preponderance of dominant workers, and the effect of these factors on colony size.

In the second season the aim of the first laboratory experiment was to discover whether the early presence of dominant workers in the colony affects the timing of male production and the consequent curtailment of colony growth (chapter 3). An experiment was also designed to determine whether sugar feeding affected the proportion of dominant workers within the colony.

Artificial feeding might be expected to reduce the colony's foraging effort resulting in more bees staying "at home" on the comb. Röseler (1967a) suggested an increased density of bees on the comb stimulates the foundress to produce male eggs, but Pomeroy and Plowright (1982) failed to demonstrate such an influence in an experimental situation. I examined this factor in the present study.