The Honeybees of the British Isles

BEOWULF A. COOPER

THE HONEYBEES OF THE BRITISH ISLES

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BRITISH ISLES BEE BREEDERS' ASSOCIATION

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by the Committee of BIBBA
to
Griselda R. Cooper

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Foreword

Beowulf Cooper's professional career was as an entomologist in the Government's Agricultural Advisory Service, helping our farmers to grow crops and raise livestock with the minimum damage from insects and other pests. In this work he was always conscious of the environment in which farmers live and work, and he did his best to preserve this by avoiding the harmful effects which pest control unfortunately often has. He had many other interests, but he decided many years ago to devote all his spare time to the study of the honeybee. His contribution to our knowledge of bees in Britain was considerable, and much of this new information was spread by the British Isles Bee Breeders' Association, which he did so much to create and to foster. However, many of the results of his research have never been published. He left a mass of unedited material, which forms the substance of this book.

We are indebted to Philip Denwood for the immense amount of work he has done in preparing Beo's results for the press. The task has in some ways been greater than writing a new book about the work. Those who knew Beo will be impressed by the way his inimitable style has been retained, so that we can often imagine as we read that he is actually speaking to us again. I am sure that the text will inspire many readers and encourage them to continue the work on breeding and cultivating the strains of bee best adapted to the different localities in the British Isles.

As stated in the editor's preface, this book is written for beekeepers, and it is assumed that readers will have at least some basic knowledge of bees and beekeeping. However, I believe that the book should have an even wider appeal. It contains much that should be of interest to those concerned with genetics, inheritance and animal behaviour, for bees are so different from the animals usually studied by workers in these disciplines. Many of these scientists are unfortunately unfamiliar with the honeybee. No doubt they could easily rectify this by reading one of many books on this insect. However in order to make their task easier we have included a short appendix (Appendix 4) describing the life history of the honeybee and the general principles of beekeeping, which should serve to enable such readers to get the most out of the text.

Professor KENNETH MELLANBY, C.B., Sc.D., F.I.Biol.
President, BIBBA

Editor's Preface

An outline of Beowulf Cooper's career as one of Britain's most active and respected entomologists, together with many personal tributes and reminiscences, may be found in BIBBA News No. 21, dated May 1982. At his sudden death in February of that year he left a mass of material which he had often said was to be incorporated, along with various existing and projected BIBBA leaflets, into a book on bee breeding. Soon afterwards Albert Knight, Secretary of BIBBA, suggested to me that I might undertake the job of putting such a book together. The proposal received the approval of Beo's widow Griselda and of the BIBBA Committee, and the present work is the result.

Beo's philosophy, as he liked to call it, of beekeeping and bee breeding was the product of thousands of hive inspections and conversations with beekeepers in all parts of the British Isles. These activities, involving a great deal of travelling, together with his very demanding professional life, left him little time to set down systematic statistical documentation; though he made a start on this for his own colonies on the record cards which he largely devised, and in his studies on wing venation. His experiences were distilled into copious notes, jotted down on record cards often in odd moments, and rough drafts of articles. From these I have tried to weave a continuous narrative, incorporating many of his published leaflets and articles which are mostly now difficult of access. Over ninety percent of the text is Beo's own words; inevitably I have had to do some rearrangement and add linking passages when developing short notes into extended themes.

I have assumed a basic knowledge of honeybee biology in the reader of this book, such as may be gained from the work by Free, listed in the Bibliography, or from other standard textbooks. Also assumed is some familiarity with the techniques of beekeeping - though the reader should be prepared to suspend his belief in some of the statements commonly made in beekeeping textbooks!

Also among the material were the diaries of Terence Theaker from 1958 to 1971, together with some of his notebooks. A study of these has confirmed the remarkable qualities seen by Beo in the Theaker strains of bee. It has also revealed ideas which Beo was to take up, some later to be discarded, others developed. Time and again in his notes Beo refers to Terence Theaker and his bees as the starting point of some observation, or as a kind of comparative touchstone. Though by no means uncritical of Theaker's ideas, Beo was delighted to acknowledge his debt to him. It was no accident that the decision to form the Village Bee Breeders' Association (later BIBBA) was taken in Theaker's apiary.

Beo also records his indebtedness to many other devotees of the native bee, too numerous to list here. No-one with an interesting strain of bee, no matter what his walk of life or where he lived, could escape the possibility of a Cooper visit. Many of them gave freely of their time and experience. Perhaps this book may stand as a tribute to such beekeepers and their forerunners, who maintained over the years many valuable strains of bee.

I am grateful to Griselda Cooper for permitting the use of Beo's written and photographic material; and to Prof. K. Mellanby, Rev. Eric Milner, and Messrs. K. Ibbotson, A. Knight, R. Price and A. Waring for reading the text and making helpful suggestions. Thanks are due to A. Waring, Pl. 15, lower & Pl. 37 upper, and H. G. Smith, Pl. 27 lower, for providing photographs, and to the Editors of *Bee Craft* and the *British Bee Journal* for permission to reproduce material first printed in those magazines. Mrs. I. C. Waring gave valuable assistance in proofreading. All remaining shortcomings are my own responsibility.

CHAPTER ONE

Introduction

Early experiences

I first handled bees in 1940, at what is now the Slough laboratory of the Agricultural Development and Advisory Service. My own stocks were built up soon afterwards from two colonies I obtained in North Yorkshire and from one wild colony taken out of the church at Great Smeaton in the same county. When, like many novices, I avidly read all the beekeeping textbooks which came my way, I was struck by the marked contrast between the contents of these books and my field experience as a research and advisory entomologist (beginning also in 1940).

According to the beekeeping texts, bees were basically all the same, and the enormous variation in their behaviour and honey production resulted from differences in the immediate environment or my management. Many authors and speakers admitted to variability in colour or prolificacy, but they treated these as if they were invariable "racial" units, not inherited on mendelian lines, and used the words "hybrid" and "mongrel" as pejorative terms, to denigrate anything of native origin. Yet in all the organisms my work touched upon, plant or animal, ecology and genetics exerted at least as big a force as the environment. Surely the honeybee could not differ so markedly from the rest of creation, natural or man-made?

My first incredulous beekeeping years clearly indicated the falsity of the notions to be found in the textbooks. The ADAS bees were mixed black and yellow-banded, followers, quick to sting, good workers and infrequent swarmers. The North Yorkshire bees were black, hard-working and docile; perhaps 1 was fortunate in that one was a superseder and the other swarmed and gave me 39 capped queencells a few weeks later. The Great Smeaton bees were infrequent swarmers with other virtues. My partner had started with bees of Italian origin: yellow-banded, prolific, followers, attackers when insufficiently smoked and with a big appetite for stores. In 1947 I moved via Cambridge to Boston, Lincolnshire, sold my 13 stocks in Yorkshire and restarted with bees from my new area. To my great surprise the bees were totally different in almost every respect, apart from being black and hardworking. Inherited behavioural differences were plainly important. There followed the phase that many learner beekeepers go through, of obtaining strains from various sources and trying to compare them. It was clear that most characteristics were to a large degree inheritable, hybridisable and eradicable by culling. This tailored in well with my work which was becoming much less involved with direct control of pests and more with research to work out indirect control strategies. Crop plants were variable, weeds were variable, pests were variable. As a taxonomist I looked for minute differences in structure and behaviour. I described several new species of cyst nematode and a number of wireworm species, whose recognition and different behaviour had not till then been noticed. And there were differences between individuals of these which we called pathotypes.

Importance of breeding

I became involved in lecturing on various beekeeping matters, particularly in management, spray poisoning and pollination. About 1949 I met Terence Theaker of Leadenham, Lincolnshire, a skilled and observant beekeeper and naturalist whose experiences had led him to very similar views to my own[1]. He had reached this position by quite different reasoning, which confirmed my conviction that the ecological approach was the right one. Clearly much of the ritual of beekeeping as taught was unnecessary and, indeed, was tending to divert attention from things of major importance.

Terry Theaker was a great believer in breeding, and his enthusiasm was infectious. He had compared his local bee against the best available Italian he could trace, six colonies of each, and four of a Yugoslav Carniolan bee, with comparable food (sugar) inputs and management, over a period of 5 years. The Italians just beat the Lincolnshire bees in 1949, but the Lincolnshire bees were well ahead in honey yield in the remaining four years. More than this: they were far less trouble, did not attempt to swarm on single broodbox management, and had plenty of food in the broodbox when the supers were taken off. Although they wintered with small and tight clusters - those who did not know their characteristics felt they "would never winter" - they had the bigger foraging population in July, the main warm period in his area.

In 1955 I moved from Boston back to Cambridge, where I saw my 4 hives of Boston bees gather vast amounts of propolis alongside another beekeeper's bees which had no such problem. Ecological genetics was seen to be vital, not only as a guide to labour-saving management, but as the potent basis of natural selection via behavioural variation, which the breeder needed to assess and evaluate to make progress. Clearly there was a need to specialise in breeding philosophy, and to propound this widely in order to arouse interest and reach kindred souls.

In 1956, after moving to Shardlow near Derby and acquiring yet another type of local bee, it became clear that I had to concentrate on native and near-native types, setting up single-strain apiaries to minimise outcrossing and improve comparability. I extended my lecturing and meeting beekeepers to all parts of the UK and Ireland, to widen the genetic field that could be surveyed.

For 5 years after 1956 I compared lowland Lincolnshire (Boston) bees and North Yorkshire high moor (Cleveland) bees, each type in both environments. I found that the North Riding bees behaved as they always had done, swarming about every third year both in their own area and at Boston, when kept on a single broodbox. But the Boston bee, which swarmed annually at sea level, continued to swarm annually at 800 feet among the rainy hills - but it did so three weeks later than at Boston. Peak queencell number was not affected in any way with either bee. This comparative study taught me that swarming is determined genetically as well as influenced by the natural environment and by the beekeeper's management. I have maintained 20-40 overwintered stocks every year since, of divers local strains originating from different parts of the East Midlands, Yorkshire and Scotland. Comparative studies have focussed on many aspects of behaviour and morphology in these native strains, most of which have proved to be excellent honey producers under the minimum-management beekeeping which my other preoccupations have increasingly forced me to adopt.

In 1957 I put a note in *Bee Craft* inviting correspondence from people interested in the merits of native strains, and it took me until 1962 to meet everyone who replied, from Devon to Ayrshire, Lincolnshire and South Wales.

During the 10 years or so up to 1964 I tried in my talks to persuade beekeepers and associations to take action to improve their own bees. This effort proved a complete flop. Those who did make the attempt merely stimulated counter-action and nett progress was nil. Large committees, with all views represented, seem unable to achieve concensus between their members. Breeding is directional. Associations are non-directional and aimed more at social activities, novice training and honey shows than at concerted effort of long duration.

Formation of VBBA

There was need of a specialist organisation of those who could show unity of purpose. By operating through groups, there could yet be variety without any straitjacket to enforce unwelcome conformity. Good floral districts could well have quite different needs from those with sparse flora; high altitude areas might have quite different needs from the lowlands, or rainy ones from dry ones.

In 1962 I spoke on bee breeding at the Northumberland College of Agriculture's beekeeping conference. There I had the good fortune to meet Donald Sims, MAFF Regional Land Commissioner and a skilled administrator. He liked the ideas, but felt that no individual by himself could achieve so big a change in attitude; breeding was so different from management. Lecturing was ephemeral, and the written word had far more lasting effect than the spoken word. An organisation would have to be formed to carry out research and promote the subject, build up funds and issue publications if the idea were to catch on. It was the only way to build up enough followers to influence action.

To me this was a shaft of light, and I returned home inspired that to do this must be my main objective in life. I rethought my work priorities and decided that several other hobbies such as folk music and dancing would have to go (not without many regrets) to find time to do justice to bee breeding. Accordingly a meeting was arranged to bring together the *Bee Craft* correspondents. It took place in Terry Theaker's apiary at Leadenham in Lincolnshire, on 27th July 1963[2]. Only six correspondents in fact came together. After considering whether such a breeding organisation could be viable, and what lines it should take, it was agreed unanimously that such a group should be convened. By the end of 1964 it had been formally constituted under the name of the Village Bee Breeders' Association (VBBA), "Village" being adopted as a descriptive title of the small-colony type of bee the group was interested in. In 1972 the name was changed to the British Isles Bee Breeders' Association (BIBBA) without any change in the original objects, which were "the conservation, restoration, study, selection, and improvement of strains of honeybees of native or near-native type suitable for Britain and Ireland".

Thus began a new phase of contacts with beekeepers in all parts of the British Isles, brought into touch with me and with each other as a result of VBBA and BIBBA publicity, lectures, annual conferences, presence at beekeeping conventions and agricultural shows, and publications. A few names from both before and after the formation of VBBA may now be mentioned. In Norfolk, Major Harold Hitchin, an enthusiast for native bees, devised a simple, logical system of record keeping and colony evaluation from about 1948. Though sceptical I tried his system - and it worked. It stimulated me to devise an improved hive record card incorporating ideas from John Ashton and others, the basis of the present BIBBA version.

In the Midlands, Richard Smailes, a schoolteacher, worked on the study and propagation of local bees up to the time of his death in 1971, one year before that of Terry Theaker. George Gardner of Leicester was a keen exponent of the reintroduction of native types of bee, superseding bees, and minimum handling to obtain good honey yields, as was H. Crowson of Selborne, Hants. George Sommerville who became Northamptonshire County Beekeeping instructor worked closely on a programme of improvement breeding, partly in collaboration with Adrian Waring who was to become his successor. Both have contributed greatly to the running of BIBBA. John Cox worked with me at Shardlow before moving to Gloucestershire.

In Wales, Griff Jenkins was and is a noted breeder and careful propagator of his local bees. In Ireland I found Mike Moynihan keeping native bees successfully on a commercial scale, and many other native apiaries large and small in many parts of the country. The fact that these Irish bees are compatible with English, Welsh and Scottish strains (they can be crossed without giving rise to bad-tempered or otherwise ill-adjusted progeny) made it essential to include Ireland within the compass of our Association.

In Scotland, Captain L. M. Thake contributed valuable experience going back to the days of the restocking scheme after the First World War. Margaret Logan, sometime Assistant Beekeeping Advisor, N. Scotland and based at Inverness, discovered and studied strains of bee resistant to American foulbrood. I was able to verify the characteristics of these strains for myself. Athole Kirkwood of Heather Hills Honey Farm, Perthshire was making a living from native bees in what was Britain's largest commercial beekeeping enterprise. Andrew Scobbie of Fife was also working commercially on a fairly large scale using the rather more prolific native bees of his district. Another Scottish acquaintance who was a careful and observant student of bee behaviour was J. A. Braithwaite.

Many others, far too numerous to mention individually, brought experiences, ideas and expertise of many kinds to help build up a pool of knowledge, and contributed to the running of VBBA and BIBBA. As I recorded in VBBA News-sheet No. 5, my car clocked up 39,000 miles in one year alone, at least three quarters of this being travelled on visits to VBBA members!

Further studies

Over the years I was able to visit other European countries to compare their bees, as well as their ideas and methods, with those of the British Isles. In Belgium, Georges Ledent, Robert Delperee, Father Reginald and others were coming to some conclusions very similar to mine after study of their own native strains, many of which are not so very different from ours[3]. In 1970 M. Louveaux, Director of the French Bee Research Station at Bures-sur-Yvette was kind enough to describe in detail to Georges Ledent and me their important work on the comparative evaluation of honey bee strains in different parts of France[4]. Later, with George Sommerville and others, I paid several visits to Germany to study their massive and highly organised national bee breeding and propagation programme. Fruitful results of these German visits were the participation of German and Dutch scientists and beekeepers in our conference in England, and in 1981 the successful international BIBBA-DIB conference in West Germany[5]. Finally I was fortunate in visiting South Africa in 1979 for the marriage of my son, and was able to study their subspecies of the honeybee at first hand.

The evidence gained from all these travels and encounters was supplemented by the morphological study of thousands of honeybee specimens dating back to the 18th century in the British Museum (Natural History) and in the National Museums in Dublin and Edinburgh. Studies of wing venation of bee samples sent in from all parts of the British Isles in the early years of VBBA enabled maps to be drawn of regional variations in British Isles honeybees at that time. The picture being built up through behavioural studies was being confirmed by these morphological studies, conducted as they were on statistically significant numbers of specimens.

Aims of this book

This book, then, is the fruit of over 40 years of personal activity in the breeding, study and management of bees, and of nearly half that duration of collective activity to the same ends by members of VBBA and BIBBA. Over this working lifetime I have become steadily more convinced that, recent imports apart, a very large proportion of the bees kept all over the British Isles - in many areas, the vast majority - can fairly be called "native" or "near-native". The ever-present forces of natural selection are constantly selecting those forms of these bees which are best fitted to survive in the various environments of these Islands. Those who have studied their needs and devised appropriate styles of management for the bees, instead of trying to fit the bees to the management, have found them labour-saving, economic and highly productive. But native-type bees like bees of any other type will not necessarily serve us well if we neglect them, if we subject them to indiscriminate cross-mating with imported types, or if we impose unsuitable styles of management on them. It is up to us to observe them, to manage them properly, and above all to maintain, extend and improve them by selective breeding, for our own benefit and that of generations to come.

To say this is not to attack or denigrate the bees which have been and are being imported into Britain and Ireland in large numbers. Many of them are excellent bees; particularly in their homelands. Many of them can be made to produce well in most parts of the British Isles; particularly if no expense is spared in looking after them. Some beekeepers, especially in Southeast England and South Wales, may find by observation and experience that imported bees suit them. Well and good - as long as these beekeepers have also observed and experienced bees of native type in an objective spirit, without making use of malicious and pejorative expressions such as "mongrel", or "hybrid"; terms no more or less applicable to the bees of Britain and Ireland than to those of Italy, New Zealand or the USA.

Beekeeping in Britain and Ireland has often been bedevilled by rancorous controversies which have caused irreparable damage. The "hive war" is a good example. At various times in the past (and sometimes today) supporters of one type or group of hives will fill the bee press, occupy lecture time and deliver field demonstrations to promote their favoured hive and decry other types. Needless to say, dogmatism begets counter-dogmatism and is self-perpetuating. Let us not fall into this trap and maintain damaging controversies, based on prejudice, in the shape of a "bee war". We should be prepared to change our hive type to suit different bees or different management systems, or in order to ease interchangeability with the beekeepers with whom we co-operate. Likewise we should be prepared to change our type of bee if, say, we move to a different area where the environment is markedly different, or where the drones of our previous strain would spoil the breeding success of beekeepers in our new area. The Village Bee Breeders' Association was formed in the belief that honeybee evaluation should be based not on prejudice, hearsay, folklore or received opinions but on observable, preferably measurable facts. Some of these facts, and the conclusions I draw from them, are set out in the pages that follow.

CHAPTER TWO

Ecological Genetics

The honeybee as a wild species

As I have mentioned, I came to realise in the course of my studies the value of the science of ecological genetics[1]. This seemed to illuminate the natural history of the honeybee no less than that of the agricultural pests with which I was professionally dealing. Ecological genetics is the study of the genetics of wild populations of animals and plants. "Wild" is here used in a very wide sense to exclude only those situations where man deliberately and successfully determines the genetic makeup of a given population. It includes many domestic or semi-domestic species insofar as their interbreeding and survival is not closely controlled by man, and indeed it includes man himself.

It is possible to keep bees by buying all one's queens from a breeder who has selectively bred them for a range of characteristics. Such bees, of predictable type, have undoubtedly been produced at many times and in many places, though it must be said that they make up only a small proportion of the queens commercially available at any one time. In any case, few beekeepers work in this way. The queens in their hives are augmented and replaced by others in the course of swarming, supersedure and other processes, and the line of least resistance is to retain some or all of these new queens rather than to kill them and go to the expense of buying replacements. Some beekeepers deliberately raise new queens for themselves, either without conscious selection or with the idea of selecting, the results of which are often the opposite of those intended.

Whenever a queen is produced in a beekeeper's hive, she will mate or attempt to do so. Here we come to a major element of "wildness", for she will mate outside the hive with a drone or drones which cannot be guaranteed to be of the beekeeper's choosing. Most beekeepers wash their hands of this problem: surprisingly so, because in fact the choice of mate, though far from 100% controllable, can be significantly influenced by the beekeeper in various ways without too much difficulty. It is this defeatist attitude over the matter of drones which causes beekeepers, many of them experienced and regarded as authorities, to dismiss the idea of bee breeding as a practical possibility.

In addition to the bees kept in hives, most parts of the country support a truly wild or perhaps more accurately feral population of bee colonies in hollow trees, cavities in buildings and suchlike places. These add to the numbers of drones which are flying about in search of queens to mate with, making the prospect of bee breeding, in the minds of many beekeepers, a hopeless one.

I shall return in the next chapter to the subject of this pessimistic attitude, which envisages the bee population of these Islands, left to itself, as a mish-mash of hopelessly mixed "mongrel" types. It is ecological genetics which reveals such notions to be quite wide of the mark. Before turning to this topic, I must mention another aspect of "wildness" which is of the utmost importance, though often ignored. This is the fact that the honeybee is continually exposed to, and heavily influenced by selection. True, a part of this selection is provided by the beekeeper's management. He may feed his bees, divide and unite his colonies, move them from place to place and subject them to all sorts of other treatments. Some of these management actions may cancel each other out in terms of the overall population; others may have profound effects on the bees, though often not ones envisaged by the beekeeper. Even allowing for management, however, the bee colony is continually being tested by its natural environment. The chief facet of this is undoubtedly climate. Temperature, humidity, rainfall and solar radiation affect not only the bees as they try to maintain their nest environment and fly around in search of food or mates, but also the type, growth, flowering and nectar secretion of their foodplants. So much so that it has been rightly remarked that of all the agricultural products of the British Isles, the one most dependent on the weather is honey.

From the point of view of the honeybee species, honey production is only an aspect (though a highly important one) of the larger question of survival. In the British Isles the honeybee is on the edge, or more likely, well beyond the edge, of its natural geographical range. Our environment is an extremely harsh one for the species. In any environment, but particularly in such a harsh one, unfit types are rapidly eliminated. Some types are more fitted to survive and reproduce than others. Most people will acknowledge the obviousness of this fact: few are prepared to explore its consequences. Add to this the equally easily acknowledged tendency for offspring to resemble their parents to a certain degree, and the whole of ecological genetics follows.

Variation

A member of a species differs from members of any other species: it also differs from all other members of its own species, so that every individual is unique. This difference is technically known as variation, and is a result of three things: 1. Age: the difference between two individuals at different stages in their developments; 2. Heredity or genetics; and 3. The environment, whether present or past. For our purposes variation is considered to be the result of a combination of heredity and environment.

For purposes of study, variation is broken up into what are called characters, which can be more or less precisely defined and measured. These include the physical or morphological, such as body size, colour, presence or length of hair; the physiological, such as enzyme or pheromone secretion; and the behavioural, such as readiness to sting or to collect propolis. No character can be said to be purely hereditary or to be purely environmental;

all bees will cluster as temperatures fall, but the precise temperature at which they will do so is determined genetically.

Chromosomes and genes

The physical and chemical basis of genetics has been well described in many books and cannot be gone into here[2]. In any case a detailed familiarity with it is not necessary to the practical bee breeder. A few of the technical terms may usefully be defined, however.

Any organism, including a honeybee, is made up of many small units called cells. Every cell contains a number of minute, elongated bodies known as chromosomes. A female honeybee, whether worker or queen, has two matching sets of these (sixteen in each set), one set originating from her mother, the other from her father. A peculiarity of the honeybee, shared with a few other organisms, is that the male or drone possesses only one set of chromosomes in each cell, derived from his mother. This condition is known as haploidy as distinct from the more usual diploidy of the females.

Along the chromosomes are strung large numbers of small particles called genes. It is these which, by controlling the synthesis of chemicals, control the growth of the individual, thereby determining the genetic or heritable part of its variation. In the queen and worker, the two corresponding genes - one on each chromosome set - will act in combination. In the drone, each gene will act alone, unaffected by any matching gene.

What is the relation between genes and characters? It is a complex one. For each pair of genes may, and usually does, have an influence on many different characters, while conversely each character may be, and usually is, affected by many different genes. As there are thousands of genes in an organism such as the honeybee, one cannot hope to untangle all the interrelationships. Nevertheless the problem is not a hopeless one; much useful information can be retrieved from this complexity.

Alleles, dominants and recessives

Each gene, in the sense of the particle occupying a given spot on a chromosome, may have two or more alternative forms, known as alleles. Genes with eight or ten or more different alleles are by no means uncommon. Let us consider a point on a chromosome whose gene has six alleles. A queen or worker will have two examples of the chromosome in question (one from each set). She might have two similar alleles of the gene; i.e. two of allele No. 1, two of No. 2, or two of No. 3, and so on. In any of these cases the queen or worker is said to be homozygous for that gene. Alternatively she may have two dissimilar alleles; Nos. 1 and 2, 2 and 5, 4 and 6 or any other combination. In all such cases the queen or worker is said to be heterozygous for the gene in question. The drone, however, has no possibility of being heterozygous, since he has only one example of the gene in question. He may have any one of the six alleles.

In a heterozygous queen or worker various effects may be observed. Imagine a hypothetical gene with an allele 1 which produces large body size and an allele 2 producing small body size. Homozygotes for allele 1 will be large; those for allele 2 will be small. Heterozygotes with alleles 1 and 2 may be medium-sized, but we should not be surprised if we find that they are all large or, alternatively, all small. It they are all large, we say that allele 1 is dominant and allele 2 is recessive to it. If they are all small, then allele 1 is recessive, allele 2 dominant. (Strictly speaking, it is the effects of the alleles which are dominant, intermediate or recessive. A given allele may be dominant in its effect on one character, recessive in its effect on another.) In the drone, of course, there is no question of dominance or recessiveness.

When an egg cell is produced in a queen's ovaries, it loses one of its sets of chromosomes. In female offspring the double set is restored by union with a sperm cell from the drone. Now a recessive allele, whose effect was completely masked in the mother, is in no way destroyed or diluted by the fact of its being recessive. It has in principle as good a chance of being passed on in an egg cell as any other allele of the same gene. If it meets with a similar allele in the sperm, the resultant queen or worker will be homozygous for it. Or it may meet an allele to which it is dominant, or one with which it produces an intermediate character.

Thus "mongrelisation" as some are wont to call the crossing of different bees, does not destroy the alleles; and therefore it does not destroy the types of character that these will produce.

Gene frequencies

If we know how common different alleles are in relation to one another, we can easily calculate the number of heterozygote and homozygote individuals in the population, and vice versa. Consider a large population of individuals who breed at random among each other. Suppose that one of their genes exists in two different alleles, which are equally common. It is easily shown mathematically that at any one time half the individuals will be heterozygotes for that gene, a quarter will be homozygotes for one of its alleles, and a quarter will be homozygotes for the other. Moreover, other things being equal, all these proportions will remain the same through successive generations. Ecological genetics is really only the extension of this principle to ever more complex situations.

Of course, other things never are equal. The relative frequency between alleles may be upset or altered in various ways, generally reckoned to be five in number. These are:

1. Very small population size. In a small population, statistical peculiarities may lead to the elimination of certain alleles. To take an extreme example, if a population which had a gene with ten alleles was suddenly reduced to a breeding population of one male and one female, the maximum possible number of alleles would be reduced to four in most species, or three in the

honeybee. Also, in small populations allele frequency may fluctuate from one generation to the next in a process known as "genetic drift".

2. Mutation. At very rare intervals, any allele is liable to mutate or change into a different one. This is presumably how all the different alleles arose in the first place.

3. Migration of individuals between isolated or semi-isolated populations may change the gene frequency by the process of "gene flow". In honeybee terms this could result from the importation of foreign strains into the British Isles, or from the moving of bees around within them.

4. Mating choice. In many species, mating is not at random. Mechanisms have been developed to divide the population up into groups whereby mating is more likely or more successful between groups rather than within the same group, or vice versa. Sex is the most obvious, but there are many others. The phenomenon of "alternative mating behaviour" in the honeybee, to be discussed in later chapters, is a case in point.

5. Natural selection. This is popularly known as "survival of the fittest". The variation in the characters controlled by the different alleles of a gene confers different degrees of "fitness" on the individuals. It is not in fact simply survival which counts, but success in reproduction. Thus the "fitter" allele will tend to become commoner in successive generations at the expense of the less fit, until a new balance is reached between contending advantages and disadvantages. Some alleles act almost wholly genetically in that they prevent their individuals from developing at all, and are known as "lethal". In most cases, however, the concept of fitness is meaningless without reference to the environment. An individual which is fit for one environment may not be fit for another.

Much controversy has surrounded the question of the relative importance of these five factors. We cannot enter these arguments here. I shall simply state that my own experience leads me to agree with the large body of scientific opinion which stresses the overwhelming importance of No. 5, natural selection. Compared with natural selection the influence of the other four factors, though certainly not absent, is reduced to insignificance in the medium or long term. No. 4, mating choice, can be important, but insofar as "alternative mating behaviour" in the honeybee is concerned (see Chapter 5), it is ultimately produced as a result of past natural selection.

Natural selection

It used to be thought that the difference in fitness conferred by different alleles, or their selective advantage or disadvantage, was typically very small, say 1% or less. Even now some scientists believe that many alleles are essentially neutral in survival value. Many more recent studies have shown, however, selective advantages of 25%, 50% and more operating. Leading workers in the subject now regard such levels as normal, and my experience would certainly confirm this. Such levels are not only a powerful means of retaining genetic stability in a population in the face of factors Nos. 1 to 4 above; they also enable a population to respond very quickly - within two or three generations - to changes in the environment.

Genetic variability

The pressures exerted by natural selection, or for that matter those exerted by the other four factors, do not lead to a population which is genetically uniform, i.e. one where each gene has only one allele. The importance of this fact is difficult to overestimate. It is to the "advantage" of a population, in the sense of increasing its chances of survival, that it should be somewhat variable. Why should this be so? One answer is, because its environment is variable. It changes both in space and in time. A population with a degree of variability will be able to adjust to temporal and spatial variation by altering the proportions of genetically different individuals as appropriate. The interplay between swarming and supersedure in the honeybee, to be discussed in Chapter 4, is a good example. The characters concerned are the product of many genes, but this does not alter the principle. By having a variable system of queen replacement, the honeybee population of the British Isles is able to exist in greater numbers and in more environments, and to maintain its numbers better in years of varying weather, than would otherwise be the case.

Another reason for variability arises out of the genetic mechanisms themselves. It often happens, for example, that heterozygotes are fitter than either homozygote. But the existence of heterozygotes necessarily implies the existence of homozygotes. Thus the cost to the population of including relatively unfit homozygotes may be a price worth paying for the increased fitness of the heterozygotes. A classic example of this is in certain human populations in malarial areas of Africa. Heterozygotes for a particular gene are resistant to a certain type of malaria. One set of homozygotes is rather susceptible to malaria, whereas the other set die in early life from anaemia. This is tough luck on the homozygotes, but more of them will inevitably be produced even when heterozygotes breed among themselves.

Geographical races

Since the environment in different parts of a population's range will vary, there will be a certain tendency for the genetic makeup of the population to vary along with it, because of natural selection. This may lead to a gradual change in one or more characters over a distance, which is known as a "cline". If parts of the population are partly or wholly isolated from each other, this will tend towards the evolution of distinct races, each with a distinct gene-complex, because there will be little or no "gene-flow" from one area to another. As will be discussed later, isolation may be geographical, but it can also be ecological, splitting the population of a single area into two or more groups which coexist but do not freely interbreed.

It is also possible for distinct geographical races to evolve in the absence of physical isolation. Sometimes one geographical race gives way suddenly to another along a well-marked line, which seems to correspond to no sharp environmental change. Examples are the carrion and hooded crows in Scotland, two races of mice in Denmark, and two races of the meadow brown butterfly in Cornwall. In these cases each race seems to have evolved a distinct gene-complex suited to the average conditions prevailing in its area. Because of the genetic disparity between the races, hybrids between them are likely to be ill-adjusted and heavily selected against. An individual migrating into the area of the other race will mate, if at all, with a member of the other race and its hybrid offspring will be unlikely to pass on the genes of the migrant's race.

Polymorphism

Some characters are subject to continuous variation. Human beings, for example, vary continuously in height, most people being somewhere near the average. Such is commonly the case with characters controlled by many genes. Others, however, vary discontinuously. Thus human eye colour may be blue or brown, but not intermediate. The blood groups are another good example. Such phenomena are known as polymorphisms, and are commonly controlled by one or a few genes.

The concept of polymorphism is of the utmost importance. The term was coined by E.B. Ford, who defined it as, "the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation." Ford is a distinguished lepidopterist, and much work on polymorphisms has resulted from studies of butterflies and moths. This is partly because their conspicuous wing patterns make the recognition of physical polymorphisms easy. Polymorphisms may also be physiological or behavioural, however.

To quote from Ford again, most polymorphisms are " 'balanced', being determined by contending advantages and disadvantages at a level determined by the relative strength of the opposing selective forces to which they are subject. Thus they ensure permanent diversity . . .". The most obvious and widespread polymorphism is sex, which is determined genetically and divides a species up into two distinct forms.

A classic study of polymorphism was carried out by Kettlewell on the peppered moth in Britain. This (to oversimplify) has a gene with two alleles. One of these alleles produces whitish wings when homozygous, the other, black wings. Since the "black" allele is dominant, the heterozygote is black in appearance. It is also much hardier than the white homozygote, and slightly hardier than the black one.

During the nineteenth century industrialisation of certain areas led to the blackening of the tree trunks on which the moth rests. Between 1848 and

1895 the proportion of black moths observed rose from zero to 98% in the Manchester area. In the most unpolluted areas, such as Cornwall, it remained zero, and in intermediate areas it reached an intermediate frequency. The main factor in this process was natural selection by predation of the moths by birds as they rested on tree trunks. In industrial areas the white form is more conspicuous, while in non-industrial areas the black form is more conspicuous. The extra hardiness of the heterozygote also played a part, as it very often does in polymorphisms.

The malaria-resistance example referred to above is another good example of a polymorphism, controlled by an allele which influences the form of the red blood cells.

Practical implications

What are the lessons of ecological genetics for the bee breeder? First perhaps is that the honeybees of the British Isles are likely to have evolved a range of forms and types suited to the varying environments of the region. These forms and types can be expected to be basically stable genetically, while yet retaining enough variation to cope with the sort of changes that are experienced here. Natural selection will be constantly keeping these forms adapted to their local environments. It will be much easier to work along with natural selection, modifying it slightly where necessary and feasible, than to work against it.

Secondly, the importation of foreign bees may not necessarily have the destructive genetic effect that many people have supposed. Native types may have all sorts of mechanisms for effectively isolating themselves genetically from the immigrants. Hybrids between the two may sometimes be self-eliminating in the long run. Above all, alleles belonging to or derived from imported bees will be ferociously selected against if they render their possessors less fit than those possessing "native" alleles. (One can even go so far as to say that if all bees were wiped out in these Islands, and then replaced by imported bees - preferably ones with plenty of variation - then the new bees could turn themselves within a few generations into something resembling the extinct natives.)

These theoretical predictions have in my experience all been confirmed in practice, and I shall develop many of these themes during the course of the present work.

CHAPTER THREE

Native Bees

Definition

In many examples of the ecological genetics of polymorphisms such as I have touched upon in the previous chapter, the different forms of the species concerned are quite easily recognised and defined, often with reference to only one character. Their very ease of recognition is the reason why they were chosen by geneticists for their studies. At a different taxonomic level, the definition of a species, though not always without problems, is also relatively simple. In comparison, forms of the nature of subspecies, breeds, races and strains vary in many different characters, are capable of interbreeding, and moreover change through time. It is often impossible to define them without generalisation or without using criteria which are differences of degree rather than of kind. This is particularly so in wild species or in those which, like the honeybee, have been kept by man but not consciously selected to an intensive level. This makes it difficult to avoid a degree of apparent confusion and vagueness in the discussion of all such forms (races, breeds, etc.) in between the level of species on the one hand and single-character variants on the other. The confusion is largely man-made. The biological data are complex: language does not affect the reality of the data. Races, breeds and subspecies may be real biological entities despite the inadequacy of our efforts to define them accurately.

During my forty years of handling and comparing bees I have become convinced that what we have at different times called "native" or "village" bees are indeed such a real entity. If we recognise the northwest European native bees as species *Apis mellifera,* subspecies *mellifera,* then the native bees of the British Isles can be regarded as a closely-related group of strains of this subspecies. In theory they are descended from the bees present here before about 1850. One convenient way of defining such a group of strains in practice is as a "temperament group", within which strains may be freely crossed without the creation of ill-adapted gene complexes, one very noticeable result of which is bad temper.

The situation is of course complicated by the fact that large numbers of bees of foreign types, of both *mellifera* and other subspecies, have been imported into the British Isles since the mid-nineteenth century. I shall speak of the actual effects of these importations later; for the moment it must be realised that at any given time there is a great diversity of bees present in these islands, from "pure" natives through crosses and hybrids to "pure" imported strains. This complicates the problems of definition. In forming VBBA to work towards the conservation and restoration of the bees native to these Islands, we had to accept that we would be dealing with a fairly wide range of types. They will range from 1. pure native strains which as far as we can tell are uncontaminated by characters of foreign origin to 2. bees that have been crossed, but which have been reselected back to their previous form. The former are native, and the latter are near-native bees. For these two groups we coined, back in 1963, the collective name of "Village Bees". The word "village" was chosen by allusion to the human village, a small community. Non-prolificacy with its attendant longevity was clearly a more meaningful indication of nativeness than the more widely used expression of colour, i.e. "black bees"; many overseas strains are darkly pigmented, but differ widely from village bees by their greater prolificacy.

In short, village bees are our British, Irish, Manx, Channel Island native bees and such other bees of subspecies *mellifera,* the dark bee of Western Europe, as show most of the characters of the native. It is profitless to engage in argument as to the "purity" of a strain; if it does what we expect the native to do and is compatible with the native, it matters little if it is derived from hybrid ancestors. Apiculturally, behavioural characters are far more important than morphological ones, and we must guard against the obsession with "race", ancestry and appearance. Biometric characters are useful in telling us where we have come from, but behavioural characters must guide where we should be going to.

Native characters

In the inaugural policy document, Bulletin No. 1 of VBBA (June 1964) we described many of the behavioural characters that we wanted to work for. In VBBA News-sheet No. 5 (September 1966) we listed ten characters as being diagnostic of our native bees. We there stated that if a strain of bee showed nine or ten of them it was a good village bee; one with eight was passable; one with seven had some way to go before meeting our standard as a village bee, but could still be acceptable to a high proportion of beekeepers, and should merit efforts to maintain and improve it. Thus we felt we could accept a yellow-banded bee needing one and a half British Standard boxes or one Modified Commercial broodbox if it showed the other eight characters.

In VBBA Leaflet 7 *Village Bees: the Native and Near-native Bees of Britain and Ireland,* the list of characters was extended to four physical and eleven behavioural. Twelve of these were reckoned to make a good village bee; a bee with ten being probably worth persevering with if possessing some special attributes to commend it enough to give it a chance of being bred into a village bee.

I now offer a list of six groups of characters, 23 in all, which are diagnostic of truly native bees. It is worth pointing out again that most if not all these characters can be found in honeybees of other countries. It is the combination of all or most of these characters together which makes a native British Isles bee.

A. Physical characters.
1. Bees "black".
2. Long abdominal overhairs.
3. Characteristic wing type.
4. Genetically large size.

B. Behavioural characters.
a) Flight pattern characters.
5. Low temperature flight.
6. Non-collection of dew at dawn.
7. Reluctance to fly when snow lying.

b) Colony population characters.
8. Longevity.
9. Non-prolificacy.

c) Characters adaptive to season and locality.
10. Heavy spring to summer pollen storage.
11. Heavy late summer pollen storage.
12. Early cessation of brood rearing in late summer.
13. Thriftiness.
14. Adaptation to local flora.
15. Tight winter clustering near hive entrance.

d) Nest characters.
16. Comb honey cappings white and convex.
17. Compact brood pattern.
18. Compact honey storage pattern.
19. Fluctuating broodnest temperature.

e) Characters affecting mating and interbreeding.
20. Minimal drifting.
21. Drones expelled earlier.
22. Alternative mating behaviour.
23. Temperament compatible with other native bees.

A. Physical characters

These characters aid survival in cool, windy conditions in accordance with several well-known general biological "laws".

1. BEES "BLACK". The typical native bee possesses dark pigmentation on the dorsal side of the abdomen. The actual colour varies from brown to jet black. Some strains are dark ventrally but this is by no means universal: bees from the East Coast of England invariably have a touch of yellow beneath, a character noted also in preserved specimens of bees from these

same areas dating from the early 19th century. Sometimes, particularly in southern strains, one finds bees with an orange or yellow spot on each side of the first, and sometimes the second abdominal tergite (a character mimicked by the hoverfly *Eristalis tenax).* In evaluating colonies for "colour" we have adopted the convention that such bees are "dark", while a bee with one or more tergites which are yellow right across is "yellow".

Colour of tomenta, which are usually narrow, of abdominal overhairs and of thoracic hairs is variable. Queens, though often very dark, may-like those of non-native types - be distinctly lighter overall than their own workers and drones. They sometimes have what we call "ginger" bands right across one or more abdominal tergites, and reddish legs.

Theoretically the honeybee is within the range of body size within which melanism (dark pigmentation) should make a big difference in body temperature through absorption of heat from solar radiation[1]. Such practical tests of this as have been made support this view.

To test the point, some years ago we did some trials with the local Boston (Lines.) black pigmented bee, and with the Brother Adam (Buckfast, Devon) yellow unpigmented bee. It had been noticed that the Brother Adam bees in May were sitting around in the sun chilled on days when the black bees were working turnipseed strongly with no sign of chilling in air at 7.2 degrees C (45 degrees F).

Worker bees were taken from the feedhole of each hive in the morning when the air temperature was 40 degrees F (4.4 degrees C) and the day dull and damp. Six bees from each hive were doused in cold tap water and then tethered with cotton to a board placed near the open window of the unheated laboratory. A 750 watt silica rod infra-red heater was placed about eight feet from the board, facing the bees, and timings made till the bees became active enough to try to fly. It was found on average the black bees flew in 19 minutes (range 12-29 minutes) and the yellow bees flew in 55 minutes (range 33-78 minutes). Whether this was due to pigmentation or to the inherent temperature requirements of the two strains is not known, but it certainly appeared as if the black bees became dry, as well as active, sooner than the yellow bees.

It was apparent in further observations that drones flying in an apiary in Lincolnshire on a sunny day with an ambient air temperature of 52 degrees F (11 degrees C) were all of the black pigmented native types, whereas yellow banded drones soon returned to their hive despite bright sun. Following this, K. Cena and J. A. Clark of Nottingham University measured with an Aga Thermovision camera the thoracic and abdominal temperature of dark and light bees leaving and returning to their hives in various intensities of solar radiation. They found that the radiation variation made differences of up to 6 degrees C to the temperature of the returning bees. The hottest black bees were warmer than the hottest light bees, and in wind tunnel tests, dark bees were 1 degree C hotter than light bees, even though the difference in pigmentation in these particular bees was not great[2].

Experiments by A. Sotavalta and others have shown that before flight, a honeybee raises its thoracic temperature to 10 or even 20 degrees C above that of the air, by "pumping" its wing muscles[3]. Absorption of heat from solar radiation during flight could be crucial in maintaining this temperature differential in some circumstances. Dark colour must assist the bee in keeping warm outside the hive in sunny but cool or windy weather, or even on dull days with high energy radiation; it also aids it in drying out after rain. Dark pigmentation is naturally selected for at times of stress by sheer survival of colonies as a result of workers bringing in more pollen or nectar, as well as by better pollen supplies enabling the production of more drones and queens. But the greatest selection for dark colour is via the ability of dark drones to fly to mate in cool air. I would estimate that in cool or average years this gives a preferential advantage to dark drones over perhaps half of the flying hours in favourable Southern English and Southern Irish conditions, and probably over 95% of flying hours in cooler and more windy situations. 1974 was such a year. In exceptionally hot, sunny years such as 1975 or 1976 this advantage may disappear (in fact, very dark bees could become too hot to fly in the middle of the day), but in most years the overall selective advantage of dark colour is of the order of 5-10%.

These effects of dark coloration are further discussed under character No. 5 below.

2. LONG ABDOMINAL OVERHA1RS. These hairs average 40% longer than those of what we are sold as "Italian" bees. This would appear to assist pollen collection in wet, cool or windy weather. They probably also have a tactile function, for example in the drone. Air trapped in the longer hair cover may also create a broader "flight envelope", to use an aeronautical term, resulting in lower heat loss, thus reinforcing the effect of dark coloration.

3. CHARACTERISTIC WING TYPE. Studies of the pattern of veins on the forewings of bees from many parts of the British Isles have been carried out along the lines of similar work in Germany and France[4]. Venation shows a characteristic negative discoidal index and low cubital index. This seems to be linked with strong thoracic wing muscles and an ability to gather very large pollen loads and probably therefore nectar loads also. In these Islands sugar concentration in nectar is often low in summer and a larger volume has to compensate for this low concentration. These wing characteristics seem to be associated with a slower flight speed and a greater tendency to rest on the journey home, but also a greater staying power in combating strong winds, than those of Italian and Carniolan types of bee we have studied.

4. GENETICALLY LARGE SIZE. When given large cell foundation of 700 cells per square decimetre instead of the "standard" type (850 or 800) normally sold in the British Isles, native strains produce appreciably larger bees, with wing length and breadth 5-10% greater than the same strains kept

on standard foundation. Italian and Carniolan strains tested respond little in this way: i.e. they appear to be full-sized on 850 or 800 comb already and some types such as the Buckfast Israeli bees of the 1960s are evidently amply stretched already. In a great many cases these bees produce drones in 700 cell comb, and they are clearly genetically smaller bees.

While all bees appear to prefer the cell size they were brought up on, and need some coaxing to work a new foundation size, just as they may need coaxing into sections, once they have made the change all the native strains so far tested have preferred the larger foundation. When native bees reared on 700 comb are allowed to build their own comb without guidance, they build appreciably larger than 850: usually 720-750. The 700 size seems a good one to start with for native strains, to allow for winter shrinkage of the comb and cocoon narrowing of the cell aperture.

It is interesting that most Belgian beekeepers employ 700 or 750 foundation, while a few, using strains very similar to some British Isles bees, have found no difficulty with foundation as large as 640!

Larger body size must tend to reduce heat loss and is probably associated with larger (if more dilute) nectar loads. The smaller, faster-flying strains from hotter, drier climates may find that with more concentrated nectar it pays to make more but shorter journeys. At any rate observation shows that native colonies, with few bees on the wing, can put honey into supers as fast during a honey flow as can much more populous Italian colonies.

B. Behavioural characters

a) FLIGHT PATTERN CHARACTERS

5. LOW TEMPERATURE FLIGHT. Doubtless dark coloration is one factor in this character, but not the only one. The character can apply in different ways to i) workers, ii) drones, and iii) queens. While many continental-climate worker bees will come out very early in the day to gather dew, pollen loads can only be gathered in cool air by workers which have this low temperature characteristic. Workers flying in bright sun should be able to gather pollen at 5.5 degrees C (42 degrees F) shade temperature in still air, or 7 degrees C (45 degrees F) in a 16 k.p.h. (10 m.p.h.) wind in a suitable site between February and May.

Drones should show a flight threshold of 8 degrees C (46 degrees F) (bright sun) or 9 degrees C (48 degrees F) in half sun in April or May. Queens also show this cool but bright weather adaptability: native queens have been known to fly and mate at 9 degrees C (48 degrees F). Queens that fail to pair in cool weather or which fail to mate fully at a season when suitable drones are available (i.e. become short-lived worker-layers) may have done so because they are not suited to our climate, and a strain producing them should be suspect. In the main this character is self-eliminating in a cool summer.

(N.B. This character is not diagnostic when the bees are in winter cluster.

In such conditions native strains fly less than other - higher-temperature - types of bee.)

6. NON-COLLECTION OF DEW AT DAWN. Bees can drink from puddle margins or dewdrops at considerably lower temperatures than they can forage for nectar or pollen. Strains of bee from sunnier climates than our own get busy very early on a summer morning gathering dew, well before sunrise. This behaviour is presumably related to conditions in their country of origin where water for cooling the hive as well as for brood rearing is likely to evaporate quickly as the sun rises and as the daytime winds rise. Our climate does not require such a habit and our native bees therefore tend to start their water-gathering later in the day, preferring nectar to water where it can be had. Our nectars tend to be more dilute than those of hot sunny climates, too, so that it saves work not to bring unnecessary water into the hive if that can be avoided. It is only when native stocks have been confined by bad weather and are already starved of moisture that early water collection is seen. I presume that in our climate dew remains on the herbage in fine weather until so late in the day that selective pressure in favour of early dew collection is absent.

7. RELUCTANCE TO FLY WHEN SNOW IS LYING. Native strains are seldom tempted to fly on sunny days in winter when snow is lying on the ground and high solar radiation warms the hive and enables individual bees to gain enough heat to fly. Many foreign strains are stimulated by these conditions and by the high level of reflected light to waste energy in flight, in many cases only to land on the snow where they become chilled and die.

The mechanism producing this effect is not known. However, according to one American account, dark bees of an Anatolian strain were able to fly and work in greenhouses made of glass fibre opaque to ultra-violet light, while other bees would not, though they behaved normally under glass. This suggests that there are strain differences in sensitivity to and dependence on ultra-violet light. The character could however be a by-product of No. 15 below.

b) COLONY POPULATION CHARACTERS

8. LONGEVITY. If 100 workers are marked in May, some can still be found ten weeks later, in an average summer. Strains with long-lived workers also tend to beget long-lived queens. Queens of any native strain should live for 36 months in full production, and those of the better strains should live for 48-60 months when kept on a single BS broodbox. If kept in a smallish colony, as in breeding or propagation work, they occasionally last much longer. This is of great value in monostrain formation, in progeny testing, and in allowing years in which their unsatisfactory offspring may be culled when hot weather has led to cross-mating with drones of high-temperature strains of bee. Longevity is the mechanism by which bees kept in hives with relatively small broodboxes manage to get such large honey crops in poor as well as in good seasons. It is the long-lived bee which builds up to a

populous colony at the season of maximal honeyflow, which shows the need for prolificacy to be false.

9. NON-PROLIFICACY. Strains from the less well-favoured parts of the British Isles should be able to do well, i.e. winter safely, gather honey well and swarm little, when confined to 10 or 11 BS broodcombs by a queen excluder. If the bees are allowed free range they would not normally place brood in more than 14 BS broodcombs (or equivalent number in larger or smaller frame sizes), though there may be a tendency to scatter during a strong pollen - or honeyflow. Inbred stocks commonly show less vigour than this, but regain prolificacy on outcrossing with another native strain.

There is no point in looking for a bee which is less prolific than needed to fill one National or Smith broodbox. The merit of this size is to minimise labour of transport to sources of forage or to crop pollination, and particularly the effort of lifting heavy weights. Whatever the strain of bee, it is always desirable for honey production to utilise a strong colony of the strain. This is not a recommendation to utilise a prolific bee, which tends to consume more food in poor weather and to need more management attention. Our climate requires populous bees with a high bee to brood ratio, and not prolificacy.

c) CHARACTERS ADAPTIVE TO SEASON AND LOCALITY

10. HEAVY SPRING TO SUMMER POLLEN STORAGE. Native bees in spring and summer store enough pollen during a good pollen flow to last 2-3 weeks, whereas Italians and most other non-native types tend to store only enough for 3-6 days. Ability to withstand siege by bad weather is a most important virtue. There is a characteristic pollen storage pattern on the comb face: native bees during such a flow will place pollen in any convenient cell, even amongst hatching brood, and will if space permits store below the brood; non-native types tend to store in an arc 2—3 cells wide, around the brood sphere to the sides and above (except on the outer combs), but not below. This may be a character selected by the exporters to this country, and not typical of overseas bees generally, but it is a noticeable distinction from our best native strains. To an apiarist with native bees, a "nice comb of brood" is a very different thing from what the apiarist conditioned to seeing Italian strains of bee is looking for.

11. HEAVY LATE SUMMER POLLEN STORAGE. Pollen stockpiling commences after midsummer, earlier than with overseas types of bee. By September the bees tend to reduce their flight activity and unless they are fed, tend to gather less pollen in late autumn. Nearly all of this late summer pollen is eaten by early October, even though the bees have ceased raising brood in August; though a cold or wet autumn may sometimes curtail consumption, so that one finds unused pollen stores in springtime. Clearly the bees prefer to eat the pollen when weather will allow cleansing flights to rid their gut of pollen waste. There is a tendency for native bees to have less waste dry pollen to throw out in springtime, unless late feeding has been

carried out. There is evidence that native bees winter to a much greater extent on fat, stored in the adult bee's fat-body, than do overseas strains; this is probably the basis of their well-known virtue of wintering on a minimum of honey or fed sugar stores. Selection takes place during prolonged cold spells, when clusters may get cut off from stores in another part of the hive; bees with the fat-wintering habit can wait for many weeks till a warm break enables them to move over safely.

12. EARLY CESSATION OF BROOD-REARING IN LATE SUMMER. This is closely related to the last character, and is evidently part of the mechanism by which native bees build up their body fat supplies, which would otherwise be expended in brood-rearing. The fat appears to be derived from oily pollens eaten at the time of reducing brood-rearing. August-fed sugar is stored without being turned into brood and the brood area contracted downwards. Most of the imported strains freely raise brood on late summer feeding. Conversely, native bees which have entered winter cluster may fail to cap over sugar fed in September or October if the weather is cold. Late feeding, however, still tends to stimulate late pollen collection if flora and weather permit. The character of early cessation of brood-rearing more than any other confers ability to winter on minimum stores.

13. THRIFT1NESS. This is the ability of a colony to adjust its breeding rate to its income and stores. While all European bees show this attribute to some extent, it is especially noticeable in British Isles strains. Some imported strains, and hybrids between them and natives, will breed flat out in spring and summer regardless of honeyflows or stores in the hive, usually dying out in the absence of a honeyflow if not fed by the beekeeper. Of all characters, thriftiness is one of the most easily lost by an over-solicitous beekeeper, and the most strongly selected for by let-alone management systems. Many good native strains are very slow to build up in spring in the absence of a honeyflow but quickly make up for lost time as soon as the nectar is coming in in quantity. Conversely they will drastically curtail brood-rearing in a nectar dearth if stores in the hive fall below a critical point, often as high as 9 kg (20 lbs).

14. ADAPTATION TO LOCAL FLORA. This is a character which varies considerably within the British Isles. Analysis of the honey diastase component by electrophoresis has shown that different strains of bee apply different salivary enzymes to nectars. This would help to explain the well-known variation in ability to winter on heather honey and honeydew. Local strains are adapted to digest honey and pollen from their local flora and will seek out nectar of their local types preferentially. In general, most British Isles strains are avid collectors of early pollens and nectars: alder, poplar and particularly willow. Like many Central European strains they are mostly assiduous in collecting honeydew and winter well on it, in marked contrast to bees of Mediterranean parentage from countries where poisonous honeydews occur. Native strains are poisoned by certain types of

rhododendron nectar and avoid them; they are also noticeably less attracted than Italian-type bees to red clover.

Many native strains are keen collectors of propolis, especially in districts where this is scarce. This trait, which confers a degree of resistance to nosema (especially when combined with the "varnishing" habit) also varies considerably with district, however.

15. TIGHT WINTER CLUSTERING NEAR HIVE ENTRANCE. Native bees tend to cluster up for winter early. The clusters are exceptionally tight and quiet, and tend to break up late. Surprisingly small clusters, if healthy, are capable of wintering through the coldest spells, although they may fail after a wet autumn when uncapped or late-fed stores remain in the hive. Where an Italian strain would die in winter with a moderate-sized cluster, despite adequate food around it, a very much smaller native cluster can survive with vigour.

Most native strains in the autumn go into winter cluster at the front of the hive. The drier conditions near the entrance and increased opportunities for cleansing flights presumably reduce the risk of dysentery, nosema and perhaps other diseases.

Particularly in the matter of tightness and size of cluster there are big variations between strains. It could be argued that this may represent degrees of introgression of behaviour patterns derived from bees of more southern type; for instance in parts of Scotland where French bees have been imported for many years in large numbers, clusters have been noticed to be less tight, with a larger minimum winter cluster size threshold, compared with districts where no such introductions have been made. The same can be said of areas of recent Italian introductions.

Against this, however, is the striking gradation or cline from coastal areas inland, and from south to north in both Ireland and Britain, and from lowland to mountain areas, in a pattern quite unlike that of importation scatter and clearly related to differences of selective pressure having acted for a long period upon bees of different environments. In the South of England and in the more populous and intensive beekeeping areas, importation and introgression have clearly had an influence, while generally in Scotland and Ireland, as well as Central and Northern England and Wales, the selective survival of advantageous characters has been the principal influence.

d) NEST CHARACTERS

16. COMB HONEY CAPPINGS WHITE AND CONVEX. The convexity is seen not only on the less permeable cappings of stored honey but also in the more porous cappings of worker and drone brood cells. In the honey storage area, such comb holds a small air layer between the underside of the capping and the upper surface of the honey, giving the capped comb a bright and, to honey connoisseurs, pleasing appearance. Cappings of many native strains start convex but later become dimpled, possibly by pressure of crowded bees jostling over them.

Natural selection for this character takes place when an early autumn curtails capping, and damp weather initiates fermentation and honey expansion within the cells. With mites carrying yeasts onto the weeping cappings, bees develop severe dysentery from the alcoholic smears. Cells with a spacious air cell beneath each capping are protected from weeping to a much greater extent than are cells beneath flatter cappings. Stocks with fermenting weeping honey tend to suffer severely in moist locations and mild and damp winters, or ones with few opportunities for cleansing flights. Under severe stress, they tend to die out preferentially, as in the winter of 1962—3 which culled heavily in favour of bees producing convex cappings. Winter cull of this type is more severe in bees which have been to the heather where flat-capping bees tend to suffer in most years from winter dysentery due to this cause, but convex-capping bees only suffer in the specially severe winter.

This character is linked with "cool air clustering" of bees on a comb being examined in still air below about 10 degrees C (50 degrees F) or somewhat higher in a wind. This is a behaviour pattern which enables numbers of bees to keep warm in cool air. It is particularly valuable when wax is being secreted for comb building or capping, and is a great asset in comb honey production. Young bees noticeably respond to cool air in this way, old bees in the same colony less so.

Cool air clustering is not easy at first to distinguish from "running". However the latter is quite distinct: running is done in warm weather too, and particularly under the influence of smoke or drumming. It is found in bees from areas where driving used to be practised, being especially of advantage to the driver of skep bees.

Cool air clustering enables bees to continue wax building and capping on cold nights; if coupled with a tall broodnest pattern (sometimes pejoratively called "chimney brood"), it helps to avoid chilling of peripheral brood on cold spring nights, and seems to minimise losses from chalk brood disease.

Another wax character of native strains is that newly built cell walls tend to be visibly thinner than those of continental bees, though when fully propolised there is little difference.

17. COMPACT BROOD PATTERN. Besides the shape of pollen stores referred to earlier, the native brood pattern is more compact: generally spherical in bees of lowland areas and southern districts, or taller than broad in those of hilly areas and northern latitudes. Continental and Mediterranean bees frequently show a broader than tall pattern in summer: in South Africa one frequently sees broodnests twice as broad as they are tall.

The spherical and tall patterns are evidently related to the need in our climate to conserve spring and summer heat, and the broad pattern to an equal need to dissipate it in hot climates. Bees with compact brood patterns have the snag that they are slower to respond to smoke, but a longer gap between smoking and opening can soon be learned to obviate this disadvantage.

18. COMPACT HONEY STORAGE PATTERN. This is the ability of a colony in late summer to compress pollen and honey stores into a minimum volume of comb within close proximity to the hive entrance. Uncapped honey in the supers is carried down to the broodchamber as evaporation causes a diminution in volume.

This has strong survival value on a number of points, particularly:

a) in autumn it facilitates defence by guard bees from the cluster against bee, wasp and mouse attack.

b) in winter it favours the making of cleansing and water collection flights and return to a cluster in close proximity to food stores.

c) as a defence against the avaricious beekeeper, by withdrawing food into the broodbox.

d) the risk of "isolation starvation" when bees cannot make contact with some of their stores is reduced.

e) proper ripening and capping of all honey stores is facilitated, lessening the risk of fermentation and dysentery.

19. FLUCTUATING BROODNEST TEMPERATURE. Italian colonies tend to maintain a remarkably constant temperature around 35 degrees C (95 degrees F) both by day and by night. In contrast, English, Irish and Scottish strains compared under similar midsummer conditions have exhibited a night-time drop in temperature as measured in the upper broodnest position following cool nights and during relatively weak nectarflow conditions. Strong colonies on double broodbox BS hives ranged from a peak temperature of 35.5 degrees C (95 degrees F) in late afternoon, falling several degrees on most nights to a trough of 18 degrees C (65 degrees F) in early morning after one clear-sky night, with the hive entrance left fully open.

The character possibly assists in survival through adverse winter and spring conditions with reduced production of heat and hence a slower depletion of food reserves. The stocks with this behaviour pattern seem to avoid death from starvation in early spring and to survive preferentially. This was particularly noticeable after the long winter of 1977-8 and especially 1978-9. This survival may however be bought at the cost of greater susceptibility to chalk brood brought about by chilling of larvae. Breeders should learn to accept low to moderate attacks of chalk brood as indicative of their bees' possession of this habit, and not to worry too much over insignificant losses which they see.

e) CHARACTERS AFFECTING MATING AND INTERBREEDING

20. MINIMAL DRIFTING. Native bees memorise their hive location very precisely and tend not to drift from hive to hive. This attribute is by no means confined to our native strains, being found among many of the strains of North Europe where hive entrances are near each other, as when hives or skeps are set in close rows or kept in formally arranged bee houses with entrances in close proximity. It is, however, an important characteristic of our native strains. The behaviour is particularly noticeable among drones

where marking has shown that little movement takes place from hive to hive within an apiary over periods of several months. This non-migratory drone character is evidently an important mechanism for maintaining within-strain matings and so keeping recessive characters like supersedure homozygous, at least under conditions when mating within or close to the apiary (see Chapter 5) is likely. Without it many of the strains we are interested in would have outcrossed and we should not today be regarding them as native. Equally, in overseas strains, where prolificacy is valued, the most prolific colonies will be those of hybrid character, i.e. where drones have migrated to other hives preparatory to the queen flying to mate and where drone congregation behaviour is of common occurrence. Where the breeder wishes to utilise hybrid vigour, it is more satisfactory to mate queens raised from one hive in a distant monostrain area of another than to rely on migratory drones within the apiary or on drone congregations further off. The latter course will give an unpredictable amount of hybrid offspring with the likelihood of abundance of multiple matings.

The character of minimal drifting of both drones and workers also tends to slow down the spread of disease and delay the onset of robbing.

21. DRONES EXPELLED EARLIER. This generally occurs during a nectar dearth, when the drones have no access to open liquid stores. Native strains soon cap over nectar, or carry it above the excluder where drones cannot reach it. With a single BS broodbox there may be several drone rejections during a poor summer, though giving a larger or multiple broodbox may mask this. In apiaries where we have studied a hive yielding migratory drones amongst several native colonies with non-migratory drones, the clear-out has restored the dominance of native drones in their own colonies, hatching from their own brood; and this could be a powerful isolation factor in a cool summer. Native queens mating close to home appear to mate with drones flying from their own hive, but not necessarily of their own rearing, during short bursts of drone activity.

22. ALTERNATIVE MATING BEHAVIOUR. (See also Chapter 5.) Native British Isles bees have three systems of mating behaviour. These we can list as:

i) Major drone assembly mating (or distant assembly mating). Queens in Central and Southern Europe and elsewhere have been shown to mate normally in major drone assemblies during spells of hot sunny weather. Drones from many apiaries within a radius of several kilometres are known to participate.

Continental workers have stated their belief that all queens mate in such drone assemblies, often far away from any apiary, and not, as was formerly believed in the British Isles, quite close to the hive.

ii) Minor drone assembly mating (or local assembly mating). Bees of native and near-native strains are quite typical in their use of major assemblies (though there is some indication that they may use them less efficiently, more often failing to return home, or sometimes not attempting to take mating flights in very hot, clear weather). Typically in warm humid periods of thundery or showery weather, smaller drone assemblies are set up near individual apiaries - usually within 200m. Drones from several colonies in the apiary are known to take part in these.

iii) Apiary vicinity mating. In the less settled weather conditions of some years, and particularly in smoky and high-rainfall regions, neither major nor minor drone assemblies may form with sufficient regularity. At such times queens of Italian and other non-native parentage may fail to mate, disappearing or becoming drone-layers. Yet under similar conditions and in the same apiaries, bees with native characteristics do mate freely and subsequently produce fertile worker brood. They may take longer to mate than normal, and in early spring and late summer we occasionally find that they have been insufficiently inseminated, leading to their being superseded after a short laying life. But this ability saves the breeding line which would otherwise die out.

Apiary vicinity mating can occur during bursts of sunshine or during dull weather when ground or plant radiation is high, or when the air is moderately warm. The queen emerges from the hive and is immediately followed by a number of drones from that hive, with one or more of which she pairs within the confines of the apiary. (It is the occasional witnessing of this event by beekeepers which must have led to the widespread belief that all matings in these Islands were of a local or apiary-vicinity nature; a belief which has surprised our continental colleagues.)

23. TEMPERAMENT COMPATIBLE WITH OTHER NATIVE BEES. This is a most important point if one's bee is not to turn speedily bad-tempered or cause other people's native bees to turn bad-tempered. To the user of imported queens the change is not serious in the "first generation" queens raised in the area (i.e. purebred queen of imported type mated with unlike local drones, yielding hybrid workers). But the "second generation" queens raised from them (i.e. hybrid queen, and still hybrid workers) are very sharp-tempered if the cross has been incompatible (see Chapter 8). In the interests of good neighbourliness and reduced management time, pain and worry, matings compatible with other native strains are essential if one is to enjoy the work of breeding and really be accepted by the beekeeping community one works with or sells to.

Supersedure

Taken as a whole, the bees of the British Isles show a high tendency to reproduce their queens by supersedure rather than swarming, as compared with bees from any other part of the world with which I am familiar. The subject is an important and complex one to which I devote a separate chapter (Chapter 4). Most native strains have at least a 10% supersedure rate (i.e. one queen in ten replaced by supersedure rather than swarming), many have a rate of 25%, and a few approach 100%.

The character is one which varies greatly from one district to another and from year to year; it is also strongly affected by management, and easily overlooked by the beekeeper.

We do not regard it as straightforwardly diagnostic of nativeness, however. As with characters 1-22 above, supersedure is found in many if not all bees of foreign origin (though usually at a rate of 5% or less). More importantly, there are undoubted native strains which are annual, biennial or triennial swarmers, seldom if ever attempting to supersede. It may be that, originally selected by certain practices of the old skep beekeepers, this strong swarming tendency has been maintained in movable-comb beekeeping by rigid adherence to management-oriented teachings, and that it would decline if these techniques were abandoned. As things are, however, one may say that while a strain with a high tendency to supersede (say, 25% or more) is likely to be native, the reverse is not true.

Historical influences on populations

Last century's strains of honeybee native to the British Isles had many admirers. With the coming of the movable-comb hive and the greater flexibility which this gave to beekeeping management, people started looking towards more prolific strains of bees from overseas, and towards management techniques demanding a more versatile bee. An age of trial and error was ushered in which did much to open up new beekeeping vistas. With larger hives and multiple broodboxes came the urge to seek out bees which would fill the larger broodboxes and increase the yield per hive.

"Isle of Wight disease"

With the coming of these foreign bees, and the greater transportation of queens and colonies from one part of these Islands to another, there arose from 1906 a malady or series of maladies collectively known as "Isle of Wight disease", whose widespread appearance caused consternation among those whose bees were affected, and something approaching panic elsewhere. Sufferers wrote to the bee press, and those whose bees were still healthy feared that they would be next to be afflicted. In this atmosphere, losses of bees from any cause were readily attributed to the "disease". Just as the heavy losses of colonies reported after the 1962-3 winter were later found to be greatly exaggerated when actual counts came to be made, so lack of precise statistics must have led to a great overestimate of the degree of loss that had occurred. This was accentuated by the large numbers of apiaries which had dwindled or been lost through the tribulations of the 1914-18 war when sugar scarcity prevented feeding, some winters and springs were exceptionally cold, colonies were neglected, honey removed was perhaps excessive, and newcomers made novice errors[5].

Defeatism

When restocking became possible, this sense of defeat seems to have been maximised for political reasons, as an inducement to persuade beekeepers to accept subsidised colonies on movable combs, in the laudable belief that the latter would assist examination of hives for disease and increase yields by eliminating skep and box beekeeping. Thus arose the idea that the native bee was dead, which subsequent authors have tended to foster and enlarge, often to the point of fantasy. Some of those personally involved in the restocking campaign have admitted to me that there was in fact no shortage of surviving native bees.

Gross exaggeration of the effects of losses

I have talked over the past 40 years to a great many beekeepers in England, Ireland, the Isle of Man, Scotland and Wales who kept bees throughout this period, as well as some of those concerned in the restocking schemes. The surprising thing is that so many of them have said that the scourge of those times passed them by, or affected one apiary but not another, from which they subsequently built up again. The pity is that so many of these old beekeepers have now gone. My estimate is that well over half of the beekeepers of that time did not suffer the scourge in their apiaries.

The worst losses were during the 1914—18 war years and shortly after, and hit especially newcomers and those restarting after the war. Most of those who suffered had lately introduced Italian or non-indigenous bees to their apiaries, or their bees were getting crossed with the new bees, or they had caught stray swarms of such types. There is considerable evidence that crawling acarine (or whatever it was) was a disease of hybrids, or segregates from hybrids, and not a disease of within-strain mated bees. Although many beekeepers and many areas suffered heavily from the scourge, at least as many did not, and the descendants of their bees are with us today.

Education

With the growth of technical education services and the employment of Regional and County Beekeeping Officers to teach beekeeping in agricultural colleges and to amateurs there was naturally an incentive to try out new techniques and to perfect the advances made possible by the movable comb hive. A snobbery arose whereby the earlier generations of skep and box beekeepers were looked down upon, and their "primitive" methods derided. An examination system gave credibility to the ascendent generation of practitioners and a new establishment grew up, as fixed in its outlook as were its predecessors. New magazines were founded to break new ground, but spent much of their effort fighting others instead of looking scientifically and dispassionately at the situation. (One editor of a periodical said to me some years ago, "Make it controversial! We've got to be controversial to keep our sales up!") County beekeeping associations even split due to the prevalent dogmatism and intolerance, far removed from the cool atmosphere needed to examine the facts and to sort the valuable ideas from the less critical and to develop them towards practical usefulness.

Literature

With more advanced techniques came literature on these techniques, generally pouring scorn on methods and types of bee other than those of the author. In particular the splendid works of R. O. B. Manley had a big influence for good on beekeeping practice, not only among large-scale and commercial beekeepers but also among the cream of amateur practitioners. A boom in large-frame hives resulted, encouraged further by the warm summers of the 1930s and 1940s and the depressed state of agriculture between the wars, when unsprayed fields were full of charlock and other weeds, unfertilised pastures full of clover, and neglected hedge bottoms provided a wealth of flora.

I too was attracted by the persuasive arguments for the Modified Dadant hive and the prolific bee, till I discovered their snags in my hedge-free, weed-free arable South Lincolnshire and found on average that I did much better with a non-prolific bee in a smaller-broodbox hive. In Scotland Athole Kirkwood found likewise, and he standardised for reasons of extracting and handling efficiency on the Langstroth hive with MD supers. In the honey-rich areas of the South of Ireland the 16" x 10" hive has been widely adopted as further proof of Manley's influence, though in the poorer and higher-rainfall areas the small broodbox still reigns supreme. Many other examples could be quoted. Even Manley in his later years complained that he could not get the high yields of his earlier days when farming conditions in his part of Oxfordshire changed after the Second World War.

Another influence has been that of the Bee Research Association (later known as the International Bee Research Association). By publishing its first-rate abstracts, scientific papers and review articles it has had an appreciable influence on beekeeping opinion and on fostering techniques specially applicable to sunnier climates and heavier honeyflows than the British Isles can normally provide. 1 am not decrying the excellent work done by 1BRA, but I have on several occasions been made aware of a refusal, derived from its work, to accept that the problems of these Islands deserve special consideration, and beekeepers have been biased against using native strains in consequence.

The "extinction" of native bees

As a result of all these events and processes, the belief became firmly entrenched in orthodox thinking that not only were native bees "inferior", but they had been eliminated or reduced to insignificant numbers by the joint effects of destruction by Isle of Wight disease and genetic swamping by the sheer weight of numbers of imported bees. What this view overlooks, however, is the potent and ever-present effect of two important processes: isolation and natural selection.

Isolation

This means the existence of barriers to cross-mating and the production of hybrids with other strains of bee. It falls into two main sorts: *geographical* and *ecological.*

The more easily understood of the two is geographical isolation: isolation by distance, by mountains and by the sea, or by belts of territory where no bees live. This has certainly been effective to a degree in some areas, particularly in upland Britain. (The isolation from new ideas of beekeepers remote from centres of population and education may also be mentioned under this head.)

To the non-biologist geographical isolation would seem to be all-important, but in fact this is not so. With increasing knowledge of the reality of drone assemblies and of how queens can mate with drones from several kilometres away in different directions, the part played by ecological isolation is now seen to be paramount.

Ecological isolation can take many forms:

1. Apiary vicinity mating (AVM). Most native strains which have been closely studied over long periods have been found to have this ability, already mentioned under character No. 22 above. AVM is their normal pattern of mating behaviour for early and late season, as well as in bad weather at any time of the year, and favours within-strain mating, while distant assembly mating (DAM) favours outcrossing. Both are desirable for the survival of the species in variable climates like that of the British Isles. AVM leads to a degree of inbreeding, favouring the elimination of certain behavioural and physiological failings and the enhancement of others, while DAM at intervals restores lost vigour and widely reassorts the genes in the inbred population. This is the favoured pattern of breeding among many bee (and other animal and plant) breeders: inbreeding followed by hybridisation of the inbred strains, and it is not surprising that nature discovered it first.

Early swarming and early supersedure both provide for the successful isolation of their possessors, as the drones of distant assembly-forming strains have not by then discovered or set up major assemblies. AVM is particularly valuable when certain recessive behavioural characters such as supersedure are advantageous, as on heavy cool soils slow to warm up, on flat fenlands or in damp woodlands where forage is scarce in a wet season. DAM is more prevalent in sunny, floriferous and hilly country where severely unfavourable conditions are rarely met with.

2. Minimal drifting. Most native strains studied have constant-homing or non-migratory drones (see character No. 20 above). Their drones do not normally migrate from hive to hive, either within the apiary or between apiaries, as do the migratory drones of Mediterranean, Central European,

and American types sold in Britain and Ireland in recent decades. Coupled with AVM this strongly confers isolation. Drones of different colonies fly during shortish bursts of activity, few hives coinciding in time, and the queen generally flies to mate during the same period as drones from the same colony. After such flights the drones return to the same colony whence they came, exhibiting marked constancy for weeks and months, always returning to the hive from which they made their first orientation flights.

It is likely that both migratory and non-migratory types of drone prevailed in native strains in the last century, but only those showing a high degree of non-migratory drone behaviour would be now classed as "native", because the others, having become crossed, would now be regarded as "hybrids". This is an example of how the distinction between native and imported types can actually be sharpened rather than blurred by natural processes.

3. The periodical summer cull of drones during a prolonged dearth of nectar (observed as early as May in native strains) appears to provide a mechanism for eliminating foreign drones which have entered a native hive.

4. The dark pigmentation of drones (character No. 1) assists their ability to fly for long periods and achieve mating in cool bright weather. This important isolation character has protected many a native apiary in the midst of those of other strains.

5. Management systems favouring a rigorous adherence to a small (10 or 11-frame BS) broodbox prove to be yet another isolation factor. More traditionally-minded beekeepers, especially in remote rural areas, have continuously maintained such systems. Hybrids tend to be too prolific for such a broodbox in midsummer, and swarm overmuch with the result that the less swarmy colonies get more honey and survive preferentially after a poor summer or are selected by the beekeeper for their honey-gathering propensities. Giving a larger brood area (larger frames or multiple broodboxes) or applying a "swarm control" system of management as some authors advise, destroys this valuable form of isolation, but is often the recommended practice advocated by teachers who are unaware of the anti-breeding pressure they are applying in so doing.

6. Non-renewal of comb has clearly assisted isolation, both in wild colonies and in let-alone apiaries. The meticulous beekeeper can simulate this by providing one drone comb per 11-comb broodbox. Strain characters are carried as much by drones as by the queen, and culling of drone comb decreases the competitive effect of the colonies to which it is applied.

While importation of foreign bees has clearly wiped out some strains of native bees, strains benefitting from one or the other of these and other ecological isolation traits have come through unharmed. I now turn to the second factor.

Natural selection

When a native bee crosses with a non-native, characters from both parents are combined. They are still present, however, even if in hidden (recessive) form in the offspring. In subsequent generations there will be "segregation" or reappearance of these characters in a random manner, i.e. not all of them will be found together in the same colony. If we consider these characters individually and not as composite "strain" units which are identical with the appearance or behaviour of either parent, then the individual characters are capable of reappearing again in subsequent generations. But the assortment of characters varies, and is for the most part randomly distributed between the colonies of these generations. Some stocks will show more characters of native origin, while others will show more of foreign origin. Beekeepers tend to dismiss all such stocks by the pejorative term "mongrels" and to forget that if enough stocks are raised, all the original characters, native and foreign, are still there. In this way such people falsely accept the superstition of the defunct native bee. It is a regrettable fact that biological understanding of such things is so woefully lacking among beekeepers - even well known figures in the beekeeping world tend to fall into this trap from time to time.

There is no sound reason for regarding hybrids - that is, hybrids between British Isles and overseas strains - as less worthy of study than their pure mated relatives. Alleles of genes are not destroyed by hybridisation, only by selective elimination of their possessors. Segregation of characters will rearrange the available genes from generation to generation, so that some will preponderate in certain colonies and not in others. It is the selective survival of those which show certain advantages ("the fittest") which will "guide" the direction in which breeding will proceed. Of course, with small numbers of colonies chance may play a big part in determining which characters will be perpetuated or disappear (genetic drift). But for the most part, in moderately native areas, numbers will be high enough to ensure directional survival: directional to the point where native characters survive preferentially.

While the crossbred progeny are reproducing among themselves, natural selection is ever-present and always acting, whether the beekeeper knows it or not. The management-oriented honey producer may try to perpetuate all the progeny he raises, but even he will have selective losses in winter, or queens that selectively fail to mate, or selectively mate with drones not of his own choosing. The less management-minded beekeeper, as well as the let-alone beekeeper and of course all colonies of bees in the wild, will clearly be subject to a very strong degree of loss and hence selection, and their drones will often dominate the population. Although part of this loss will be due to chance and be non-directional (colonies lost by hives being knocked over by cattle or by flooding of apiaries, for example), a very high proportion will be directional and guided by one or more characters aiding survival. Such characters will include dark body colour, low temperature working or mating, heavy pollen collection, high load-carrying ability, tolerance of wind, minimum breeding out of season, longevity, supersedure and many other things, including resistance to certain diseases. Possession of such characters will inevitably assist preferential survival under pressure of natural selection.

As a result, many of the characters which go to make up a native bee become reselected from bees of mixed parentage, and tend to reassort themselves together in the same stocks. Some characters sort themselves out quickly, some slowly, the majority independently of conscious selection by the beekeeper. This reassortment was particularly noticeable during the import-free years of the Second World War, and in individual years of great stress since then. A beekeeper who selects for yellow body colour, for example, may find that nature has at the same time been selecting for long body hairs or native wing venation, nosema resistance or non-prolificacy; he may end up with a yellow-pigmented bee with otherwise native characters, as in at least one case within my experience. Appearances may be deceptive. That is why, in assessing a strain, the breeder must evaluate a wide range of characters as precisely as is practicable and not just go by the overall impression of the bee. The impression may be all that the honey-producer sees, but the breeder must look beyond.

Assessment

In assessing a colony for "nativeness", the breeder has to remember that the genetic constitution of any organism is no simple matter. Two factors must always be kept in mind: 1. the fact that the colonies under assessment may be undergoing the process of reassortment under the influence of natural selection, and 2. the natural variability of native bees among themselves.

1. REASSORTMENT. Many people misjudge the implications of nativeness in a strain of bee, because a strain possesses some conspicuous native trait, e.g. in colour or prolificacy, they in their minds automatically attribute to it various virtues or faults, about which they ought to hold an open mind. A bee which is black (a summer virtue in our climate) probably derives little advantage in wintering from this pigmentation, except some marginal advantage in very bright periods suitable for cleansing or early pollen-gathering flights. A prolific bee which winters as a large cluster, excellent for gathering an early spring crop off kaleseed or winter rape, may in fact be at a wintering disadvantage if the winter starts wet and the cold is prolonged.

A bee showing some virtues is not thereby automatically gifted with the rest. It may be - or it may not. The beekeeper who selects for too few attributes or lets his own choice overrule that of natural selection too strongly, is likely to lose important attributes in his search for perfection.

It is too easy to talk about "the black bee" having certain attributes. In fact colour is not *ipso facto* linked with many of the desired attributes of nativeness, and in selecting for black pigmentation one may in fact be rejecting other native characters.

It is better to speak of "native characters" and to refer to "adapted natives" in the case of those colonies which have a high proportion of native traits, and "non-adapted bees" in the case of those having too great a mixture of opposites in one strain. This is not to say that the latter are automatically undesirable, since they are often likely to show hybrid vigour and may be excellent honey producers in the hands of an intensive manager. But for the breeder they make unreliable parents. It is easier to recreate one's hybrids by re-crossing one's inbred lines than to breed from too varied an assemblage of parents.

If one is thinking of an adapted native strain, it is legitimate (if not always precise) to talk of a "native bee". But for the more variable and less, adapted strain, it is less accurate to refer to it as a native bee. "Near-native" may be a good description, however.

2. VARIABILITY. Since they have been largely moulded by natural selection, one would expect native bees to have evolved a range of types to match the beekeeping environments of the British Isles, which have always varied both in space and in time. I have spent a considerable time studying preserved specimens of *Apis mellifera* in museums and collections in Britain and Ireland, and have seen that there are notable morphological differences both between the bees of these Islands and those of Europe and the rest of the world, and to a lesser extent between the bees of different parts of these Islands: differences stretching back well before the days of the Italian queen bee trade and the "Isle of Wight disease" era.

It is on the behavioural side, however, that differences are so marked, and it is the behavioural side that has so much to give to bee breeders. Some old authors refer to bees of good temper and others to bees of stingy or followy nature; some describe large and populous colonies while others clearly know bees of non-prolific type and relatively small colony size. Some must have been early to develop and others late. Some were reluctant swarmers and had to be crammed into hives too small for them in order to force them to swarm - the only method of increase then available. And there were many other differences.

Moreover, many strains are dissimilar to those of the same area a hundred or more years ago. Climate, forage, hives and management have changed, and it would be surprising if the resulting selection pressures had not caused some alteration in the gene pool of populations.

Some newly imported strains, having been highly selected by the exporter, will show a high degree of uniformity between stocks (though this is not always so: for instance the Buckfast bees in some years have been very variable). If they are being compared with bees of native or near-native type, allowances must be made for the variability of the latter, caused by the genetic reassortment and regional diversity; unless of course a very highly adapted and/or carefully bred native strain is being considered.

Avoidance of pejorative terms

By taking a balanced view of all these considerations, it is to be hoped that beekeepers can avoid the use of certain pejorative expressions for types of bee that they disapprove of. This practice is strongly to be deprecated. I cannot overemphasise the tremendous harm this tendency has caused to the proper consideration of bee breeding's contribution to apiculture, and will continue to cause if it is not positively resisted by fair-minded exponents of the craft.

MONGRELS. Perhaps the most objectionable term to those who have the conservation of native strains and characters at heart is the term "mongrel" applied to a native or near-native bee. Honeybees are outcrossing and variable organisms, and the presence of some yellow banding or prolificacy in an otherwise largely native strain does not deserve the pejorative "mongrel" connotation.

If bees are crosses of recent origin, say one to three generations back, probably the word "hybrid" is justified. Beyond that it becomes less and less applicable. Almost certainly degrees of natural selection or backcrossing will have so completely altered the fifty-fifty balance of characteristics from each component parent of the original hybrid that in most parts of these Islands it could better be described as near-native, even if the bee is yellow-banded or has broad tomenta or is more than normally prolific. There are islands of non-native populations where this would not be so, particularly in the South of England and South Wales, but they are the exception rather than the rule.

The term "mongrel" is not a precise beekeeping term. It is certainly no more relevant to the bees of Britain and Ireland than to those of Italy or France or the USA. Let us not besmirch our own or anyone else's bee by its use.

OLD ENGLISH BEE. Another ill-used expression is that of the "old English bee" (or Irish, Scottish or Welsh etc. as the case may be). The implication is that the bees of today are not like those of yesteryear and that there is therefore no urgency to promote their conservation, maintenance or propagation.

Today we are breeding today's and tomorrow's British Isles bees, not those of a century ago. Breeds of cattle, sheep, pigs and poultry and many crop plant cultivars are very different from their ancestors, yet we do not decry the basic continuity of species, subspecies or group. Why attack honeybees because they have undergone recognisable variation, in most cases much less than in the species mentioned above? We who are breeding bees are not genetically identical with our forbears of a century ago. We do not call a person French or Italian because of a French or Italian ancestor several generations back, mated to British Isles spouses ever since. It is quite illogical to do so with bees.

Another bad effect of this term is the embarrassment caused by those who claim to have discovered a last remnant of "old English bees", usually in some remote area. Our bees - probably 90% of them in most areas - are the native or near-native British Isles bees of today, not hybrids, mongrels or "old" bees. Let us call them what they are and not undersell our product. Many areas where selection is against dark pigmentation may yet have bees which are predominantly near-native despite appearances to the contrary. We must not let prejudice deter us from recognising this fact.

CHAPTER FOUR

Supersedure

Queen reproduction, replacement or renewal may be said, broadly speaking, to take place in our bees of Britain and Ireland under three broad divisions (or "impulses" as many authors call them): 1. Swarming, 2. Queenlessness (or "emergency" or "orphanage"), and 3. Supersedure.

There are many intermediates between, combinations of, and variations in these categories, depending on the strain of bee as well as the circumstances. For example, some swarming strains do not supersede, whereas others will do so as a last resort. A stock that goes queenless because of nosema may raise several "emergency" queencells and, if it is strong enough, end up by swarming. When a hive is overcrowded and overheated so that the bees crowd out over the front of the hive a superseder may swarm on a hot day even with no queencell in the hive; or if a virgin queen comes out to mate in such conditions the bees may decide to swarm off with her. This is one of the problems with the overstocked nucleus and mininuc.

Swarming and supersedure are not opposites, and can even occur together. One of my stocks in 1976, for instance, on being examined after swarming, showed three emerged queencells and three broken down; a virgin queen was found in the stock, and also the old marked queen. I have heard of a stock which overwintered with an old queen and her daughter, the latter departing with a swarm the following summer and leaving the mother behind.

There are even strains which have been selected through the operation of particular management and propagation systems to the point where they will neither swarm nor supersede.

These complications have led to problems of definition, so that different authors have drawn the lines between the different categories in different places. It is as well therefore to attempt our own definitions before going on to consider the problem in greater detail.

1. Swarming

Although a complex and variable process, the outlines of swarming are well enough known; so much so as to become an obsession with many beekeepers and to dominate unduly many systems of beekeeping. In its classic form, the bees first construct a number of queencells: anything from a single cell to over two hundred, but in these Islands most commonly between six and thirteen, generally in batches of successively decreasing ages. While the cells are under construction the bees normally slacken off foraging activity and cluster beneath and among the bottom combs, and the queen slackens off her laying. About the time the cells are sealed a portion of the bees swarms off (the prime swarm), usually with the old queen, to found a new colony elsewhere. The prime swarm is often followed by further swarms (casts), headed by young queens emerged from the cells, leaving behind a further portion of bees to carry on the old colony under a single new queen. Modifications of this classic pattern are usually the result of some complicating factor such as bad weather, overheating, or some interference by the beekeeper.

2. Queenlessness

"Queenlessness" may be defined as the condition in which the old queen disappears before, or shortly after, queencell initiation, and certainly before the young queens mate. The necessary cause is absence or serious deficiency of the old queen, which may result from many causes such as death or debility through disease (usually nosema or amoeba), extreme old age, or the accident of hive disturbance or some untoward action of the beekeeper.

3. Supersedure

"Supersedure" we define as the act of queen reproduction in which the bees make no preparation for swarming (such as slackening off work or clustering beneath the combs), and in which the queen mother goes on moving about among the bees - unless she is nearly spent - laying normally until a virgin queen emerges, and onwards until the virgin queen is mated, and usually on until the new queen has been laying for some time. The essence is that the virgin queen mates IN THE PRESENCE OF THE OLD QUEEN, who does not decamp with a prime swarm.

By insisting on the presence of two queens together we can term this category "queenright supersedure", to distinguish it from processes of queen replacement which are called supersedure by many authors, but which are better regarded as forms of "queenlessness" (as defined above), or of thwarted swarming.

4. "Supersedure swarming"

Authors of beekeeping books have been in violent disagreement over whether there is such a thing as a "supersedure swarm". One could argue that such a phenomenon is a contradiction in terms. Undoubtedly, most superseding strains will occasionally throw off swarms, which often prove to contain virgin queens. One can envisage a stock on a hot day, with the bees crowding out and the colony in a position either to swarm or supersede, balanced on a knife edge between the two. If the hive is overheated and perhaps the spare queencells are not being "guarded", emergence of two or more virgins may stimulate workers to swarm and take a virgin with them.

Some superseding strains send out "mating swarms". Terry Theaker recorded many of these. Here the workers follow the virgin queen when she comes out to mate: i.e. a few days later than the previous type of swarm would have emerged. A mating swarm is usually small and often returns to the hive with the virgin. Sometimes it flies away after clustering; occasionally it has been observed to fly into another occupied hive in the apiary. Such swarms, like those of the previous type, are more likely when there is more than one queencell and when the strain is one liable to excitement in the presence of a virgin (see below, under "tertiary component No. 6").

The first type of swarm is perhaps not really distinct from a cast, albeit a cast which is not preceded by a prime swarm. Thus of the three types of swarm - prime swarm, cast and mating swarm - it is the absence of a prime swarm which is crucial in the definition of supersedure.

Ignorance on supersedure

Ignorance is great on the matter of supersedure: most books give it very short measure and fail to recognise the opportunities it offers in honey production and labour-saving management. Because colony propagation does not force itself upon the beekeeper during supersedure, the unmethodical or idle handler is apt to lose the character through lack of provision for propagation. There is an immense mythology prevalent about this mode of reproduction, ranging from those who fear the characteristic as unnatural, degenerate and useless, to those who regard it as a form of immortality. All of these beliefs are very wide of the mark.

In order to discover how deep people's experience of supersedure was, 1 have made a point of asking audiences to whom I have been lecturing how many of them have experienced the finding of two queens, the queen mother and her daughter, living and laying side by side in one of their own hives. Following that I have asked how many of the audience believed in the existence of supersedure. The replies have been revealing.

An audience in London had never experienced a two-queen hive in nature, although several of them had tried the skyscraper hive method, which involves having two or more colonies working one above the other, with queen excluders between. An audience on the South Coast of England had never met supersedure, but about ten percent believed it to exist. Of an audience in the English Midlands I found that about ten percent had experienced two-queen hives, and nearly everyone believed in supersedure. A Yorkshire audience contained one man who had experienced a two-queen hive, but about eighty percent believed in supersedure: evidently all readers of William Hamilton. About five percent of a Cheshire audience had met a two-queen hive, and all appeared to know about supersedure: evidently someone had been educating them. In South Wales they all professed to know about supersedure, but none had seen a two-queen hive ("But it's unnatural!" shouted one disbeliever).

In Scotland supersedure was more taken for granted - perhaps it is commoner - and about thirty percent claimed to have experience of the two-queen colony at one meeting on the East Coast; but a meeting in the

South-West was too shy to voice an opinion (though I have myself seen a two-queen colony in their area).

Ireland exhibited a wide divergence of opinion. Dublin seems to know of supersedure by book knowledge but not experience, but several observant Midland and rural beekeepers know it well and value the characteristic as a money-spinner, though few plausibly claim to have seen a two-queen hive. In the North I have met only sceptics, and in the South and South-East they were too engrossed in counting the supers to have time to look for two queens.

In the Isle of Man supersedure also exists, but seems to be regarded as a great oddity.

Knowledge of supersedure seems to be centred largely on areas of native and near-native bees and belief in its existence seems to be reduced in proportion to the number who keep imported types of bee or who have learned from those who keep non-native bees. The power of the written word seems very strong amongst townsfolk and "educated" beekeepers, in that they believe literally what they have read in their textbooks, to the point where they reject what they can see for themselves in their own hives. Such is the brainwashing power of dogmatic bee education!

In the following account we shall discuss the nature of supersedure, see how it differs from swarming, and look at forms of management which will maintain and increase the character, discuss how to propagate superseders and mention some management methods which are appropriate to a superseding strain of bee. A great deal of management which is suitable for swarming bees is quite unsuitable for superseders, and the reverse is also true. It is therefore important to know when you have supersedure in your strain, so as to know which system of management to apply.

Components of supersedure

Like successful honey production, supersedure is a complex of many contributory components. A WELL ADAPTED superseding strain will possess many of them, and an incipient superseding strain will possess very few. This is why a long-term breeding process is essential in the selection of a good strain of superseding bee.

These components are all separately inherited: some may be linked but the possibility exists of having one without another. The breeder must therefore analyse with care what attributes are possessed by the stocks he intends to become his queen mothers, the aim being to enhance the degree of adaptation without losing too much vigour. During the breeding process - a sort of "purification" process - some loss of vigour is inevitable unless a large number of colonies are available and many are used as parents in each generation. This lost vigour is restored on crossing the inbred lines, in the process of obtaining the honey-production colonies. This is why breeding must be given due priority, and the mistake should not be made of breeding only "from one's best colony" (in the honey production sense). One needs also to breed from stocks showing a heavy loading of components of supersedure. We can divide the components of supersedure into; 1. primary: i.e. those which are essential to our definition of supersedure; 2. secondary: i.e. those which greatly support the success of a strain showing the primary characters; and 3. tertiary: i.e. those which make an advantageous contribution under some conditions of selection, but are by no means essential.

Primary components

1. LACK OF ANIMOSITY BETWEEN QUEENS. Supersedure, biologically, succeeds because of one fact: a lack of animosity between the queens moving about in the hive together. It is almost as if the two were either ignorant of each other's presence, or uninterested, or even (with some queens) repelled, queens retreating from each other after an encounter. (This lack of animosity is a living example of tolerance in action, and is the same source of strength and has the same weaknesses as in human society. As the workers show an equal readiness to defend their colony as do bees of a swarming strain, one cannot apply the term "pacifist" to the colony as a whole!)

This tolerance between queens exists a) between the old mated queen and the virgin queen; b) between the old mated queen and a newly mated queen; c) between a virgin queen and another virgin out of another cell in the same hive; and d) between mated sister queens. I have on several occasions tested case c) by opening cells in a hive where one virgin has emerged and the others have not yet been destroyed (which the workers, not the queen seem to be responsible for), and putting the queens together. With superseders, the queens have always run apart.

This inherited lack of animosity contrasts with the clear hostility between queens of all ages and conditions from swarming strains, and even between their queens and capped queencells. Whenever I have put virgins from swarming strains together, they have fought.

(Dr. Simpson in *The Reproductive Behaviour of European Honeybee Colonies* writes, "I once saw an old queen in an observation hive killed by a young queen several weeks after the young one had begun laying and had often been close to the old one." This seems to be a switch from non-hostile to hostile behaviour. Possibly exposure to light or other disturbance on observing the hive had this effect. L. E. Snelgrove claimed that queens would fight in the light but not in the dark. This may be true of some strains but needs further investigation[1].)

It would be interesting to discover whether the lack of animosity between queens extends to workers of different colonies of the same strain and to workers and strange queens. Stocks of superseding strains have been observed to accept strange queens, and sometimes their swarms, without hositility[2]. Terry Theaker on one occasion saw a marked queen (probably still a virgin) from one hive alight on and then enter another hive which she was subsequently found to be heading, the previous queen being thrown out. On another occasion he saw a small swarm (probably a mating swarm) come out of one hive, circle round and then enter another hive where the queen was accepted. More than once he witnessed small queenless swarms entering hives or nuclei containing virgin queens. Several users of superseding strains have also noticed that within-strain direct introduction of queens is usually successful.

2. ABSENCE OF PIPING. Working with strains from Lincolnshire, Leicestershire and the North Riding of Yorkshire (mostly), I have never heard piping in a superseding colony, though queens of the same strains which are swarmers pipe strongly. Terry Theaker, who worked with between 50 and 100 colonies for something like 30 years, had the same experience. Other beekeepers from Hampshire, Cumberland, Fifeshire (Scotland) and Co. Leix (Ireland) have made the same observation, so that it seems reasonable to generalise. This character is closely associated with lack of animosity between queens.

3. CHARACTERISTIC HIVE SOUND SPECTRUM. Eddie Woods claimed to be able to spot supersedure by the sound spectrum made audible by amplifying the signal picked up by a microphone placed in the broodnest of a hive. This is the basis of one of his tests with his "Apidictor" equipment. I was present when he demonstrated the device to George Gardner in the latter's apiary at Leicester, on which occasion the Apidictor picked out a superseding stock from a line of 8 hives, despite Mr. Gardner having (in fun) assured Mr. Woods that the hive was preparing to swarm. It did in fact supersede a few days later.

Briefly, Mr. Woods distinguished two characteristic sounds (among others) emanating from a colony of bees: a "warble" and a "hiss'. The warble, he claimed, was a concomitant of the reduction in the amount of queen substance available to nurse bees which is a feature leading to both swarming and supersedure. It comes into existence some days or even weeks before the hatching of the new queen or queens, gradually increasing in volume during this time. Typically, the warble does not reach as great a volume in supersedure as in swarming, presumably because the reduction in queen substance is less drastic, though the difference may be difficult to detect in practice.

The hiss is a short sharp sound heard from a normal queenright colony, not preparing to swarm or to supersede, when its hive is struck sharply with the palm of the hand. In a colony preparing to swarm this hiss progressively declines in volume, while becoming very much prolonged in duration. In a colony preparing to supersede, however, the hiss remains the same as in a "normal" colony.

Thus, to oversimplify, a colony which hisses but does not warble is not raising queencells at all; one which warbles but does not hiss is preparing to swarm; and one which both hisses and warbles is preparing to supersede.

We are not certain that Mr. Woods' observations on supersedure are universally applicable to all strains of honeybee, since some of his other remarks on supersedure are by no means valid generalisations. But this could without too much difficulty be investigated more deeply, and the picture completed[3].

4. PHEROMONE REQUIREMENTS. These are evidently different for superseders than for swarmers. A dequeened stock does not immediately become excited, and is much slower to commence raising a queen - in many instances none is raised before it is too late (the larvae being too old) to do so. It is my impression (confirmed by Terry Theaker) that laying workers are rather slow to appear in superseding strains, and that mated queens of related strain are easy to introduce to stocks with laying workers[4].

I have never been privileged to undertake any work on honeybee pheromones so can offer no personal comment. One could ask several questions. Have the workers of superseding stocks a low requirement or craving for queen substance? Or do the workers themselves produce more of the active pheromone, so that a slackening off in production by the queen has less effect? Does the queen pheromone break down less easily in the less populous and lower-temperature colony? Do superseders yield a different queen substance which would explain the repellance which the queens show towards each other?

Secondary components

These are characteristics which, although not essential to supersedure, in the long run add strength (and likelihood of success) to a superseding strain possessing them. The well adapted superseder will possess all or most of these characters. After hybridisation with a non-superseder, however, these characters may well be seen in non-superseding stocks, although transmission may be complete to a future generation. One may be tempted to confuse the shadow with the substance and unwisely rely on selection for these secondary components. While to do so may be convenient practically, one must periodically re-test for the primary components to make sure that one is still on the right track. If queens are not clipped, and the stock is permitted to go on swarming, those with the secondary components but not the primary ones can be eliminated. But a breeder would not dare to risk this until his programme is well on the way to perfection in respect of supersedure!

la. LOW PEAK SWARMING NUMBER (PSN). This is the highest (peak) number of occupied queencells to be found together at time of swarming or supersedure. An adapted superseder usually raises only two to three, often only one, rarely up to five. It is as if the stock knew it was not going to swarm and only raised just enough to reproduce, with a small surplus in case one of them should fail. More than this: if it cannot raise a good queen, well fed and physically large, it may not raise one at all; it is very rare to get an undersized scrub queen, such as is all too common with the queen of a swarming strain raised by division or in a nucleus. Such reluctance to raise cells is very noticeable when there is a shortage of pollen in the hive, whether caused by bad weather or by a heavy nectar flow leaving no room for pollen. When a dequeened superseder does raise cells, my records show that all the queens emerge on the 12th-15th day, i.e. all are reared from an egg or a very young larva.

lb. LOW PEAK ORPHANAGE NUMBER (PON). This is clearly related to the last, and is the peak number of queencells raised by a colony under orphanage conditions. It is closely related to the PSN, but somewhat higher; presumably the complete cessation of queen substance income alarms the bees more than under conditions of supersedure, when there is some income, if reduced, in queen substance from the queen still in residence, as there will be also in the swarming stock before the old queen is lost with the prime swarm. After the swarm has left, and for a period of six days, orphanage conditions prevail and queencells can still be raised, so that in a swarming stock PON and PSN are likely to be the same, at similar times of year. Since one cannot ascertain the PSN to order, measurement of PON, which can be produced artificially merely by dequeening or division, is a useful and reliable substitute.

2. SLOW BUILDUP IN SPRING. A slow buildup in worker bee numbers in springtime is a marked characteristic of most superseding strains. This is a contrast to the "build up and bust" habit of swarmers. To compensate, brood rearing tends to start early, large pollen collection in the previous autumn enabling rearing to go ahead when weather prohibits flight, and a long-lived bee enables adequate colony population in springtime to re-establish the summer breeding pattern securely. Those attuned to the brood appearance of rapid-buildup strains are apt to be deceived by the slow buildup into thinking that superseding bees are not going to have a large enough population to be successful honey gatherers, but if they can hold back their impatience, the June-July flow will prove their fears groundless. For an early flow area with a less reliable late flow, a superseding strain may be less satisfactory. For early fruit pollination work superseders will provide fewer bees for work on hot days, but their low-temperature working ability may yet make them more effective pollinators in years of cool blossom periods.

3. COMPRESSIBILITY. This is the ability to withstand compression of the broodnest from a norm of more than eleven frames of brood (of British Standard size or equivalent) down to eleven or less by insertion of a queen excluder, or by reason of insufficient super room, without recourse to swarming. In fact most superseding strains will swarm (sometimes even without building queencells) under provocation of extreme overcrowding and/or overheating, but very much less readily than will swarming strains.

It is important to distinguish this reluctant or infrequent swarming characteristic of superseders from "changeable non-swarming" exhibited by strains which readily construct numbers of queencells but equally readily break down queencells already raised, capped and even ready to emerge. This breaking-down can happen immediately the swarming stimulus is removed; e.g. when a nectar flow causes hive cooling by virtue of removal of field bees and evaporation of nectar.

4. OVERWINTERING OF DRONES AND EARLY DRONE-RAISING. Many superseding strains retain a few drones over winter. Some also rear them in small numbers very early in spring. The same strains frequently supersede in spring, sometimes as early as late March. The presence of these drones ensures mating, as well as keeping the supersedure in the strain by inbreeding.

Tertiary components

These are mostly characters found just as much among swarmers as superseders. But their presence in a superseding strain tends to reinforce the superseding habit and establish their possessors as "adapted superseders".

1. NON-MIGRATORY DRONES. This maximises within-strain mating just as distant drone-assembly mating maximises outcrossing. Where supersedure is favoured in its homozygous (i.e. invariably superseding) expression, the character is clearly an advantage; where the heterozygous condition is favoured (i.e. by reduced swarming) it is of some value, enabling the breeder to hang on to some degree of supersedure, which might be lost by dilution in an area where most beekeepers are selecting for swarming. With migratory drones, queens mating with drones emerging from the hive with them may yet be outcrossing.

2. LONGEVITY i) of workers, and ii) of queens. With both there is a maximal chance of colony and queen survival if the queen is failing in autumn or winter or in prolonged summer bad weather. Many swarmers of northern temperate strains of bee, however, are also long-lived.

3. THRIFTINESS. Bees that will curtail brood-raising when income falls off and when honey stores are below a certain minimum are at a particular advantage in dearth conditions, poor seasons and poor districts: circumstances in which superseders can do well.

4. HEAVY POLLEN STORAGE. This, though common in native swarming strains too, is of great value to superseders in enabling them to rear good queens at short notice at most seasons of the year.

5. APIARY VICINITY MATING. When queens are seen mating near the hive, they nearly always turn out to be of superseding strains. This is to be expected since drone assembly mating maximises outcrossing and supersedure is favoured by inbreeding as it is largely recessive in character.

6. MINIMAL MATING EXCITEMENT. In the absence of severe overheating, overcrowding, or other causes of alarm, when the queen comes out to mate the bees should not fly off with her as a mating swarm, and there should be no panic. Bees which are good ventilators would appear to be at an advantage in supersedure. Possibly the queen is not driven out to

mate as in some strains, but comes out of her own volition as on an orientation flight. Supersedure queens usually mate very quickly.

7. HOLDING SPARE VIRGIN QUEENS IN THEIR CELLS. In stocks with this behaviour, the old queen or first emerged young queen does not go round destroying the extra cells. Subsequent cells are allowed to hatch if required, or if not they are sealed in so that their inmates die of starvation. In superseding strains this component is a corollary of primary component 1 (lack of animosity between queens), while in some swarming strains the queens are prevented by the workers from attacking the cells.

In most swarming strains the cells may be attacked by the first virgin, but in many cases I have no reason to believe that the queen does this, as workers are seen busily breaking down cells after the virgin queen emerges. This is particularly noticeable when queencells raised from superseder eggs are being raised in a colony of swarmers.

In adapted superseding strains the workers do not break down any remaining queencells until after the first virgin is mated, thus keeping a queen or queens in reserve against the failure of the first queen to mate. Some swarming strains do this as well, but it is particularly valuable in a superseder.

8. MATING IN THE PRESENCE OF BROOD. Some strains seem to hold back their queens from mating if brood, or in some cases open brood, is present. Superseders usually mate on the 5th day after emergence, or soon after, irrespective of the presence of brood (or, for that matter, of a laying queen).

9. BALLING OF CROSSBRED QUEENS. The curious phenomenon of queen balling, in which the bees form a tight ball around the queen for a time, often damaging or killing her, is far from being fully understood. It occurs in several apparently distinct sets of circumstances (see Appendix 3). One of these arises in colonies of superseding strains, particularly when the hive is disturbed by the beekeeper or some other agency. A "crossbred" queen, that is, one whose mother mated with a different temperament group or perhaps even just a different strain, is then likely to be balled. Such a queen often provokes general bad temper in her workers (see Chapter 7) who are of course themselves likely to be of admixed strain. Some imbalance in the composition of her queen substance is thought to be responsible.

Users of superseding strains have often noted that when a queencell from one colony is hatched in a nucleus formed from another, the young queen is balled immediately on her return from a successful mating flight, often at the hive entrance[5].

In the probably quite frequent cases where a queen has mated with drones of both the same and different temperament groups, this mechanism will favour the "pure" daughter queens at the expense of the "crossbred" daughters. Sometimes this will lead to the death of colonies, but in cases where the old queen is still alive or there is more than one queencell, it may lead to a crossbred queen being replaced by a pure one.

Population dynamics

In certain areas and on certain soils supersedure confers a special advantage on stocks displaying this character. While it may exist to a small degree in most areas, it becomes of major importance in areas of clay soils, scarce pollen plants and high rainfall. Clearly these are appreciably less favourable to success in a swarming strain, and although they are also less favourable to superseders, the balance is altered so that supersedure becomes relatively very much more successful in the ecology of the species.

Where climate and flora and that great variable, the season are favourable, not only do swarms find homes to carry on their characteristic, and next year produce both drones and swarms to populate the area, but the parent colony is also more likely to succeed and carry on, but with a young queen. In the case of annual swarmers, favourable summers increase their proportion in a population. Beekeepers tend to follow suit, by breaking up frames with queencells into many hives. By management, these can be fed and aided to survive. Annual swarming is most common in good districts where there is nearly always a heavy nectar and pollen flow early in the year; for example in lowland brassica or charlock districts.

In a wet season however (or in the year after a dull one, when trees fail to yield so much nectar or pollen), a swarming strain not only loses its overwintered queen with the prime swarm, but the young emerging queens may either fail to mate, or may mate but fail to store enough food to winter successfully, whether in a new site or in the continuing colony on the old site. The prime swarm, too, is at risk. The management beekeeper, of course, takes steps to remedy this drawback by feeding, but the colony in the wild and in the hands of the let-alone beekeeper in such a situation is liable to fail more often under swarming as its means of queen propagation than under supersedure.

Biennial swarming obviates some of the uncertainties of annual swarming, in that it halves the chance of dying out after a bad summer. Since biennial-swarmer queens are normally long-lived, there is little chance of such a queen, raised in preparation for one swarm, dying of old age before the next swarm two years later. And in the winter following the year of non-swarming there is a greatly enhanced chance of survival due to having more honey to winter on, and therefore a more than doubled chance of weathering the dearth. Moreover, in the non-swarming year all such colonies are putting out a large number of drones, whereas annual swarmers which only just scrape through the winter may put out very few early on, though perhaps as many by the end of the season. Thus after a bad winter, queens are more likely to mate with biennial-swarmer drones than with annual-swarmer drones.

On the face of it swarming would appear to have all the trump cards. It certainly has the trump cards that management beekeepers are on the lookout for. The swarming strain increases its number of colonies at a rather rapid rate: it has to be rapid enough to maintain colony numbers in the face of mortality due to starvation or disease, accidental loss of queens on mating, orientation or cleansing flights, winter loss, the hive getting knocked over, mice or careless manipulation. So great are these losses in certain seasons that swarming strains tend to be over-prolific to compensate, and the management beekeeper has his work cut out not to increase his numbers of stocks. Besides direct colony increase via the queen, however, we have also to consider the equally important propagation of characters via the drone. In an area of swarmer dominance, most of the young queens that arise (in an old hive and in the casts) will tend to pair with swarmer drones. In an area of balanced polymorphism (i.e. some colonies being swarmers and some superseders) many of the queens will mate with the drones of their own character, but some will crossmate with the other character, and hybrid (or heterozygous) offspring will result. Since good seasons will favour survival of those showing the swarming character, there will be an increase in swarminess in the population following a good summer (i.e. good for buildup, mating and overwintering).

But a poor summer for some of these factors will show a swing the other way. Swarmers will decrease in proportion to superseders, who have husbanded their food supplies and not squandered them on riotous propagation, whose queens have not ventured out in carefree swarming, and whose virgins have not in consequence been forced to mate under unsuitable weather conditions. Supersedure has a strong survival advantage following poor seasons. In my studies of apiarists who use supersedure, the chance of successful queen-replacement is often 10:1 (against 5:1 with swarmers), since if the queen is lost on a mating flight, fails to mate or is killed by disease, there is a second, third and often fourth chance to succeed.

Following particular years unfavourable to swarmers, as in 1963 after a prolonged winter and in 1969 in Eastern England following the wet summer of 1968, I witnessed a jump of approximately three times (from 12% to 38%) in the proportion of superseders in three strains which I was studying and on which I have reliable data. Had two seasons of severe selective pressure succeeded each other - which does happen sometimes - the gain in supersedure would have been even more spectacular.

The significant point is that when a swing in colony numbers of this kind occurs, it is followed by an equally spectacular swing in the proportion of drones carrying the character of supersedure. Instead of most swarmers mating with drones carrying the swarming character, there is a greatly enhanced likelihood of the swarming survivors mating with supersedure-carrying drones, and a bigger chance of the formerly scarce superseding queens mating with superseding drones. Not only is the supersedure character carried by the homozygous (both parents alike) queens, but equally by the haploid drones bearing this character. A good percentage of swarming virgins will pair with these superseding drones, and although the colonies will be likely to swarm and suffer the hazards of this swarming behaviour, they will (if they survive) beget equal numbers of swarming and superseding drones in the next generation. Thus, one season of heavy selection pressure in favour of supersedure begets a big, continuing resulting swing towards supersedure for several years thereafter, before successive favourable seasons again cause swarming to outweigh the selective advantage of supersedure.

Thus we see that in nature swarming is propagated by queens and by drones; supersedure is propagated by drones alone. The management beekeeper accentuates this advantage of swarming by division (in effect increasing the success rate of casts), by feeding swarms, casts and divisions, and by division under conditions harmful to the success of superseders (as well as by other actions to be mentioned later). It is this anti-supersedure bias in management as at present taught that has done much harm to many fine native strains, and it is this ignorance of what is a valuable and biologically advantageous character (in the appropriate context) that this chapter hopes to combat, so that beekeepers may be encouraged to study supersedure, to understand it and be enabled to exploit it profitably in those areas to which it is fully appropriate. Some voices clamour that "swarming is natural", and infer that supersedure is unnatural. Both are natural, the one just as much as the other. Man can devise management and breeding methods to get the best out of each. Beekeeping in these Islands would have died out long ago if all our bees were of one type or the other. It is said that it takes all types to make a world, and this is as true of bee populations as of human society. A beekeeper who is not prepared to value both is only half a beekeeper. The narrow and sectarian dogmatism which has bedevilled beekeeping in the British Isles for the past century or more must wake up to the world of reality around us, and transform itself into a more open-minded and versatile system.

We thus see that supersedure is an adaptation towards survival - indeed, success - under adverse conditions. Whereas swarming is at its most successful under conditions of plenty, and predictable plenty. In our climate we are blessed with a random mixture of both, sometimes alternating, sometimes consecutive, sometimes some of each, with the extremes (in which the selection pressure is highest) relatively uncommon but highly significant when they do occur. It is not surprising that our bees show this character of balanced polymorphism, which allows the species to mould itself towards the prevailing most favourable method.

It is possible that this polymorphism of swarming and supersedure may contribute to the success of the species by high viability of the heterozygotes: i.e. the crosses between swarmers and superseders. Although we regard swarming as a dominant character in that the crosses are almost invariably swarmers in behaviour, it is likely that they will swarm less frequently than homozygous swarmers. This combined with a greater vigour perhaps than either "pure" swarmers or "pure" superseders could give them a high overall success rate, especially in average weather conditions. The possibility needs to be further investigated before it can be regarded as established, however.

Recognition

The beginner will have great difficulty in recognising the presence of supersedure. As his first aid to doing so, he should mark his queens with paint or an adherent disk, in such a way that each is separately identifiable. Unless, like Terry Theaker, one has the time, patience and observational skill to note down each queen's physical appearance in detail so that they are individually recognisable, this marking of queens, with each mark individually recorded, is an essential operation for every bee breeder, despite its slight risks. So much so that I devote a section of Chapter 8 to it.

Some beekeepers prefer to clip one wing of a queen, which combines a form of identification with a means of delaying swarming. Clipping is not to be recommended however for the beekeeper on the lookout for supersedure. Mated queens of native strains have been known to take the occasional flight, particularly in early spring (perhaps for cleansing purposes), a habit which may be much commoner than normally supposed[6]. Clipping can therefore lead to unnatural loss of queens, leading in turn to false assessment of colony characters and putting stocks at a disadvantage.

Whenever an unmarked queen is found, therefore, it should be marked (whatever the year) with a colour and/or number distinct from that of the queen last known in that hive. Marking does have the psychological disadvantage that the quick examiner generally stops looking for a queen once he has seen one, and particularly a marked one. I know I have made this mistake myself on many occasions. The reverse mistake is less common: sometimes one chances to see an unmarked queen when one expected to find a marked queen, and one is prompted to go on looking to see if the marked queen is still there - and sometimes she is. It is important therefore to train oneself to go on looking after spotting one queen, whether she is marked or not.

Two queens

The presence of two queens in the hive simultaneously, together with eggs or young larvae and only emerged queencells or none at all, is the crucial evidence to look for. Of course you could have a swarming stock, with takeoff delayed by prolonged bad weather, at the point where a virgin has emerged during the disturbance caused by manipulating the hive, or several virgins have emerged together after the prime swarm has left the hive, but piping should give the game away[7]. I have never heard queens pipe during supersedure. The workers must have some other way of knowing which queen to leave and which to stifle when there is more than one cell.

The mere presence of an unmarked queen in the place of the expected marked one is not proof of supersedure. This may have been an emergency replacement after orphanage. Alternatively the colony's original intention may have been to swarm, but bad weather or the start of a nectar flow may have delayed the exit of the swarm until a new queen emerged. The old queen may have been killed and the queencells broken down. This is what I have called "thwarted swarming".

In searching for two queens it is worth bearing in mind that they are in some strains likely to be in different parts of the hive - i.e. at opposite ends of the broodnest or at the top and bottom of a multiple-box hive where no excluder is present. Terry Theaker and his partner Frank King used to examine a hive together, each working inwards from both sides, and often each would find a queen. It is also worth being on the lookout when dividing hives. Surprisingly often a queen is eventually found in each division without any queencell being produced. If the newer queen is slow to come into lay (as in a wet summer), the beekeeper is apt to deduce that the stock is queenless. This is often a cause of new queens being killed on introduction.

Another point worth looking for when searching for queens in general is that when going through a hive, particularly when not using smoke, bees tend to be more jumpy when one lifts out the comb bearing the queen or an adjacent comb. The bees seem more excited, with more running about on the top bar, at least in the case of a less sedate-natured bee.

On one occasion 1 was going through a hive and found the old queen at the back, moving very sedately. A young agile queen was found at the front; fat and short as if just mated. In the vicinity of the young queen the bees were very excited, and I was stung by the new queen. I have often been stung when handling the comb with the queen or an adjacent comb, particularly with jumpy bees during a dearth, or in cold or thundery weather.

Queencells

The beekeeper, of course, wants to be able to recognise cells destined for supersedure and to distinguish them from those that will lead to swarming. In my experience there is no infallible rule which applies to all strains. An orphanage cell (i.e. emergency queencell) is generally built out from the midrib and not designed initially as a queencell. But superseding strains do sometimes have to resort to orphanage if they have left queen replacement too late: rare in nature but not uncommon where the beekeeper has broken cells open during manipulation or has been using the supersedure cells as a source of increase. So an orphanage cell built out from the midrib may be either a swarm or a supersedure cell. As a rule - that is, with most strains - a supersedure cell is placed well up on the comb face, and on a comb where there is (during its young stages at least) plenty of pollen stored. But my Leicestershire superseding strain repeatedly puts its cells right on the bottom of the comb just like many types of swarm cell, though my Yorkshire and Lincolnshire superseding strains prefer to site them on the comb centre.

It is stated by Wedmore that "supersedure cells are few in number, built as one batch, most usually on the face of the comb and, in any but weak stocks are heavily covered with wax so that surface pittings may be deep enough to take on hexagonal form. Drones are usually flying before the cells are formed, and there is no increase of drone brood. Egg-laying of the queen is not reduced and comb-building does not cease." I would tend to agree with this for South of England and Midlands strains, but some Irish and Scottish strains reputed to be superseders build cells that are not excessively thickened or pitted, and it may be that this is a matter of strain.

He adds, however, "If one of the queen cells is cut open and found to extend back to the midrib, retaining the original base of a worker cell, one may be sure that it is not a cell built for swarming." My experience confounds this: in my colonies such cells usually result from orphanage, past if not present. The stimulus which caused them to be started has nothing to do with either supersedure or swarming; though if the colony is of a superseding strain such cells may *result* in supersedure, while in a swarming strain they can likewise result in swarming. No doubt our experience is of different strains and we should not generalise[8].

All the superseding strains that I have known have raised few queencells, and probably built as one batch. Terry Theaker found it difficult to decide whether a colony's intention was to swarm or supersede. He concluded that "supersedure cells are always of the same age. If cells are of two or three age groups it is wise to assume that colony reproduction (swarming) is their aim." This observation, however, conflicts with that of Wadey, who states that "There are intervals between the dates of starting the cells, in order that the queens may not be able to emerge in batches as in the case with swarm-reared queens." There could be a difference between strains here, some staggering the buildup of successive cells as an alternative to holding virgins within them later.

Theaker also postulated that "the number of queencells made is directly proportional to the swarming influence." I regard these last two characters as secondary supersedure characters, not essential to supersedure but likely to contribute to its efficiency and success. Some swarming strains, however, raise few cells. Douglas Adams of Derby, noting my strain which both superseded and had a low PSN, increased his stocks with a low PSN. He ended up with bees which swarmed at a low PSN, but did not supersede. At the other extreme, some infrequently swarming strains raise many cells (15-30), but break them down rapidly if the weather goes against them.

Other clues

Three characters commonly (though not always) accompany the process of supersedure: loss of vigour, reduction in the number of bees, and a deterioration of temper. In themselves they may be due to many causes and are in no way diagnostic of supersedure, but taken together with the clues already mentioned they may serve to alert the beekeeper's suspicion that supersedure may be taking place.

In many cases of supersedure the superseding stock shows reduced vigour and reduced honey storage either in the year of supersedure or in the first year of building up after supersedure. In fact if queens of Terry Theaker's strain are judged on the first year's performance, many will be thrown out as useless, but subsequently, during their 2nd-5th years, they would have done wonderfully.

A superseding stock usually becomes low in bees before supersedure is observed, and a top super usually empties of bees (especially in bad weather - e.g. May-June 1972).

It is commonly observed that stocks which are normally good-tempered display a slight to marked worsening of temper during the period of supersedure. This out-of-nature sharpness is often the first symptom of impending supersedure detected by the beekeeper. The colony is "out of sorts" and liable to show this by uncontrollable following and stinging j without provocation, with temperamental bouts of "jumping" when combs are prised apart and put back. This is presumably what Wadey means in referring to "a subtle difference in the behaviour and demeanour of the bees that is recognisable to those who know what to look for and listen for."

Presumably some pheromone which signals contentment is lacking, or another that puts the colony on edge is being collected from the queen and shared around the workers. This state of affairs seems to persist throughout the queencell phase of supersedure, is modified slightly from emergence to mating, and generally normal docile behaviour is resumed once the new queen is in full lay (unless the new queen is genetically one which provokes bad temper in the colony: see Chapter 7).

With a swarming stock, lack of queen substance pheromone causes queencell production without apparent loss of good temper. At the time of swarming the stock is usually very good-tempered, perhaps because of the satiated young bees which are clustered to produce wax secretions. In my experience temper deteriorates after the queen has gone in the swarm and few queencells are left (either as a result of breaking down by the bees or the beekeeper or of small initial production). Possibly the bees are frustrated by lack of "queencell substance" as a substitute for queen substance, and have no queen to feed to produce more. Once a new queen is laying or laying workers have developed, the colony returns to its normal behaviour.

A final point worth noting is that adapted superseders normally supersede when the queen is a certain number of full seasons old. Although queens of the Theaker strain occasionally live into their eighth year, they usually supersede in their fourth full season. I know of other strains superseding regularly in their third and second full seasons respectively. The keeper of such bees will be on the lookout for supersedure particularly in the appropriate year.

Why promote supersedure?

Supersedure, as we have seen, is an adaptation towards thriftiness; swarming a gamble which comes off in better seasons but fails in poor ones. In our human stop-go society we have a ready parallel, the gamblers doing well in boom times, but the thrifty ones coming best through hard times. In the British Isles, this historical ebb and flow has likewise left it imprint on human genetics: the thrifty Yorkshireman or Scotsman surviving to become the major part of the population of their home districts, the more spendthrift and perhaps more enterprising genes having migrated to the centres of prosperity and sought their fortunes in overseas lands, depleting the home populations of the gene balance they once had, but leaving behind a population more fitted to survive in their home area than the original broader-based population would have been. In human evolution customs, beliefs and a range of other factors come into play which we could not attribute to honeybee populations, but the relevance of the comparison is apt in many ways.

With the loss of so much of our native bee flora through the advance of arable agriculture, use of weedkillers and elimination of hedges and trees, much former superb bee country is now of very mediocre value to bees. Areas that were formerly ideal for a swarming type of bee are no longer so; but the thrifty superseder can still be profitable to the beekeeper.

We now have a position in which the management-minded beekeeper tends to feed more, and thus enlarges the effective area of the country in which there is swarmer-superiority, at the same time as the declining honey-productivity of much of the countryside is tending to enlarge the actual area of supersedure-superiority. We predict that supersedure beekeeping has a big future for the man prepared to learn its handling, though it will never appeal to those who prefer to process factory-produced sugar through the hive feeder on its way into the honey-bottle.

In the past it has been customary to equate high yield per stock with efficient beekeeping. Today it is high yield per manhour and per unit capital outlay that is valued. In this the contribution of the superseding bee may be considerable, cutting down much peak-of-season management and the discomforts of bad-weather stock examinations. This advantage can be felt both by the large-scale commercial beekeeper and the small-scale producer, and the bee breeder and propagator will have his part to play in enabling them to succeed.

Whom will supersedure bees suit?

Superseding strains are particularly good for those whose work or other interests keep them away from their bees and oblige them to carry out irregular or infrequent management. Manipulations do not have to be carried out to the rigorous timetable of, for example, nine- or fourteen-day swarm cell inspections; nor are such operations as artificial swarming, clipping of queens or requeening, with their attendant labour, precise timing and risks of failure, necessary parts of supersedure beekeeping.

Having said this, to succeed in managing superseding strains requires a higher standard of beemanship (understanding of bees) than does success with swarming bees. Supersedure-based management is not synonymous with neglect. Perhaps the commonest mistake made is to treat queens of superseding strains as immortal. They are not!

Superseding strains therefore will not suit the indecisive man, who will not have the courage, determination and judgement to divide or propagate a superseder when it is collecting honey well. He will leave it "till next year", or "till the honeyflow is over" - and till it is too late. Swarmers propagate themselves and indecision encourages propagation, not the reverse.

The process of selection - by allowing bees to swarm - may not be possible for many town beekeepers with resentful neighbours. But the products of breeding - selected strains - are eminently suited to town beekeeping.

Strain maintenance

The maintenance of a strain of bees can best be done in the home area of that strain, or one ecologically very like it. Any strain will change in time when transferred to a new area or when put under a different system of management. Yet when a district is undergoing profound land use changes, for example changing from grassland or woodland to arable, or to town or industry, some change in the character of the bee is inevitable, and it may be wise to accept the inevitable. In other cases, however, it may be possible for a group of beekeepers to set up out-apiaries further away, in order to keep the bee selected for the conditions for which it is already most suited.

In the past, there has been too strong a tendency to lose sight of the adaptation of a bee to its soil, flora and management, and for it to be brought away and propagated under quite different conditions, so often to fail. By working as a group, there is less need for this to happen. The mating of queens in their home area can often be managed through the use of mininucs (small mating nucleus hives), serviced by someone on the spot, even though the actual propagation is undertaken in apiaries under closer control many miles, nay, tens and even hundreds of miles away. This is where cooperation between groups can be valuable.

It is important that strain maintenance be attempted under the guidance of someone specially interested in this aspect of beekeeping. It should not be subservient to honey production, otherwise there will be the inevitable tendency to "breed from the best colonies" or, in other words, to propagate from hybrids crossing outside the strain instead of maintaining the characters of the strain. In strain maintenance one must eliminate the very prolific brood producers as well as the colonies which are very poor, for whatever reason, in order to keep the strain close to the previously recorded characters for that strain.

Management of superseding strains

This should aim at facilitating the detection of supersedure and encouraging its successful occurrence, as well as propagating queens so as to maintain the superseding characteristics. If the manager of superseding bees is to reduce his management time and the number of his hive visits, he needs to be all the more astute in order to ensure that the manipulations he does carry out are the right ones.

For the most part, management guidelines will follow those recommended for native and near-native bees in general, discussed in Chapter 6, but it will be as well to mention here some of the more important principles which apply to superseding strains in particular - and to strains in which the degree of supersedure is to be assessed and enhanced. These may be divided into "do's" and "don'ts".

Do's

1. DO KEEP LOOKING. The only test of supersedure is the presence of two queens in the hive, and the only way to discover this condition is to look for it. What counts is not the queen which ought to be there, or the one which you or someone else assumes to be there, but the one or ones actually present. The remarks on "recognition" above are relevant here.

2. DO KEEP RECORDS. Be meticulous about identifying each queen seen on every occasion, and about recording their existence at the appropriate point on the record card, paying particular attention to parentage. This is especially important when dealing with a character such as supersedure which is recessive in expression. The genes for supersedure may be present in their masked state even in a swarmy colony, and it is only careful record keeping which can pick up the significance of the appearance of supersedure in a hitherto swarmy strain and point to the likelihood of its recurrence.

There is another mechanism whereby supersedure may be present in masked form, and that is admixture of characters through multiple mating. All the bees of a colony are not identical; it is normal for there to be admixture of half-sister workers, due to their mother being mated to several different drones. This may sometimes be apparent from colour differences in workers and even drones (if the queen is not homozygous for colour), but it is behaviour characters, not so easily spotted, which may puzzle the breeder.

If bees swarm, this may be due to the behaviour of those workers inheriting swarminess from one mating, even if the queen in the swarm may be genetically of the non-swarming character. Since the swarming behaviour always overrides the superseding one, and high peak queencell number tends to override low peak queencell number (or raise it to a midway position), one can get the inherited superseding tendency carrying on despite the occurrence of swarms in a strain.

For example, supposing a supersedure-inheriting queen mates with five drones of her own character and one drone carrying the swarming character.

Although perhaps only one sixth of the workers are mild swarmers (i.e. 50% swarmer, 50% superseder), if the colony comes under pressure during overcrowding or hot weather it will swarm. But the chances are 5:1 that the queens raised will carry supersedure, and 1:5 that they are heterozygous for supersedure and swarming. Moreover, if mated in isolation, i.e. not with drones from other hives in the apiary, there is a 5:1 chance of mating with supersedure drones. Thus swarms can produce offspring which are pure superseders. However, unless a conscious policy of not propagating, indeed of culling homozygous swarmers is carried out (but perhaps permitting some heterozygous swarmers with low peak swarming numbers to remain), the situation outlined above will rarely occur. But that it can occur should be appreciated, and the value of record keeping should be held in high regard despite such apparent anomalies. The need to fathom why anomalies do occur should be persevered with, as the decision whether to proceed with a breeding line may depend on why the anomaly occurred.

3. DO ALLOW THE BEES TO SWARM if they want to. Most of the manipulations applied to prevent swarming will also prevent supersedure, thus making it impossible to tell whether the bees are truly swarmers or superseders. Taking off an artificial swarm will reduce the number of bees dependent on the queen's pheromone production and may therefore tend to defer supersedure. Replacing a queen early in her life destroys the opportunity of letting her show us whether she would have ultimately been superseded. Clipping a queen's wings may cause her to be lost on a springtime cleansing flight, and one may wrongly deduce that supersedure has taken place. Even if one realises what has happened, one has lost the chance of assessing her for supersedure.

One of the most damaging fetishes of some beekeepers is that of queencell destruction. It has great appeal to the negative side of human nature and it seems to be their only technique of management in summertime.

At a conference I once attended the local bee advisor suggested he opened a particular colony where he had observed a single capped queencell in the "textbook" position in the centre of the frame, and which he thought would by now have emerged. On opening the hive no queencell was found, either emerged or unemerged. It was later discovered that the beginners' class had used the stock as a practice hive, and the operator had pulled off the queencell. If beginners are taught to do this from the outset, what hope is there of changing their ways when they graduate beyond the novice stage?

4. DO USE SMALL BROODCHAMBERS. The only test for the character of "compressibility" is to restrict the colony normally to a single broodbox of 10-11 British Standard frames or equivalent, which in any case is likely to suit the relatively non-prolific habit of most native superseders. Of course, extra brood chamber room may be necessary for certain manipulations in connection with, for example, propagation or drawing out of combs.

5. DO GUARD AGAINST FORCING SWARMS. Readiness to allow bees

to swarm need not be equated with providing conditions which practically force them to do so. Most superseding strains will swarm under extreme provocation, particularly that of severe overheating in hot weather in a crowded hive. One has to strike a balance here between testing for "compressibility" on the one hand and allowing bees to swarm. Measures which avoid giving the bees extreme provocation to swarm include using wide comb spacing and allowing wide entrances in summer to facilitate ventilation, and giving ample super room in good time to relieve extreme pressure on the broodnest.

6. DO ENCOURAGE DRONE REARING. Drones are essential for the maintenance of supersedure within the species. By mating with swarmer as well as superseder queens they ensure the continuance of the relevant genes in both hidden and visible forms. Drones are all the more important for supersedure in that it is a process frequently taking place in spring or autumn when drones are few or absent from many colonies. All stocks that are known or suspected superseders should be given at least one frame of drone comb, which can well be transferred to swarmer colonies when filled with brood, as described in Chapter 7.

7. DO MARK QUEENS (see above).

Don'ts

1. DON'T DELAY QUEEN RAISING. Superseding bees are not immortal. Because your bees do not swarm, you must not be lured into a false belief that they are self-perpetuating. If they are left too long, you may one day find yourself landed with a drone-layer - or no queen at all - at a time of year when no replacement can be reared or mated. Some strains are good at providing replacement in good time, but others choose less opportune seasons for this necessary event.

A point should therefore be made of raising daughters in the second year of a queen's life, not to replace her with but as an insurance against her possible failure. By all means keep a useful breeder queen beyond this age, but do not rely on her continuing for ever as a first class honey producer. She may be of more value to you after this time as a parent of first class colonies than as a honey producer. In a smaller colony she stands to live longer and can still provide all the eggs you need for producing queens of that strain. In a big colony she is more likely to fail in springtime when you least expect it. The same principle applies in the management of infrequent swarmers.

2. DON'T CREATE ADMIXTURE OF BEES by a) uniting, b) donating brood, c) switching flying bees, or d) equalising colonies, unless for some very good reason and unless your procedure is carefully recorded. Apart from its general disadvantage in falsifying assessment, admixture, even on a small scale, masks the superseding character when bees from swarmer colonies are added to superseders. Since swarming overrides supersedure the converse is

not true; superseder workers added to swarmer colonies will seldom reduce their swarminess significantly. For the same reason one should try to avoid e) admixture by multiple mating. Steps towards minimising this are the encouragement of superseder drones at the expense of swarmers (see above) and the creation of monostrain mating zones.

3. DON'T DESTROY QUEENS. In breeding for a character such as supersedure it is desirable to undertake progeny testing. The daughters of a queen mother, raised early in her lifetime, must be assessed for desirable characters and if they prove positive, further batches of daughters must be raised from the same mother. This cannot be done if the mother has been killed in the process of "requeening" for management reasons, or because her colony was "weak". Besides, if killed, the queen mother cannot herself be tested for supersedure which often takes place in her third or even fourth or later year. Weakness of her colony may itself be the prelude to supersedure.

4. DON'T CLIP QUEENS (see above).

5. DON'T DESTROY QUEEN CELLS. This is in part the corollary of "do allow the bees to swarm" (see above). Another reason for avoiding the practice is that it is often difficult or impossible to be sure whether the bees are about to swarm or to supersede - or to tear down the cells themselves and do neither.

Propagation of superseders

The special problems involved in making increase from superseder colonies arise from their general reluctance, in both the short and the long term, to raise large quantities of queen cells. It is common for adapted superseders to refuse to raise cells at all even when dequeened, if this operation is performed outside the period of peak colony prosperity or at a time when pollen is in short supply. Methods of making increase which have proved effective include the following:

1. TRANSFER OF LARVAE TO SWARMERS. Superseding strains may be propagated by any of the usual methods involving grafting, punching or specially prepared comb, provided that the cell-raising stock is a swarmer or, at least, of a high PQN strain. Large numbers of queens may be raised by these methods. Care must of course be taken that the swarmer's drones are not present in the mating apiary. One way of doing this is to remove and destroy drone brood from the swarmer before drones have hatched, replacing it with drone brood from the superseder queen mother colony, which should then be encouraged to rear more.

One slight doubt about this method is that there is a suggestion that feeding of the queen larvae by swarmer workers may encourage them to mate preferentially with swarmer-type drones, presumably due to the composition of their brood-food. Although borne out by some evidence this is only a theory. In any case mating the queens in a monostrain apiary must be one of the breeder's top priorities.

If the resulting queens are to be introduced into colonies as virgins, it should be noted that the usually successful practice of running virgins "pulled" from their cells straight into queenright colonies often fails with superseders. This is presumably because the superseder virgin does not show enough animosity towards the reigning queen, and is killed herself.

2. REMOVAL OF SUPERSEDURE CELLS TO NUCLEI. If one or more capped queencells are discovered when the bees are preparing to supersede, they can, if at a suitable season, be removed and put into queenless nuclei, taking the usual precautions to avoid robbing, chilling, cell destruction, etc. The mother queen, if left on the old site with plenty of pollen-gathering foragers, will often go on to raise more cells. This may sometimes be done three or four times before she eventually gives out; as she increasingly fails (to give out queen substance?) the number of cells raised may tend to increase. (But the lower the PQN, the less likely is the number to increase.)

3. DIVISION. A stock to be divided should be built up early by steady feeding from March onwards. It may be useful to winter on two broodboxes, or a second broodbox may be added in spring before the lower box is overcrowded. There should be a frame of drone comb in the centre of each box. When good weather has permitted a good supply of pollen to be accumulated and drones are flying, the division may be made.

The queenless stock, with eggs, young larvae, and emerging drone brood and plenty of pollen should be left on the old site, the queenright portion going to a new site some yards away (perhaps being given a super of bees from another apiary over a newspaper to keep the queen in full lay).

The queenless stock must be fed thin syrup during the cell-raising period to maintain high colony temperature and high pollen intake. Without such feeding and without the stock being on the old site, bad weather may lead to a refusal to raise cells by a true superseder. If particularly bad weather supervenes, no cells may yet be raised, in which case a comb of young larvae should be given from the parent queen's stock one week later, and feeding kept up. The manoeuvre is almost always successful from mid-June to early July; it is at other times that failure is most likely.

By this method only a few cells will be raised, but of very good quality. They may be distributed to nuclei as in the previous method. Or the queenless stock may be divided into a number of nuclei, each with a cell.

4. REMOVAL OF YOUNG QUEEN. The process of supersedure may be allowed to continue until there is both an old queen and a young one (whether virgin or mated). The young one may then be removed either with a nucleus or for introduction into another colony. The risk here is that one may leave it too late and find the mother queen gone. It is safer to remove the new queen as a capped cell.

5. USE OF NATURAL SWARM CELLS. If a colony of a superseding strain swarms naturally (which it may do at rare intervals), the swarmed colony may be split into nuclei with one queencell to each. The parent swarm,

if captured, may well prove to supersede later the same season and will sometimes produce more than one further queencell at that time.

6. ADMIXTURE WITH SWARMERS. To obtain more queencells from a low PQN superseder strain it is possible to add bees to the colony from a swarmer or high PQN colony. This may be done either by adding a frame or two of brood (worker only) or by switching flying bees (which is quicker). These added bees will turn the stock into a high or medium PQN stock, though genetically any queens raised will have the character of their mother. This practice can be effective when followed by some form of dequeening to initiate cell production. It is however risky in that the stock can easily swarm, and if this happens unobserved the old queen and all virgins but one will be lost.

CHAPTER FIVE

Mating Behaviour

Importance of drones

It was stated in Chapter 3 that in the British Isles there are three types of mating behaviour: major (distant) assembly mating; minor (local) assembly mating; and apiary vicinity mating. Although we should not underestimate the importance of queen behaviour in the mating process (e.g. whether she seeks, or does not seek a mating assembly), the subject has mostly been approached from the angle of the drones[1]. It is drones which set up assemblies, usually some time before they are sought by the queens, and it is the drone which seems to pursue the queen, whether in or out of an assembly. It is important that we devote a considerable amount of effort to studying the behaviour of drones, because the characters of the strains we are trying to perpetuate and improve are carried as much by drones as by the queens. If our queens are flying to mate in drone assemblies where drones of other strains consort, it will make the job of monostrain building much slower and a far bigger job than if they do not. If drone assemblies are only utilised (as I believe) during and after prolonged bright and settled weather, we must devise our strain isolation tactics for the production of drones early in the season, when sunny weather is at a premium, and must cull queens mated during spells of prolonged hot weather. Is it advantageous to site a mating apiary near to an assembly place, or is this a foolish procedure? We need to know much more about drone behaviour in planning our propagation and our breeding programmes.

Alternative mating

It seems reasonable to assume that both assembly and non-assembly mating behaviour are normal and of frequent occurrence in the native and near-native strains of the honeybee. One would expect strains selected for hybrid vigour and outcrossing to show the assembly type of mating behaviour particularly well, while those selected for non-prolificacy and within-strain mating would tend to maximise local mating. This, indeed, is what the limited evidence bears out.

It is our climate which would clearly put a premium on having two distinct, but each in its way perfect, sets of mating behaviour. One for fine and settled weather, and another for prolonged cold and wet weather, when no self-respecting drone would wander too far from home. Superseding strains, in particular, which but rarely send out swarms to spread their characters, must be sure of rearing replacement queens or they would die out, and their characters vanish. The swarmers can be profligate; if most die out, some will survive. But when an ageing superseder has to be replaced, the queen must be mated: and so rarely does a queen of an infrequently swarming strain, or a superseder, fail to mate. Yet how often does a frequent swarmer fail to do so! Breeding works by a series of negatives: the unsuccessful disappear from the breeding line, and the successful produce the future generations.

1. APIARY VICINITY MATING. It is more than a coincidence that most of the superseding characters which we know are, as the geneticist says, recessive. It is only under conditions of a moderate degree of inbreeding that the character shows up. Apart from my own experiences, four beekeepers who possess non-swarming strains all describe to me undoubted apiary-vicinity mating behaviour, and the continuance of such bees in recognisable form through many generations: a clear sign of repeated mating within the drone family of the parent. One beekeeper has shown me a hive, in an apiary of 50 colonies or more, which has shown the superseding character for 24 years, having been headed by six queens in this time. Local mating must have occurred in this stock repeatedly over this time. It has the added character of always superseding early in the year - late March, April or early May - at a time when many of the other more normal and in many cases swarmy stocks may have few or no drones on the wing (and when assemblies are most unlikely to have been set up).

Another beekeeper kept detailed records of a stock which did not swarm for twelve years although it had four queens during that time. H.J. Wadey refers in 1943 to "a colony which since 1921 has never swarmed at all, only once made swarm cells, and on six occasions superseded its queen, each time preserving her for some time with her daughter. Similar occurrences have been common with related colonies."[2]

One of these four beekeepers once witnessed a marked virgin from a nucleus running up and down the branch of an apple tree in the apiary, with a number of drones and some workers flying around. (The spot was definitely not a drone assembly place either before or after this event.) She then returned to the hive, but after 15 minutes came out and went back to the same spot. This behaviour was repeated several times before she eventually returned mated. It seems certain that she had mated in or near the tree.

On another occasion the same beekeeper witnessed a queen coming out of the hive entrance and walking over the face of the hive (having appeared at the entrance several times before), accompanied by an excited crowd of bees. After about two minutes the commotion subsided without the queen having flown, and the bees hurried back into the hive, fanning vigorously and leaving a dead drone in post-mating condition lying on the alighting board. The hive was immediately opened and the queen was found to be carrying the mating sign. A similar event had been observed some years earlier.

On yet another occasion he witnessed a drone hovering over a queen who was resting on a raspberry leaf. Unfortunately he disturbed her and she flew off. Another virgin was seen flying back and forth about 2 metres above the ground "like a dragonfly over a pool". A drone flew to her, clasped her, and then fell to the ground, but mating was not accomplished. (The queen did mate the same afternoon.)

Corresponding behaviour by what was almost certainly a drone bee has been described to me by another beekeeper. The drone was hovering and approaching and grappling with worker bees as they flew in a regular flight path.

A third beekeeper was surprised to notice that while he was sucking a swarm out of a hedge with an industrial vacuum cleaner, a number of drones were flying in the vertical air column blowing out of the cleaner, doubtless attracted by queen pheromone.

A fourth beekeeper described to me the unusual experience of witnessing a queen and drone, coupled together, flying slowly across the apiary at head height. (The incident was preceded by a buzzing noise as if of a swarm.)

Drone comets (such as are known to form in assemblies also) have been seen moving or hovering in apiaries, often crashing into the ground, by a number of beekeepers including my wife and myself, particularly (though not exclusively) when virgins were known to be present in hives.

These incidents (which can be parallelled in the literature) show that both queens and drones can behave in ways likely to lead to mating close to the ground, or even on it, often within the confines of the apiary; and several of them provide practically conclusive evidence of mating actually taking place in such circumstances. Despite the growing evidence and personal experience of drone assemblies in our Islands, therefore, my faith in the existence of "apiary vicinity" mating remains undiminished[3].

The effect of this type of mating behaviour is that a queen is likely to mate with one or more drones from her own hive, which in the case of strains with non-migratory drones, are likely to be her own "brothers". Alternatively she may well be fertilised by drones from other hives in the apiary, whose bees are, more likely than not, related to her. Thus we have here a powerful mechanism for securing some degree of inbreeding, with all its consequent advantages and disadvantages.

Since this type of mating is practicable in cool as well as in warm weather, it must be of particular value to queens trying to mate very early or very late in the season, or at any time when the weather is too cold for prolonged flight.

2. MINOR (LOCAL) ASSEMBLY MATING. A local assembly, as I have already indicated, usually forms not far from an apiary, often within 200 metres, and drones from several or all the apiary's hives are known to take part in them.

One beekeeper has described to me how he followed a virgin queen from a nucleus in his apiary towards a spot some 15 metres away where drones were known to assemble. He saw there a drone comet, from which a queen fell to the ground and then flew off. Hastening back to the nucleus, he saw the virgin return some 10 minutes later with the mating sign. Again, not conclusive, but highly suggestive evidence.

Using small pocket thermometers I have been able to measure temperatures in places where I had previously observed drone comets, and where I have known queens to mate close to an apiary. In the past I used a small pocket mercury thermometer; more recently a small digital thermometer with a very fine thermocouple attached. This may be carried aloft by a balloon. All my measurements have given me a clear idea of why drones are where they are; namely in warm air. Because of this I now prefer to call this type of assembly a "bubble assembly". It occurs in a bubble of warm air which generally forms during a sunny period of the day, or when a brief gap in the clouds permits sunshine for a few minutes. The bubble of warm air then forms in a place which is well sheltered from the winds.

Typically such assemblies form, often lasting for short periods only, in weather which is unsuitable for intensive and long-distance bee flight for one reason or another. Cool days when temperatures hover just above the 10 degree C mark show one such type of weather; days which are warm but also cloudy, often thundery and showery, show another. Humidity is often high on such days, discouraging long-distance bee flight (particularly in cool weather) but assisting the warming up of vegetation when the sun does shine. Humid air, being more unstable than dry air, can also conduce to the formation of "thermals".

The shelter required for such a bubble to form may be provided by a group of buildings, hedges or trees, or even by some physical feature such as a hill or hollow. Even a brief burst of sunshine will warm the buildings, vegetation or ground, which will immediately begin to transfer some of this heat to the neighbouring air. Because of the lack of wind, warm air will build up a bubble of distinctly higher temperature than that of its surroundings.

The use of buildings and walls to provide shelter and store solar energy has of course been well known to gardeners for centuries. It seems as well that in the weather conditions described, trees and hedges can not only give shelter but also heat their surrounding air significantly. Dark-coloured leaves with their large surface area rapidly warm up under solar radiation, and just as rapidly transfer heat to the neighbouring air. In conditions of high humidity, counteractive cooling by evaporation of water will be reduced. The same is true when the leaves are sticky with honeydew. The shelter provided by the tree canopy allows a bubble to form. Sometimes a tree or group of trees can create a "mini-thermal" as the air heated by them rises, drawing up air warmed by contact with the ground to be further heated and maintain a rising or eddying column of air.

In the cooler variety of weather conditions just described, it has been found that dark-pigmented drones of *mellifera* type may fly freely, while Italian drones come out of the hive and go straight back in again because it is too cold for them. At such times, as in 1981, mating success of native queens is noticeably better than that of Italians. It is not certain how much of this effect is due to dark colouring and how much to other, unknown factors. At any rate it tends to ensure that drones and queens of predominantly native type will find and use bubble assemblies during many of the weather conditions favouring their formation. Altogether this type of assembly would seem to promote inbreeding and within-strain mating, though not to the extreme degree of apiary vicinity mating.

3. MAJOR (DISTANT) ASSEMBLY MATING. Although heated air may well play a part in assemblies of this type, and there are doubtless intermediates between them and the bubble type, major assemblies are distinctive in a number of ways. They are usually made possible by the interaction of wind and topography, producing a vortex of twisting, rising air. I have often referred to this type therefore as the "vortex assembly".

Such vortices generally form regularly in particular, widely-spaced spots whenever wind conditions are right. The energy contained within them is usually much greater than that in a bubble assembly. Drones use them only in fairly prolonged warm or hot periods, when long-distance bee flight is feasible and the drones can learn their location on successive flights.

Since marked drones have been recaptured twelve miles from the point of release, it is reasonable to assume that drones can, under ideal conditions, fly very much further. It would not be absurd to assume that individual drones may on rare occasions fly 20-25 miles. Queens probably fly for very much shorter distances, but even so a queen which can reach a major assembly could mate with a drone from 20 miles or more away. In such an assembly, drones closely related to the queen may be greatly outnumbered by unrelated drones from far away. Although the possibility of inbreeding is not eliminated, its likelihood is greatly reduced in favour of a high degree of outcrossing.

There is some indication that queens of native type may be less inclined than others to seek distant assemblies and less good at finding their way home from them, so that their genetic effect may be somewhat diminished. Nevertheless such queens and drones do use these assemblies; after a hot summer the percentage of native queens producing hybrid offspring usually increases markedly.

Thermal turbulence[4]

Let us first consider those types of major assembly in which heated air plays a part. It is well known that, during warm sunny weather in the British Isles, differential heating of the land surface by the sun commonly causes thermal turbulence, in which rising bubbles and columns of air, typically 150-300 metres across, are heated by contact with warmer patches of ground, and balanced by descending currents elsewhere.

Much of this turbulence may be irregular and effectively random as bubbles break away and drift off with the wind, in which case it may be of little value to drones and queens seeking stable up-currents. There are situations however where such heat-induced turbulence is regular and predictable because of the physical nature or configuration of the ground.

Patches of sandy soil, sparsely covered with vegetation, are one such case in point. Around midday the surface of the ground there begins to get significantly hotter than that of the surrounding areas. This temperature differential can be quite extreme in some circumstances. The film of heated air in contact with the ground will ascend, particularly around any rise in the land, and such ascent will be a regular afternoon phenomenon as long as the right weather conditions persist. Golf courses, commons and heaths, usually found on poor sandy soils in the British Isles, are therefore good places to listen for drone assemblies (particularly as they tend to be quiet places! One would expect assemblies in similar thermals which rise from towns and villages - perhaps the noisiness of such places has led to a dearth of drone-assembly reports from them.)

A number of drone assemblies have been recorded over marshes. These are often situated in sheltered hollows where the air can easily become heated and, because of its high humidity, can become unstable and so encourage rising thermal movement.

Sea breezes

The sea breeze is another heat-induced phenomenon known to be associated with drone assemblies. Heating of the land increases air pressure and starts a seaward drift of air at higher levels, which is balanced by a breeze blowing in off the cooler sea onto the land at the surface. Part of this rotational movement is a belt of warm rising air at a short distance inland. This belt of rising air may even develop into a kind of front, sucking air from further inland into a zone of converging, rising air perhaps 20 miles or more from the coast. Sea breezes in the British Isles develop mostly in settled, anticyclonic conditions, and are strongest in the afternoons. They are seldom very pronounced, but can reinforce other effects locally. On offshore islands and peninsulas, sea breezes from different directions may meet and create stronger updraughts and vortices.

Valley winds

The "anabatic" valley wind is another means of creating updraughts or vortices. Under the same weather conditions, heated air on the slopes of hills and mountains tends to move upwards. Where such slopes face each other across a valley, a wind blowing upwards along the valley bottom will eventually be generated. Funnelling effects increase the updraught at the head of the valley, particularly where two or more such valleys meet at a pass or col between higher ground on each side. The air here has no alternative but to go on rising, and the meeting of two airstreams can easily initiate a twisting motion. The development of such winds as the day progresses is quite complex, but for our purposes it is sufficient to note that the maximum effect is usually in the early afternoon. Anabatic winds are generally of low velocity in the British Isles, but where they meet or where they are reinforced by a sea breeze or the prevailing wind they can certainly be significant.

Topographic turbulence

The other main kind of turbulence is that induced when a wind blows against a raised object, which for our purposes is usually a hill or range of hills. In passing over or around it (or both) there may be generated eddies (frictional turbulence) or standing waves to the lee of the hill. Standing waves may be accompanied by "rotor zones" of revolving air at ground level. At very high windspeeds "rotor streaming" develops in which the whole airstream rotates to the lee of the hills.

It would seem that most of these effects are observable only when prevailing windspeeds are too high for drones and queens to fly. These effects are probably significant only where some peculiar topography is capable of creating vortices and eddies even when winds are light. Where winds are funnelled by valleys this may happen, especially where valleys converge. Possibly the main significance of prevailing-wind-induced turbulence is to reinforce and interact with thermal turbulence (sea breezes, anabatic winds etc.) during anticyclonic periods of fairly low windspeeds. An upper level wind, for example, may "cut off" the top of a rising column of air, setting an upper limit to the assembly. Another common effect is for the upper parts of the assembly to be deflected sideways by the prevailing wind. Local topography, by directing two airstreams towards each other, may also induce a twisting motion in heated, rising air, thus helping to initiate a true vortex.

It is also possible for topography to have a similar effect as in the case of "bubble" assemblies; i.e. to create a sheltered area of lower windspeed where thermal movements can have their effect. One would expect this to happen where the prevailing windspeed is around the maximum for queen and drone flight.

Visual stimuli

Dr. J. Van Praagh[5] working from Utrecht University has investigated drone assemblies in the Netherlands, Germany and Austria from an optical point of view. Using a special measuring device he found that known drone assemblies are in a kind of "optical trap" where light intensity is fairly uniform from all directions. He postulates that drones reaching such areas are automatically sensitised to queen pheromones, and that air movements within the "trap" may then determine the exact location of the assembly. This interesting possibility needs to be investigated in the British Isles.

Observing drone assemblies

Although sight, touch and even smell can be of assistance in their search, it is with the sense of hearing that most observers have experienced drone assemblies; though seldom with any idea of what they were listening to. A few quotations from literature and hearsay will make the point:

(9th July 1779) "A surprizing humming of bees all over the common, tho' none can be seen! This is frequently the case in hot weather."

(1st July 1792) "There is a natural occurrence to be met with upon the highest part of our down in hot summer days, which always amuses me much, without giving me any satisfaction with respect to the cause of it; and that is a loud audible humming of bees in the air, tho' not one insect is to be seen. This sound is to be heard distinctly the whole common through, from the Money-dells, to Mr.White's avenue-gate (at Newton). Any person would suppose that a large swarm of bees was in motion, and playing about over his head."

Gilbert White, *Journals.*[6]

"The haymakers sometimes talk of mysterious noises heard in the very finest weather, when it is calm, resembling distant thunder, but they were convinced it was something in the air."

Richard Jefferies, *Wild Life in a Southern County.*[1]

"Oh, that's nothing: that's only the midsummer hum!"

Hampshire farmworker, c. 1934.

"The summer joy is singing in the air."

Saying of Carinthian beekeepers.

The sound of a drone assembly has often been described as that of a "swarm", especially by those with little or no experience of beekeeping. It is a loud but low-pitched hum resembling that in an apiary when a multitude of drones are on the wing, but far off and more mellow, without the shriller pitch of worker bees. J.G. Hayden has written, "I am fully acquainted with the 'hum' of swarming bees but I was always mystified by this deeper, louder, yet pleasing constant droning . . .", elsewhere he refers to the sounds as "weird reverberations". He found the noise "pleasing", Gilbert White found it "amusing"; some observers have called it "terrifying"! Most observers have been quite baffled as to the true nature of the phenomenon, often looking around for swarms or foraging bees, without success. There is evidence, however, that a few beekeepers in some parts of the British Isles did know what they were listening to; an old Northamptonshire beekeeper is quoted as referring to the "courting place of the queens" (the assembly at Gretton), while I have heard of a Scottish beekeeper who used to take his queens to a particular spot on the moors where he knew he could be sure of getting them mated quickly.

The sound is heard over a patch of ground which is plottable into sound-level contours with a central area, or more than one discrete area of high audibility, surrounded by areas of decreasing audibility; at the latter the sound may well be inaudible to those with less acute hearing.

The area of maximum sound is variable in that wind strength, direction and gusting are variable, as also are the altitude, flight direction and numbers of flying drones. The whole area over which the sound is audible may appear to move about according to the time of day, and according to the changes in energy value and relative directional strengths of the different winds involved. The area of maximum volume is not always synonymous with the "eye" of the vortex or assembly. It may seem to be downwind of where the drones are seen to be actually flying.

The "eye" is the term used to denote the cone of stationary and near-stationary rising air at the base of a vortex, below which the flight of drones flying to and fro in numbers produces the volume of sound which we recognise as constituting the drone assembly. Within the eye, the onlooker feels it to be calm, hot and sultry compared with surrounding areas, because there is little cooling movement of air across his face. Such little wind as there is is variable in direction, as slight eddies press in from one side or another. The eye is the point of balance where energy supply from one direction exactly balances that from at least two other directions (a triangulation effect). If the wind strength from one of the three directions is less than the combined moment of the two others, the eye will move downwind until balance is reached, forcing the horizontally moving air to move vertically upwards.

Although it is usually by sound that a drone assembly is first suspected and identified, the actual drones in it are sometimes visible. In assemblies on passes it is often possible to look down on the vortex from adjacent hills, and to watch the drones flying up and down, according to the slope of the vortexing tube of warm air, and doubling back at the end of their traverse. It may be easy to see them, aided by binoculars and sunglasses, at the lower end of their trajectory, but less easy to see where they turn back at their zenith. In bubble assemblies drones are often not hard to see turning back in more or less horizontal flight.

Terence Theaker attempted to follow the drones which were making off in one definite direction from his apiary towards a presumed drone assembly, with only partial success. A trick which often works at assembly places is to throw small pebbles high in the air and watch to see if they are chased by drones as they fall. Helium-filled balloons with queens tethered to them were successfully used by BIBBA in the Isle of Man to lure drones downwards in an assembly place, where it was possible to photograph, film and tape them. Increasing windspeeds sometimes make assembling drones descend almost to ground level before being forced to disband the assembly altogether. Occasionally, high buildings make useful observation points, and light aircraft would seem to have possibilities.

A few indicators of the warm, anticyclonic weather conducive to the formation of distant drone assemblies are: mirages seen over roads, fields and roofs; tar starting to melt on the roads; and in areas of coniferous woodland the smell of pine needles. At such times the beekeeper visiting his apiary should watch to see if all the drones appear to be making off in one direction. One drone assembly known to me is noted for its attraction to glider pilots in search of rising air, another as a good place for kite flying, and a third as a place where seagulls may often be seen soaring.

The serious investigator of drone assemblies can usefully provide himself with a small pocket thermometer for identifying "bubbles" and thermals, a hand-held anemometer for confirming the relatively still air at the eye of a vortex, and perhaps some gadget for emitting smoke or soap bubbles, or balloons filled with helium, for tracking wind directions. In further research one can envisage the creation of artificial drone assemblies using equipment such as large fans or heat sources which could set up rising columns of air.

List of drone assemblies

After the name and grid reference of each drone assembly site are listed (a) the date(s) it was observed, (b) the observer(s), (c) any details relating to the site, and (d) the weather conditions and any other remarks. Grid references within the UK are to the Ordnance Survey's National Grid. References are 6-figure or 4-figure according to the precision of our information. In some cases there is an element of guesswork, and the most doubtful references are followed by (?). In nearly all cases, however, any error is likely to be less than one kilometre.

England

CORNWALL

1. Perranporth, SW 764 547. (a) "Several years" down to 1982. (b) W.G.Lyne. (c) Coastal golf course on sandy soil, (d) Weather warm.

2. Trevose, SW 863 752. (a)-{d) As No.l.

CUMBERLAND

3. Brampton, NY 538 585. (a) July 1975. (b) T.Davison, (c) Golfcourse fairway and adjacent ridge, (d) Weather very hot.

DERBYSHIRE

4. Darley Dale, SK 253 632. (a) Several years down to 1973. (b) A.J.Graham, (c) On a hillslope. (d) Only heard on really hot high summer days; peak at l-2pm BST, but heard till 7pm.

5. Elvaston, SK 413 329. (a) June-July 1980. (b) G.Cooper, (c) Over walled ha-ha bordering country park, (d) Weather still and hot.

6. Hopton Wood, SK 561 262. (a) Late May 1973, early June 1974. (b) D.Robinson, (c) Deep wooded valley, (d) Bright sunny day.

7. Thulston, SK 410 320. (a) 10th & 13th July 1975. (b) B.A.Cooper, (c) Over part of BAC's apiary in back garden - level ground, (d) Assembly in patch of still air, stopped when wind rose. Weather dullish, temperature approx. 21 degrees C (70 degrees F). Drones seen.

8. Whatstandwell, SK 340 545. (a) Three times in 1975, twice in 1976, all mid-July, (b) Mr. & Mrs.R.Burleigh, (c) No details, (d) "Terrifying" humming sound; early evening in hot weather.

9. Willington, SK 500 299. (a) Before 1968. (b) B.A.Cooper, (c) Not heard since building of power station.

DEVON

10. Doddiscombsleigh, SX 845 864. (a) 4th-10th July 1976. (b) W.Davie, (c) Hollow beside a 600 foot hilltop (highest spot for miles around), or slope on other side of hill, (d) Hot, sunny or hazy humid weather, light local winds. Drones seen.

11. Tiverton, SS 97 12 (?). (a) Early July 1974. (b) P.Burdett. (c) Over large oak tree on canal bank, (d) Midday to early afternoon; still, humid weather.

ESSEX

12. Gilwell Park, TQ 389 965. (a) Mid-May 1971. (b) B.Clarke, (c) No details, (d) Average spring weather, bright and sunny, low breeze; "swarms of bees circling above the highest trees like smoke".

HAMPSHIRE

13. Redenham Park, SU 295 492. (a) About 1945. (b) H.W.Crowson. (c) Over hazel/oak plantation, level country, (d) No details.

14. Selborne, SU 735 333. (a) 9th July 1779; 1st July 1792; approx. 27th

June & 4th July 1973. (b) Gilbert White; H.W.Crowson, B.A.Cooper, (c) High common with trees on downland. (d) Weather hot and sunny; audible half a km away.

15. Waltham Chase, SU 560 140. (a) August 1940. (b) J.G.Hayden. (c) No details, (d) Atmosphere "slightly disturbed."

HEREFORDSHIRE

16. Hergest Ridge, SO 255 563. (a) 25th June 1976. (b) E.A.Tunbridge.
(c) Two flattish areas on ridgetop. (d) Drones clearly visible 10-15 feet above the ground, but they went up to a considerable height.

17. King's Caple, SO 560 288. (a) 13th June 1973 (approx.). (b) T.Grimwood, E.Brown & J.Williams, (c) Orchard on lowish hill in the centre of a plain surrounded by higher hills, (d) Weather still, bright, sunny.

LEICESTERSHIRE

18. Breedon, SK 400 233. (a) 1st July 1975; 30th July 1981. (b) D.Shields, B.A.Cooper, (c) "Pass" near electricity pylon and old buildings, (d) Weather hot (approx. 24 degrees C), still or with light breeze. Drones seen.

19. Wilson, SK 404 242. (a) 13th July 1980. (b) D.Shields, (c) No details.
(d) Overcast but hot, humid and still; heard early to mid-afternoon.

20. Medbourne, SP 814 932. (a) 1st half of July 1979. (b) K.Grant & Mr. Cramp, (c) In and near disused quarry towards top of a hill, "like a sun trap", (d) Weather very hot and still.

NORTHAMPTONSHIRE

21. Gretton, SP 904 954. (a) June or July 1944, (b) C. Shillaker. (c) Slight depression on side of escarpment, (d) Hot and sunny day around noon, slight wind. Drones seen.

NORTHUMBERLAND

22. Allendale Moor, NY 81 55. (a) Many occasions over a number of years, (b) T. Davison, (c) Sites variable - some ridges, others over open, flat places, (d) Hot, sunny days. Drones seen.

23. Alnwick, NU 173 163. (a) July 1973. (b) A. Lawson. (c) South face of a hill over spruce trees, (d) About lunchtime on a hot, sunny day; weather hot for 3-4 days previously.

35. Petworth, location uncertain; perhaps TQ 010 213. (a) July 1974. (b) H. Holland, (c) Over evergreen tree in quarry, (d) Very still in quarry, light breeze outside; bright sun after rain, sultry; time 2 pm. Drones seen ascending and descending over tree.

WARWICKSHIRE

36. Snitterfield, SP 202 592. (a)-(d) No details.

WORCESTERSHIRE

37. Severn Stoke, SO 866 445. (a) Haymaking time, year unknown, (b) J. Crundwell, A. D. Williams, (c) High point with panoramic views, (d) No details.

YORKSHIRE, EAST

38. Spurn Point, TA 400 108. (a) 2nd July 1983. (b) W. Bielby, A. Knight.
(c) Over a depression in front of coastguard tower, (d) Observed near mininuc mating apiary provided with drone colonies: no other bees within flying range. Drones seen.

YORKSHIRE, NORTH

39. Scarborough, TA 027 908. (a) May or June 1947. (b) C. Breech, (c) Between river and high drainage bank, S-facing. (d) Weather very hot.

40. Terrington Carr, SE 686 718. (a) Probably July 1944, 1945 or 1946. (b) B. A. Cooper & F. W. Kimber. (c) Marsh, (d) Present on hot, sunny days, absent on dull days.

YORKSHIRE, WEST

41. Rycroft, SE 072 382. (a) 11th June 1975, & one other occasion, (b) A. Carruthers. (c) Between wood and field, (d) Clear hot day (temperature approx. 86 degrees F), strong breeze.

42. Seacroft, SE 35 36 (?). (a)-(d) No details.

IRELAND

CO. KILKENNY

43. Derrylacky. (a) July 1955. (b) F. Dineen. (c) Plateau between valleys.
(d) Very dry, sunny weather.

24. Langley, NY 850 612. (a) Haymaking time, 1945. (b) T. Davison, (c) Slight hollow between two ridges, (c) Weather hot.

25. Wallington Hall, Cambo, NZ 033 844. (a) July 1968; July 1972. (b) N. M. Sinnister; C. I. Richardson, (c) Over woodland and lake, (d) Weather warm & sunny.

SHROPSHIRE

26. Styche Hall, Longford, SJ 644 345. (a) "Nearly every year for 40 years" (to 1975). (b) W. H. Masters, (c) Marshy hollow, (d) Heard on very hot days.

27. Two Crosses, Clun, SO 239 867. (a) July 1981. (b) D. Davies. (c) 8-10 feet above a sycamore tree, (c) Drones seen.

28. Two Crosses, Clun, SO 240 868. (a) 15th August 1981. (b) D. Davies. (c) Over bottom of narrow dell and nearby field, (d) Hot, sunny, still & humid; time 2-2.30 pm BST.

29. Two Crosses, Clun, SO 243 863. (a) 16th Aguust 1981. (b) G. & B. A. Cooper, Mr. & Mrs. Davies. (c) Top of low hill, (d) Temperature 17-22 degrees C, force 3 wind but assembly area calmer; time 3-4.30 pm BST.

STAFFORDSHIRE

30. Anslow Gate, SK 200 253. (a) July 1977. (b) Mr. F. Sharman. (c) Over shallow valley, (d) Sunny day; time pm BST; about 120 feet above ground. Drones seen.

SURREY

31. Chessington, TQ 18 63 (?). (a) Several times between 1957 & 1964. (b) Mrs. Deakin. (c) Slight SE-facing slope, sheltered from cold wind, (d) In hot, sunny, humid weather.

32. Churt, SU 840 388 (?). (a) Many times down to 1969. (b) Mr. Baggs. (c) Over former coniferous woodland on slight rise, (d) Heard when temperature was over 70 degrees F and pine needles smelt strongly.

33. Puttenham/Wanborough area, SU 485 925. (a) About 1934, in June, (b) Mr. Baggs. (c)-(d) No details.

SUSSEX

34. Eastbourne, TV 601 969. (a) Not recorded, (b) Member of Eastbourne BKA. (c) At end of promenade on sea front, (d) No details.

CO. MEATH

44. Gormanston. (a) 22nd July 1971. (b) B. A. Cooper, (c) No details, (d) Sunny afternoon, coolish breeze; time about 3 pm.

CO. WEXFORD

45. Forth Mountain, (a) 27th July 1971. (b) G. & B. A. Cooper, D. Ost. (c) Marsh to north of mountain peak, (d) Air calm despite strong wind elsewhere, hot day.

ISLE OF MAN

46. Ballaghennie, NX 439 025 (?). (a) Summer 1966. (b) B. A. Cooper, (c)-(d) No details.

47. Kerrowmoor, SC 402 947. (a) June 1968. (b) G. Ball, (c) Sheltered corner below brow of hill, (d) Drone comet seen flying around chasing queens, queen fell to ground and seen to return mated to nearby hive 10—15 minutes later.

48. Port Erin, SC 198 697. (a) August 1966 (twice); August 1972 (many times); June 1973 (several times); 9th August 1975. (b) A. Palmer; B. A. Cooper; many participants in BIBBA Conference 1973. (c) Golfcourse green between low hills on peninsula, (d) Always on bright, sunny days, often breezy. Drones seen, photographed, filmed and taped.

SCOTLAND

AYRSHIRE

49. (Location unknown), (a) Approx. 1940. (b) J. L. Burgoyne. (c)-(d) No details.

50. Carrick Hills, NS 291 162. (a) Approx. 1955. (b) J. Mackay. (c) Over two hilltops, (d) No details.

BANFFSHIRE

51. Portsoy, NJ 531 602. (a) 22nd June 1975. (b) B. Mobus. (c) Heathy hilltop, (d) Day was a "scorcher". Seagulls using rising air currents.

DUMFRIESSHIRE

52. Glencaple, NY 00 68 (?). (a) Several times down to 1950. (b) J. G. Hayden.

(c) Ridgetop. (d) Weather always hot, sunny and perfectly still; time approx. midday GMT.

53. Moniaive, NX 773 911. (a) About 1965. (b) Mrs. Davidson, (c) Over trees in a garden below a hillside, (d) Hot, thundery weather; late afternoon.

INVERNESS-SHIRE

54. Crask of Aigas, NH 465 429. (a) 22nd June 1975. (b) B. A. Cooper, A. G. Edwardes. (c) Pass between hills with dead air focus, (d) 60 degrees F in bright sun; time 2-2.30 pm; isolated drones seen next day at 59 degrees F.

55. Kilmorack, location uncertain; possibly the same as No. 54. (a) 20-25th August 1966; late August 1973. (b) A. McRae, B. A. Cooper, (c) Top of a pass, (d) Very hot sunny weather. 1973 observation (BAC) was of drones flying towards this point.

MIDLOTHIAN

56. Edinburgh, Braid Hills, NT 254 694. (a) 28th June 1975. (b) B. J. Sproule.
(c) Rocky hills with grass and gorse - golf course, (d) Hot, cloudless day with light northerly breeze; time 3-6 pm BST. Drone comet seen 8 ft from ground, otherwise no drones visible.

PERTHSHIRE

57. Forgandenny, NO 091 180. (a) About 1966, late June or July, (b) R. Couston. (c) North side of and above trees on North-sloping hill, (d) No details.

ROSS-SHIRE

58. Knock Farrell, NH 505 585. (a) 8th August 1975. (b) D. Hulme. (c) On high ridge, (d) Clear sky, temperature 83 degrees F, light southerly breeze; time 2.50 pm BST.

WIGTOWNSHIRE

59. Lochnaw Castle, NX 998 631. (a) Often in July between 1971 and 1974.
(b) C. Munro. (c) Over mixed patchy woodland immediately NE of loch.
(d) Hot, sunny weather.

WALES

60. Near Cwrtnewydd, SN 48 47. (a) Frequently, (b) G. Jenkins, (c) Over trees in mating apiary, (d) In "suitable weather".

Remarks

We shall not attempt an exhaustive statistical analysis of the above data, though a trained statistician might care to do so. Some definite conclusions seem to emerge, however:

1. Time of year. When mentioned this is usually July. The earliest date is around mid-May, the latest is 25th August.

2. Weather. There seems a clear positive correlation with temperature. Several observers went out of their way to comment that the phenomena were experienced on very hot, sunny, often humid high summer afternoons. The lowest measured temperature was 60 degrees F. There are cases of winds of up to force 3 (Beaufort scale), however, though when investigated many drone assemblies have proved to be points of relatively calm air when winds are blowing all around. Occasionally drone assemblies have been observed in hazy conditions or even under overcast skies when appreciable solar radiation was still getting through the cloud cover.

3. Time of day. Early to mid-afternoon is the commonest time mentioned, the earliest observations being "around midday" (BST) or "around lunchtime". No assembly is known to have been observed in the morning; the latest time noted is 7 pm BST.

4. The type of site varied enormously: hilltops, valley bottoms, slopes, level ground, over trees and marshes are all mentioned more than once.

CHAPTER SIX

Management of Native Bees

Aims of management

The Village Bee Breeders' Association was formed in part as a reaction against the overwhelmingly management-oriented approach to beekeeping which was and is still predominant in this country. Excessive concentration on (often time-consuming) management techniques for solving all problems, it seemed to us, was responsible for the neglect of the study of variability within the honeybee species, and for the failure to adopt breeding solutions. These latter, though demanding far-sightedness and the pursuit of long-term aims, could, we felt, often solve the problems more radically and with a greater long-term economy.

An appropriate system of management is however obviously a *sine qua non* for every serious beekeeper including, or rather especially, the breeder.

The breeder of native bees must adopt a scheme of management which satisfies the following requirements: - 1. It must suit the strain of bee being used. 2. It must suit the beekeeper's available capital and labour resources, as well as his district's peculiarities of climate, soil, flora etc. 3. It must leave the beekeeper time to concentrate on evaluation and breeding. 4. It must facilitate the progress of breeding work by, for instance, enabling variability between colonies to manifest itself and be detected, and by encouraging the survival of the desired type of bee and the elimination of undesirable types.

Since the above factors and their relative importance will vary greatly between one beekeeper and the next, even among those keeping native bees, it is impossible to lay down a standard system of management to which all such beekeepers should adhere. In any case an undue degree of standardisation can hinder experimentation and progress. British and Irish beekeeping has been bedevilled by the dogmas of rival "do as we tell you" groups, whose company we have no wish to join.

In what follows I shall therefore merely outline some of my own management techniques as practised in my years at Thulston, showing where possible how they are governed by the above criteria. I shall take these in order.

1. The strains of bee I have been keeping in and around Thulston have been mainly of East Midland and North Yorkshire origin, long-lived and generally non-prolific even by native standards. They are infrequent swarmers, making preparations to swarm, if at all, usually only every 3rd or 4th year. The habit of queenright supersedure is well-developed in most colonies.

2. I have generally been prepared to spend money on equipment of proven

worth, where this will save on management time later. Hence my insistence on equipment well-made from good quality materials. My spare time available for management, never great, has declined almost to vanishing point, and thus my system has become a "minimum-management", semi-let-alone, or "extensive" one (see below).

The districts in which I have been keeping bees have been generally poor: districts of light soils and increasingly arable agriculture with meagre flows of both nectar and pollen. However heather and, more recently, oilseed rape, have provided supplementary flows. I have generally run around 30 stocks. Although short of time, I am always prepared to move my bees to a nectar-yielding crop, finding this well worth while in my nectar-starved district.

3-4. It has been my concern to observe and evaluate my bees above all short-term management considerations, and to propagate particularly bees of pronounced native type. My interest has been particularly in the habit of supersedure.

Altogether my management has moved in the direction of what the French call "extensive" as opposed to "intensive" management. In the former (labour-oriented) system, the weight of honey per man-hour is the criterion of success or failure, whereas in the opposite (capital-oriented) type, it is generally weight of honey per hive roof which is the criterion. Thus I have been prepared to buy and run extra hives, in order to save on management and transport time. This policy I believe to have been a success, suiting my bees and my lack of spare time. Even judged by intensive standards I think my system shows up well - I expect 100 lbs of honey per hive in an average year, even in a poor district.

Every beekeeper must of course work out his or her own scale of priorities, adding perhaps factors not mentioned here. Some, for example, like Terry Theaker, may want to devise a "minimum weight" management system, whether through age, disability or disinclination for lifting heavy weights.

Equipment

1. HIVES. In my early years of beekeeping I gained extensive experience of single and double broodbox National, WBC and Smith hives, as well as single broodbox Modified Dadant. The WBC I found took 33% more time in manipulation than the National/Smith, and as it seemed to offer little advantage in my area in return for its high cost, I discarded it. The MD I found too heavy to be easily moved, while less prolific strains of bee stored an unduly large proportion of their surplus honey in the large brood chambers, and sometimes left the entrances insufficiently guarded against robbers. The choice lay then between the National and the Smith.

My choice eventually rested on the Modified National hive (similar to the Irish "Dublin" hive) for two main reasons: its superior handhold and the bottom beespace enabling a framed glass quilt to be used [1]. Having studied and photographed people engaged in hive manipulations I have found that the deep handhold materially eases handling of boxes: an advantage which is felt every time a box is lifted, and which becomes ever more beneficial as one gets older. The advantages of glass quilts are dealt with below.

Having settled on a hive type, one has to decide whether to run it on a single, double or "one and a half" system.

From 1947 to 1955 a colleague and I kept about 25 stocks of the prolific Fenland bee on double broodbox Nationals on the management teachings of my old friend William Hamilton. These bees built up big colonies early on such a system, harvesting well from turnipseed (flowering in May). But I found the practice of early artificial swarming necessary for this swarmy strain too much work. The double broodbox, like the MD hives, I found had no effect whatsoever on the incidence of swarming compared with single box Nationals.

With the much less prolific North Yorkshire, Lincolnshire and East Midland strains I found definite disadvantages in double broodboxes. Often the bees would work up into the upper part of its brood area in late summer, leaving comb near the entrance open to robbing by wasps and other bees. I, and other users of similar strains, have lost many stocks in this way.

Another problem is that the double broodbox may encourage normally non-prolific strains to "overbrood" and become out of phase with the nectar-secreting flora. In a good year this may pay off, but in a poor year it can be disastrous, the stock producing much less surplus than if left on a single box or even needing summer feeding. Such overbrooding may greatly shorten the life of the queen, upsetting one's breeding programme where this depends on progeny testing and selection for longevity. The bees may also spread honey over too large an area and have difficulty in ripening it all.

Prolific strains, I have found, may be divided into the "compressible" and "non-compressible". The former are not encouraged to swarm by being kept in a small broodbox, while the latter are. The use of a single broodchamber acts as a filter, showing up the "non-compressible" types and allowing them to be culled, whether naturally or deliberately by the beekeeper. (Non-prolific strains, on the other hand, may actually be encouraged to swarm in a double broodbox because of the increased number of bees, when they would not have done so in a single box.)

For these reasons I came to adopt single-broodbox management for honey-producing stocks (though using double boxes for other purposes such as propagation and drawing foundation). My costs, management time and effort have thereby been greatly reduced, while my honey production has not fallen.

The official standard for the Modified National hive specified a bottom beespace. The bees don't mind whether their beespace is at the top or bottom of the box, but arguments have raged as to their comparative merits for the beekeeper. Boxes with top beespace are undoubtedly easier and cheaper to construct, and the use of a shallower floor can eliminate brace comb below the frames (at some cost in ventilation). Against this, the bottom-beespace frames are somewhat easier to handle, particularly if one has left one's hive tool at home, while the excluder does not need to be framed. If the boxes are accurately assembled, and particularly if chevron-ended frames and Hoffman spacing are used, no more brace comb and propolis is used between boxes than in a top beespace hive. The deeper space above the floor attracts brace comb, but also allows ventilation and clustering space in hot weather.

2. QUILTS AND COVERS. These points are of small significance, in my view, compared with the possibility of using framed single-sheet glass quilts with correct beeways on bottom-beespace hives. In 1980 I had the pleasure of celebrating 30 years of use of exclusively single-sheet glass quilts. In my early days as a novice I acquired experience of cloth quilts, wooden crownboards and two-sheet glass quilts (two glass panels with a wooden divider). All had big demerits which to my mind quickly outweighed the apparent merit of low first cost. It did not take long to see the advantage of gauging what was going on within the hive, both visually and by sliding the back of one's knuckles over the glass to sense colony temperature contours. The glass quilt can give a lot of information which cannot be deduced from entrance watching, and can give similar information more quickly, and without disturbing the bees or getting stung.

In winter the glass quilt enables the size and tightness of the cluster to be gauged. Restlessness or the presence of drones may be apparent. Excreta stains and dampness warn of dysentery, nosema and amoeba, and the need for more ventilation. Amounts of remaining stores can be quickly estimated in conjunction with "hefting" (i.e. alternately lifting opposite sides of a hive to judge its weight). Bees actively running about may be warming comb for the start of brood-rearing, or in order to dry out a damp cluster.

In spring the warmth readily detectable on the glass indicates the presence and size of the brood nest. Appearance of drones can signal the time to begin preparations for queen-raising. Symptoms of diseases such as braula and paralysis can be spotted.

Concentration of workers round the edge of the box, because of overheating, or capped stores in the centre with nectar being sealed on the periphery, may show that more room is urgently required. Bees head upwards in rows along the top bar, secreting wax, warn of swarm preparations. Several days before the swarm emerges, such bees seem to disappear as they descend to near the entrance prior to the departure of the swarm.

Concentration of drones round the outside of the box is a sign that they will soon be expelled, while the sight of a queen running up and down the top bars of a broodbox can mean she has run out of room to lay.

Robbing may be spotted through the glass: expose the glass quilt of each hive in turn, block the entrance and tap the hive. The one which is being robbed will display robbers coming up to the light, running about frantically to escape, often chased by occupant bees. Bees in the colony doing the robbing will not exhibit this desire to escape. Appreciable wasp attack may be similarly detected.

When supers are removed from hives, glass quilts enable one to be sure they are bee-free - an important point when extracting is being done by non-beekeepers.

From the evaluation point of view, bee characters such as jumpiness, non-excitability, propolising and comb varnishing can readily be assessed through a glass quilt.

For a fuller treatment of the subject the reader is referred to BIBBA Leaflet No. 12[2].

3. FLOORS. I have standardised on the deep ($^7/_8$", 22 mm) floor, finding its entrance block useful for closing or restricting the entrance. It provides a good ventilation space in summer and allows observation of bees clustering below the comb. It does have one big snag, however: the brace or ladder comb which is built beneath the frame has to be scraped off if the combs are to be placed above others (e.g. in uniting).

4. ROOFS. I have found the deep 9" (225 mm) roof to be of value; it gives near-double wall conditions in winter, has special merits in wet situations and shows an appreciable advantage in hard or prolonged winters in addition to its better-known benefits against prying fingers. I have modified all my roofs by providing them with eight vent holes, two on each side. Experiments have shown that these assist moisture dispersal from the hive in damp or hard weather if used in conjunction with top ventilation of the hive boxes.

5. FRAMES. To minimise propolisation and maintain correct beeways between and above combs I prefer Hoffman sidebars and chevron (or "V") ends (see BIBBA Leaflet No. 12). Several aspects of the older convention of frame spacing have been observed to be weighted against British and Irish native strains; in particular the $1^3/_8$″ (35 mm) sidebar standardised for the Hoffman frame, which it turned out was suitable only for the physically smaller strains, causing larger bees to swarm unduly. Its use also results in undue crushing of bees when a comb of drone cells is withdrawn quickly: a big drawback to speedy handling. The old metal-end spacing of 1.45 inch (37 mm) is about right for all native strains to exhibit their best.

6. FOUNDATION. As mentioned above, native bees seem to do best on a cell size of 700 per square decimetre, and it has been my practice to give them this. Not all strains will make the change easily from larger to smaller, or smaller to larger cell size, but once they have been persuaded to do so, native strains seem to prefer the larger size.

7. DRONE FOUNDATION. I have found many merits in placing deep combs built on drone foundation into each broodnest. Most stocks will use one to one and a half combs per broodbox; some more, some less. My practice is to place one drone comb in each broodbox: i.e. one in a 10 or 11 frame box, two in a double box, and so on. I identify them with two nicks in the edge of the top bar to make these frames readily distinguishable in use.

Drone comb has important advantages in breeding, to be discussed in Chapter 7. It is also useful in management. If bees are given all-worker foundation in the broodnest, they will use every opportunity to remedy this imbalance by modifying worker comb to drone comb, and by building ladder and brace comb in any vacant space. This slows up handling of the colony and produces bulges and concavities which inhibit one's finding of queens, queen cups and cells and spotting of disease.

Bulges and concavities formed in this way make combs like a jigsaw puzzle; one cannot reverse them or move them to other positions without crushing bees when combs are pressed tightly together, and they also crush bees when withdrawing single combs vertically (which is all that is necessary in many management programmes to see the state of brood raising, queenrightness or colony development). Crushed bees are unnecessary, may spread disease, and will antagonise a whole colony and slow up examination. If the bees are "followers" this may in turn antagonise nearby colonies and lead to false evaluations.

It is because of the discomfort caused by bee crushing ("rolling the bees") that many people replace comb frequently. This is an unnecessary chore if adequate marked drone frames are used.

Wintering

During the exceptionally severe and prolonged winter of 1946-7 I was obliged to leave a number of hives on the bleak North Yorkshire Moors without any special preparation for wintering. They came through the winter splendidly, and ever since then I have made a practice of wintering normal-sized stocks without packing or insulation, and with through ventilation. The latter is achieved by having a deep floor and full-width entrance covered with perforated zinc of large diameter holes to exclude mice, a glass quilt raised on matchsticks at the corners and with its central feedhole uncovered, and a roof freely ventilating on all sides.

I have consistently found with native strains that with through ventilation the bees may eat more food and emerge with fewer bees in the cluster than stocks wintered warmly packed, but that they emerge more vigorous, and quicker to start brood raising, particularly in areas with few pollen sources. Possibly bees warmly packed have used up their protein/fat in winter and are starved of these substitutes for pollen for spring brood rearing. I also find that warmly packed stocks are worse affected by acarine disease: this is also true of very small stocks kept warm by artificial heating with electric light bulbs in cold periods.

An exception must be made, however, for nuclei and weak stocks. These do need mollycoddling, and will benefit from small boxes, top insulation and no through ventilation.

Most native strains in the autumn go into winter cluster at the front of the hive. I have seen this in the Midlands, in Essex, Yorkshire, North Wales and Scotland. Clearly there must be a selection pressure resulting in preferential survival under some conditions of wintering which favours bees which do this. The reason is not far to seek. Bees which have occasional winter cleansing flights will suffer less from dysentery, from nosema and maybe other diseases, and it may help bees to move to new supplies of food after prolonged confinement by bad weather. A cluster at the front of the hive is also good for defence against wasps and robber bees in autumn.

If the combs are placed "warm way" (parallel with the entrance) the bees gradually eat their way back towards the rear of the hive, never running short of food, whereas if the combs are "cold way" (at the right angles to the entrance), the cluster can move to one side and die with food still left on the other side of the hive. As a management practice I have for some years made a point of placing small nucs (two and three framers) warm-way right at the front of full-sized boxes with food combs placed behind them (to the north in hives facing south) to give them the greatest chance of strong wintering. When placed further back in the hive, such tiny colonies have fared less successfully - maybe due to damp as well as cold. Little colonies resulting from late propagation are quite unnatural things, and to allow them to succumb during winter would be a wasteful procedure, and useless from the breeding point of view.

Other colonies which I like to protect from undue hardship are stocks that have been robbed by wasps, and those with old queens being kept for propagation. Management dodges to minimise loss are to place the hives in a dry and airy spot, preferably on the south side of a hill where they can get the midday sun. An air-pervious barrier (i.e. not a wall) behind them assists air flow and permits cleansing flights most frequently; these are often necessary with heather honey or late-gathered and therefore uncapped stores.

It is surprising what bees can stand in winter and still come through: mice, minimal food, leaky roofs, damp from a host of causes, and even mild degrees of flooding. Damp is probably more harmful than any other single factor, particularly in a very cold winter, when the moisture produced by respiration freezes into stalactites from the quilt or crownboard, to conduct away the warmth of the cluster. This was what killed many very large colonies in the 1962-3 winter, when the smaller colonies, producing less total moisture, wintered safely. Management practices such as choosing dry sites, small broodboxes, sound hives and through ventilation go far to combat dampness. But it is remarkable how a vigorous stock comes to no harm at all when right behind the hive entrance, even if the floor slopes back and rain may turn the rear part of it into a pond. Bees can stand a lot of damp if fed early and if in possession of well-sealed stores in the comb and fat (from pollen) in their fat-bodies.

Stocks which are to be run for honey production, and all colonies whose queens are in their first winter, are wintered on a single broodbox. This helps to combat robbing and dampness, but also has important breeding purposes.

Bees that are genetically inefficient in packing honey round the cluster, or which consume too much food, are automatically culled by winter starvation. The same process tends to cull disease-susceptible stocks. The healthier the colony, the less likely it is to fly, even on warm days, and the shorter will be its flight period. Thus fewer bees will become chilled and lost on cleansing flights. This seems to apply whether the colony suffers from acarine, nosema, mice or AFB: appreciably affected colonies can be picked out in an apiary by the frequency of flight during the winter period. Presumably the colony is disturbed, loses cluster warmth, has to manufacture more heat by exercise, and in consequence tends more to early breeding.

A stock with a moderate dose of acarine eats more food in winter than a healthy stock, so that a great many of its bees are lost on cleansing flights during the period when the colony should be dormant. I found, as a voluntary "expert" in Lincolnshire, that the proportion of stocks with detectable acarine was much higher in those that died than in those that wintered successfully. But the ones that died were mostly on single broodboxes, whereas acarine-infested stocks wintered on double or on one and a half broodboxes usually survived - although they consumed very much more food than did healthy stocks. In other words, the smaller broodbox appears to select strongly for acarine resistance where the larger one does not.

The practice of wintering on a double broodbox can however be useful for stimulating spring buildup, particularly if the stock was strong in the autumn and was fed early. Colonies so treated are in a good condition for raising queen cells early in the season, for increase by division, for early pollination work or for harvesting early honey surpluses from crops such as oilseed rape.

Spring management

The truly "minimum management" beekeeper will take no special steps to stimulate the growth of his colonies in spring. If time permits, however, I find it useful to encourage broodrearing by cutting down on ventilation and providing insulation, by early opening of hives, and in some cases by early sugar feeding and providing extra pollen.

Usually in March I replace the mouseguard by an entrance block giving a reduced entrance, remove the matchsticks from below the quilt, cover the feedhole and place an insulating cover of polystyrene and insulation board over the broodbox. Experiments have shown that the broodnests of native strains exhibit a night-time drop in temperature during cold spring nights (see Chapter 3). This is a valuable aid to survival in adverse conditions and reduces the need for spring feeding, but is bought at the price of an increased susceptibility to chalk brood disease. Such loss of brood can hold back colony development and reduce the number of foragers available for later nectar flows.

The practice of opening hives and lifting out frames in cool conditions in early spring is much frowned upon by writers of beekeeping textbooks. This can indeed be dangerous in very cold weather, at least for small colonies which cannot replace heat loss and may chill overnight. There are some circumstances in which a colony should not be opened, or when a stock under examination should be closed up without delay. One instance would be a very small stock, perhaps building up on a single seam of bees. Or if frost is just descending and the bees are still in cluster: the bees cannot manufacture enough metabolic warmth to re-establish a proper cluster temperature. This is an October-March situation, and I have lost small stocks by disturbing them injudiciously at this time.

Normal sized colonies on the other hand may lose a few bees, but it takes a lot to really damage them. Owing to brood rearing, breaking cluster and movement activity, heat loss is fairly quickly replaced, though at some cost in stores consumed. This activity seems to stimulate brood rearing, flight activity and pollen gathering. In fact I would recommend early opening up to the beekeeper with healthy native stocks wanted for, say, fruit pollination.

It is possible that other strains of bee, from warmer climates, may behave differently, or suffer more. But I do not believe that consideration for these should be allowed to penalise those of more native type, which we are recommending because of their management versatility among other things: and for those like me with limited spare time, this can be their most endearing aspect.

As I wrote on 8th April to a correspondent,

> "Yesterday - very dull, air temperature 42 degrees F, strong ENE wind straight from the steppes! - I opened and went through an apiary of eight stocks of mine, and moved frames of one (due to a faulty box) into a new hive. There wasn't a glimmer of sun. Mad! These were the stocks I hope to propagate from in 1971, my chosen tested hives. A few adult bees would be chilled, but with taller-than-broad broodnests, these would be minimised. I also put a drone comb in the centre of each broodnest. I feel certain that by today they're back to normal, will produce earlier drones, get no less honey, and prepare me for earlier queen raising. Early season examination with this aim is well worth while!"

I much prefer not to feed bees with sugar syrup in the spring. Native strains, well-provisioned in the autumn, should winter well on what they have stored in a single broodbox, and should require no extra feeding in all but exceptionally unfavourable springs. There is always the risk of adulteration of extracted or section honey with honey derived from sugar syrup which the bees have shifted up into the supers to make room for an expanding broodnest.

Users of native strains have found that stimulative feeding has far less effect on brood raising than does the same procedure on Italian or Carniolan strains.

And yet for special purposes - particularly early drone raising and early pollination work - early stimulation with sugar syrup does have an effect on getting brood raising started, and in encouraging early flight (for pollen or water collection, and perhaps for excretion). Terry Theaker, for example, believed strongly in feeding 1:1 syrup (1 kg sugar to 1 litre water) from about mid-February onwards, if weather permitted. But he fed only very small amounts of syrup, as the bees did not take more, believing in small but frequent feeds of warm syrup. His bees would go into very tight clusters and it may be that few bees would leave the cluster to discover the food above, in 1 lb inverted honey jars.

This does not conflict with B.Mobus's observations on winter cluster water relations. A big stock will consume more honey/syrup and release more moisture by respiration. It will raise more total warmth even if cluster temperature is the same. Feeding syrup cold will have a bigger chilling effect on the smaller cluster - and cold bees will not take cold syrup due to its chilling effect.

More valuable than sugar syrup for early stimulation, in my view, is an abundance of pollen. The expression "pollen-clogged combs" is a derogatory term used by beekeepers favouring strains of bees which gather less pollen, and is aimed against users of the more pollen-loving strains.

Such combs, if stored over winter, can become the lifeblood of colonies in spring, enabling them to raise more brood early, and earlier drones. They are of most value if given to colonies one wishes to use for propagation of queens and/or drones. Some beekeepers prefer to leave such combs of pollen on the colony in an upper chamber over winter, to supply pollen and honey in spring (a form of "winter food chamber" management). But they can alternatively be stored over winter in a dry place and be given to bees in spring in an area with little natural pollen. They undoubtedly stimulate broodrearing and may be specially desirable in superseding strains from which one wishes to obtain early season drones and queens before distant drone assemblies are set up.

If the hives were in districts with abundant pollen sources the previous autumn, this supplying of combs of pollen may be unnecessary. Such is often the case when the bees have been to the heather.

I feel it important to ensure that frames of drone comb are adjacent to the brood area from late March onward, or mature drones will not be available in time for early queen raising (a drone takes 14 days to attain sexual maturity from hatching) and other advantages of drone comb may be lost.

I have wintered stocks quite happily with the drone comb right in the centre of the broodnest, but if the comb is empty it may seem worthwhile to move drone combs to the outside of the broodnest in autumn. I have also tried removing drone comb from hives in autumn and restoring them in spring. Reduction from 11 to 10 combs has merits in keeping the hive dry in winter. But invariably lack of time in spring has delayed their return and the residue of combs have been widened, so I have not persevered with this practice. On balance, I find the time involved outweighs the merits.

Early spring is not too soon to begin preparations for the production of combs. Perfect combs are worth their weight in gold, and I believe in going out of my way to produce them in advance of my requirements. Spare drawn comb is always desirable and a store of this, well built and disease-free, is needed for many operations in summer, and particularly for housing swarms and divisions, and filling nuclei out to full size.

Any colonies which happen to have been wintered on a double broodbox can be profitably employed in drawing out a few combs. The best combs, fully drawn out with no beeway left at the bottom and no undrawn corners, are produced in a top box. At the end of winter double-broodbox colonies are often concentrated in the top box. All or some of the bottom box combs can be removed and put into store for summer use. Alternatively the two boxes may be inverted, with some of the combs in the new top box exchanged for foundation, taking care not to divide any brood. This may be done when the dandelion is out, or when the queen in the top box has begun laying eggs at the top end of the lower box; i.e. is spreading its brood downwards instead of the more normal upward spread. One cannot seriously chill eggs! When a flow comes the bees will draw out the foundation perfectly, without bottom or side passages within the wooden frame. If poorer combs are put near the outside of the new bottom box, next year they will be empty of brood or stores in spring, and can then be withdrawn.

The reader may have guessed by now that swarm control programmes, nine-day inspections and the like play no part in my system of beekeeping. I find it far more worthwhile to devote any available time in spring and early summer to the propagation of queens and drones from my selected colonies. There are many merits in early queen raising (say in May), the chief ones being the increased likelihood of within-strain mating, and the longer time available for building up nuclei in order to withstand wasp attack in autumn and ensure survival over the winter. In most years bees from which propagation will take place need special preparation to force early drone production, as well as early large broodnests which can provide eggs for queen rearing and nurse bees for cell raising, and which can act as support stocks to enable pairing of queens to take place from well-stocked nuclei. Although simple division of normal stocks can be a good method of propagation, it makes breeding a slow process and it is seldom good enough to rely on this alone if real progress is to be made.

Honey-producing stocks are essentially left alone from March to May (and beyond), apart from one inspection for checking health and general colony evaluation, moving to nectar-yielding crops or pollination sites if appropriate, and adding supers as required. It is important to super in advance of the flow at this time of year, allowing the bees to prepare the combs above, store incoming nectar, open up overwintered stores and use them or carry them up, and ensuring that the broodnest is not cluttered with honey and nectar which may restrict the queen's laying.

Summer management

Summer management of honey-producing colonies is on much the same lines as spring management, except that the hives are kept cool by removing entrance blocks and top insulation. Although I take no special steps to discourage swarming, bees of almost every strain will construct queencells and swarm, or even swarm without constructing cells, if seriously overheated for only quite a short time. In cooler hive conditions the difference between determined and reluctant swarmers is easier to detect. The insulation may usefully be replaced over the top super in late summer, particularly at the heather or when producing sections, when nights can be cold enough to inhibit comb-building.

Overheating while hives are being moved during summer quite commonly leads to queen cell construction, to swarming and sometimes apparently to queen balling. If severe, suffocation of bees and collapse of combs may easily result. I like to give the bees plenty of clustering space when they are being moved, as well as empty comb in which they can store water sprayed on them, and adequate top ventilation via a screen board. If possible I avoid moving very populous colonies in hot weather. Another point I watch for is to make sure the hive, in its new position, faces the same point of the compass as it did before the move. If it does not, many bees flying out may fail to find the entrance, clustering on the face of the hive pointing in the accustomed direction and chilling at night, or even entering other hives with a risk of spreading disease.

I like to use some of the stronger single broodbox colonies for drawing out foundation in summer. My preferred method is to add a deep box with nine frames of foundation above the broodchamber, lifting up two already occupied combs and putting them on the flanks of the new upper box. The two combs are replaced by two drawn combs from store. If a broodnest is divided by one or more combs of foundation this will often lead to swarming or supersedure, which can happen in both single and double broodchamber hives as the side without a queen raises queencells.

Feeding dilute (rather than concentrated) sugar syrup assists comb drawing in the absence of a stong nectar flow, but risks the storage of some of the syrup. Prolonged feeding of this sort may lead to acarine buildup, and in cold weather to chalk brood. Populous stocks make a better job of drawing comb, especially late in the season. Feeding less populous stocks over an upper box at this time may attract so many bees upwards that the entrance is left insufficiently defended.

Autumn management

Whereas in spring it is important to super colonies in advance of the flow, in autumn I guard against over-supering, which encourages the bees to spread the nectar out too much and then have difficulty in evaporating and capping it. This increases the beekeeper's work in uncapping and extracting, if it does no worse.

One hears a lot about "spring cleaning" hives to make summer working easier, and to spot disease, queenlessness or colony deaths. Equally worthwhile is an autumn, "pre-winter" cleanup and inspection. If queenless colonies are found they can be united and those short of stores can be fed; "hefting" is not enough, as the weight felt may be largely propolis and pollen. Records made in autumn can help one to interpret one's spring inspection findings. Was the queen there in autumn? Were there two queens in autumn? Did they have separate clusters? Was each marked in a unique way so that one can see which one (or both) survived the winter?

Since I like saving time from chores at busy periods, I always find it worth cleaning top bars of wax and propolis. Under a properly designed glass quilt they do not get built up again, because of the perfect beeway provided, and bees are less disturbed than if this job is left to the spring. A spring observation of excreta on the scraped top bars will then alert one to possible disease, and "comb varnishing" (see Chapter 8) will be easily spotted.

The bees themselves do a lot of pre-winter comb refashioning and polishing. One can help them by flattening bulging combs, rubbing them flat with the hive tool and placing them alongside a flat-faced comb. Next year these flat combs can be put where they are needed, without fear of their being reshaped in the old pattern. (But beware of robbing when flattening combs on a sunny day.)

Mention of robbing reminds me that I and my collaborators have had a great deal of trouble from this habit over the years. It is not that native strains as a whole are particularly bad robbers (though some certainly are!), but that their often small colonies can be vulnerable to robbing without vigilance on the part of the beekeeper. In good weather at the end of the honeyflow, or in poor weather if bees are idle, robbing is very apt to commence. It can lead to the deaths of nuclei and even quite strong stocks if not taken in hand rapidly. It may cause one to move queenless stocks to apiaries far away, where the wrong strain of drones may be flying. And it can lead to the spread of diseases, e.g. braula, AFB, EFB, nosema and potentially varroa, which may be very expensive to eliminate once they have been acquired.

Robbing tends to be worse between colonies which have something in common: thus bees of the same bloodgroup are likely to rob each other more than those of different bloodgroups. Divided stocks are more likely to rob each other than ones unrelated by management handling. This could be due to bees remembering their old site and "silent" robbing each other at a gradually increasing rate, the robbers "telling" their fellows of the source, or perhaps due to bees following a scent trail to its source. When robbing occurs, a common "hive odour" will tend to be set up as a result of food from one hive filling up the other. Bees which have worked a common source tend to rob each other; thus bees brought back from the heather will often rob each other but not their sugar-fed neighbours. This might be a reason for including a drop of peppermint, clove or aniseed to the feed of individual colonies. Bees of hives which have been interchanged may also rob each other; if this is done when there is not a strong honeyflow, the weaker stock may end up weaker still instead of the reverse, because of the robbing.

Small or even medium-sized colonies in large single broodchambers or double boxes, or hives with wide entrances can often be at risk, especially when being fed at the top of the hive. Queenraising nuclei are particularly liable to be robbed out by strong stocks especially in a large apiary or when being fed. Colonies with aged queens also succumb at times, as do queenless stocks and dronelayers.

It is easy to trigger off robbing by exposing the interior of hives, combs, wax and propolis, honey or sugar syrup, especially early in the day.

A careful policy of robbing avoidance can, I find, keep the apiary largely free of this trouble. Not giving the bees broodboxes too large for them, fitting entrance blocks with small entrances at high-risk times, and making sure all hive parts fit tightly will do much to discourage robbing. If hives are opened only late in the day for as short a time as possible, robbing, if started, is soon quenched by nightfall.

In manipulation, no nectar, honey or comb is spilt or dropped on the ground, or left lying around where bees have access to it. Bee-proof covers are placed above and below all piles of supers being moved. Cut-off portions of comb and scrapings of propolis are put immediately into a tray or box, if possible with a lid, for removal to a solar wax extractor or bee-proof store. Cover cloths are employed so as not to expose stocks unduly.

When feeding, entrances are narrow particularly during a nectar dearth, and preferably near the cluster. With "warm-way" combs the box is turned if necessary so that the cluster is at the front of the hive. Autumn feeding commences as soon as the honey is removed, or on August 1st if it is removed earlier. It finishes in the case of small stocks by early September, and in the case of large ones, late September. (Italian bees can successfully be fed much later.) Smaller stocks with young queens need to build up slowly and are better fed slowly. Large stocks are better fed rapidly, and capped combs are taken away from them to be given to less populous stocks unable to cap later on. Stocks thoughts to have nosema or amoeba are not fed, to avoid spread of the disease by robbing. As soon as queens are mated in nuclei I try to move their hives to a separate "build-up" apiary far away from testing, production and comb-drawing or drone-producing stocks.

In order to detect robbing an eye is kept on stocks which show the habit of "following" (see Chapter 8), as these are often the ones which do the robbing, and on stocks which are likely victims. It is difficult, when a spate of robbing has begun, to tell which stock is robbing and which is being robbed. Both display undue activity when other stocks are doing little.

Orientation flights by young bees and drone killing may simulate robbing. A stock which is robbing can itself be being robbed by a third stock, so the tugging at a strange bee is not evidence of its being seriously robbed out. One method of detection using a glass quilt has already been given. Another is to close the entrance of all active stocks with grass. Ten minutes later the grass is removed from each hive in turn. The robbers will then largely and pretty rapidly enter their own hive; the robbed will rush out in a continuous stream.

Often a robbed stock can be detected at dusk, when many bees may be seen flying out of it, but few returning. The robbing colony shows the reverse behaviour, but so do normal colonies if there is a honeyflow on or the bees are coming home late.

When a single hive is being seriously robbed it is moved, preferably to a distant apiary with no big stocks, and an empty hive placed on its site. The robbers continue to investigate the hive on the robbed site instead of attacking adjacent hives.

A mass outbreak of robbing can be stopped dead in its tracks even in a commercial apiary of 50 stocks, by piling up straw or hay loosely over every hive front, using balks of timber or string to hold it in place. This should be done without delay - waiting till evening will allow stocks to be robbed out. Robbing usually starts during a nectar dearth, so shutting the bees in is not losing appreciable quantities of honey. A bale or two of straw is the cheapest way to acquire the necessary material.

Since running apiaries in areas of sandy and gravelly soils I have learned to regard wasps as a serious menace, especially following a warm spring. Late in the season, about the time of taking off the honey, they enter hives to steal honey, pollen and sometimes grubs; they can rob out nuclei easily, and full stocks also on occasion. As with robbing by bees, trouble often starts when hives are opened for management purposes and the wasps call in their friends to join in the feast. Colonies vary in their resistance to wasps (see Chapter 8); often continued attack even by small numbers of wasps manages to undermine colony morale, and the stock succumbs to further attack even if moved to another site.

Wasps will also pounce on and eat bees on the alighting board, biting off their wings and legs and flying off with them to the nest. I have photographed them pouncing on and killing bees on flowers early in the season.

Management to avoid robbing by bees will simultaneously protect against wasp attack. In addition it is well worthwhile walking around to discover wasp nests and killing them with an appropriate non-persistent wasp killer. Baiting with accessible food such as jam will aid tracking down nests once regular foraging trips are being made. Or jam with a suitable insecticide stirred in in small quantities will be carried home and fed to the grubs and ultimately to the queen. This is worth doing up to the end of August, and very profitable in July. Wasps can be killed at the hive entrance if one has the time, and this may be worth doing if the nest is not too close and the wasps not too numerous.

CHAPTER SEVEN

Bee Breeding

Definitions

Beekeepers in these Islands use the word "breeding" in a very slapdash manner. They put their hands on the top of their hives in February, feel a warm patch and say, "Ah, the queen is breeding." What they mean is that her colony is raising brood, or "brooding", as we might put it.

Some use the term "breeding" to mean raising queens by the beekeeper. This is best referred to as "propagation", which includes the raising of two sexes: queens and drones.

The term "breeding" as used by BIBBA and throughout this book means something different. Suppose that in the horticultural industry there is someone who intends to raise some new variety of plant to be sold in a chain of shops. He sows 10,000 seeds which he gathers either from his selected parents or just at random, or he makes purposeful crosses, and of these 10,000 seeds 9,500 come up. 500 never come up; we have lost some already. He grows them on for a year or two and likes the sort of flower that appears, but he throws away all but a hundred of them because they lack the right scent or they are not anything new. So he has one hundred plants from his 10,000 seeds. He grows these on to get a full-sized plant and has another look at them, and he ends up with two which he likes, and we say he has bred two. Then he goes to the shops and they only want one of them. And so he has bred one variety of plant. This is breeding. Breeding is propagation followed by culling: nature's culling, the raiser's culling, the shops' culling.

Bee breeding in many ways operates as a sort of alternative procedure to bee management. Instead of performing ritual operations of management, you can substitute almost the exact opposite operations in breeding, to the same ultimate ends. The manager who has bees with swarming propensities would provide plenty of room for brood and might apply swarm-control measures, i.e. management measures. The breeder would keep his bees in a smaller broodbox with the result that three-quarters of them would swarm, and he would then propagate or multiply the ones that did not swarm.

The breeding method for combatting acarine disease is to give all one's bees acarine and then propagate from those stocks in which the mite does not build up. Again, the manager whose bees are found to be suffering from acarine disease will probably dose them with Frow or Folbex, or apply some management manipulation to reduce the number of mites.

Management is the direct strategy; breeding is the indirect strategy. Having two operational strategies gives the beekeeper a much more powerful array of tools than limiting himself to one strategy. Management and breeding, though in a way apparently contradictory, in practice complement each other. Thus bees which have had most of their swarminess bred out of them are much more amenable to swarm control measures; bees which are acarine-resistant will need medication less often and will respond to it better.

Though management and breeding are quite different in basic approach, because people understand one there is no reason why they should not understand the other. At school we can learn numeracy alongside literacy, and the one does not obviate the need for, or have to precede, the other.

The breeding cycle

As I wrote in the introduction to Bernhard Mobus's *Mating in Miniature:* "apigenics or bee breeding moves through a threefold cycle of practical stages which must be repeated over and over again. First there is the evaluation of colonies: the measurement of their heritable characteristics as objectively as is possible. Secondly there is the selection of the evaluated colonies, leading to a choice of the parents whose workers show characters nearest to those of the desired type. Thirdly there is the propagation of the queens and the drones of the chosen types, together with the union of the two sexes. The cycle then begins again on the new generation."

A TRIENNIAL PROGRAMME. A breeding programme based on natural matings in isolation and not on artificial insemination can most conveniently be organised on a triennial cycle of operation.

In the summer of year one, queencells are obtained from the selected desirable stock A, and mated in the same apiary to provide F1 offspring. This first round of queens raised may well produce workers that are crosses, but their drones should be of the right type. Indeed, unless A's parent stock (P) was also highly desirable to breed from, then stock A's drones may be less suitable than those of her F1 offspring. If stock A is placed with them, therefore, all drone comb is removed from it and given to the F1 hives to produce as many drones carrying the stock A characteristics as possible. The formation of a "monostrain" apiary of several stocks (with no stocks yielding drones from any other strain) is the first step towards monostraining an area.

To describe these F1 queens I coined the name "hemi-queens" from the Greek "hemi", meaning "half", to denote a kind of halfway stage in the upgrading of the strain. Beekeepers often fail in their practical approach to strain improvement by not giving due attention to this important intermediate stage in their programme.

The hemi-queen is valued as a drone-producer even if she herself pairs with drones of undesired or unknown characteristics. Her great merit is that she may be expected to produce drones between them carrying the characters so admired in the colony of queen A. No single drone will carry all the desired genes — only half of them - so one needs big numbers of drones to obtain a wide enough gene pool for success in transmitting to the next generation the desired attributes of A's strain. It is necessary to raise many hemi-queens to ensure adequate coverage of the gene pool, i.e. to ensure that the drone really does give a hemi-strain.

Although the hemi-queen is bred primarily for her production of males (drones), she can be used to continue the breeding line on the female side as well if her workers prove satisfactory in the desired qualities. Hemis are often excellent honey producers due to the hybrid nature of their workers. This attractive honey-producing capability, unless guarded against by strict attention to evaluation, may cause one to overlook the faults one is breeding against and be tempted to use them for future female progeny raising against one's better judgement.

In the summer of year two a further batch of queens are raised from stock A, but paired in nuclei placed in the isolation apiary flooded with F1 type A drones. The second year queens so produced, still F1 queens, now stand a far better chance of pairing with the desired and related type A drones, than did those mated in the first year, many of which would be likely to contact distant "mis-matings".

Meanwhile, the year one, F1 hemi-queens have built up stocks which can be assessed, and if one likes their qualities, can be bred from. Owing to the fact of multiple mating, it does not follow that a desirable stock early in the season will be desirable at the time queens are being raised. Many more queens therefore have to be raised than are needed, and the less desirable types culled from the breeding line.

If you have run out of hives, then reasonably good queens of the first year's raising can be given to other local beekeepers. Their stocks will begin putting out drones of your type into the area. Your swarms will likewise escape into the district and colonise trees and vacant hives.

In year three, the F1 queens raised in year two are "tested" to see whether their characteristics are up to expectation. Some will be bad-tempered, or swarmy or disease-tolerant, and may be removed from the breeding apiary, but unless their faults are extreme they may still be utilised in the honey-producing apiaries.

Year four begins once more, like year one, with the building up of a new set of drone-producing colonies; year five like year two continues with the queen-raising proper, and year six, like year three, is a testing year. F1 off-types may be used as drone producers, but no F2 queens should be bred from them for drone production in the primary queen-producing apiary.

As the strain becomes more uniform and inbred, it is legitimate to curtail the programme to a biennial one, since the year one mating can be bred from straight away without waiting for a full year to elapse. If they do show undesirable characters, they and their progeny can be relegated to the honey producing apiaries. And if a high proportion of the progeny of an otherwise satisfactory stock show undesirable traits, then that parent, as well as her progeny, should be culled from the breeding line.

NEVER CULL A DESIRABLE MOTHER ON ACCOUNT OF AGE. Keep your mother queen as long as she can be persuaded to totter on.

Propagate from her to your and your friends' maximum. Her offspring may be crosses, less suitable as queen-parents but still first-class as drone-parents. If these daughter queens are crosses, their daughters may produce wrong drones but they should not. So it is essential to mark all queens to show what generation they belong to. Once the mother queen has been lost, you are faced with the question, "which shall be the new mother?" Only careful observation and recording will provide you with the information needed to guide you in your choice. In the main, you should obtain some degree of monostrain isolation in three years, and a fair degree of it in six years, if you cull stocks bearing any signs of hybridity - of which bad temper is the most reliable.

SEVERAL GENERATIONS IN ONE YEAR. In order to speed up a breeding programme, it is commonly possible to rear two and even three generations in one year. By stimulative feeding of a colony well supplied with drone comb, queens may in an early season be raised in May. Their first batch of brood may be utilised by another strong but de-queened stock to raise a second batch of queens in early July, from which yet another generation can sometimes, in an apiary of stocks de-queened to make them retain their drones, be raised in late August. All these queens will have to be "tested" the following year, but breeding may go on simultaneously, and time can be saved.

CHAPTER EIGHT

Evaluation

The most complex part of breeding is evaluation: a skill which has to be learned over a considerable period of time. Many beekeepers imagine that it is simple. Quite common, for example, is the belief that by propagating from one's "best colony" (in the honey-production sense), one is automatically selecting for those factors and characters in the bees which are desirable, and selecting against those that are undesirable. There are several reasons why this belief, and others like it, are mistaken.

Firstly, the good honey yield from the colony may be largely an environmental effect. The colony may be located in a very good apiary site, other colonies may have been subjected to some treatment by the beekeeper which held them back at a crucial stage, and so on. The stock may not even be able to repeat its superior performance in a season with a different weather pattern.

Secondly, the good performance, though genetic, may be due to hybrid vigour, the queen having mated with drones of a different strain. In the next generation the colonies will be very variable, of relatively low average performance, and most likely bad-tempered into the bargain.

Thirdly, the high honey yield may be due to the bees being efficient robbers. Terry Theaker at one stage made the mistake of propagating from his best honey-getters, and ended up with bees that were very productive as long as their apiary was sited near to someone else's colonies!

Fourthly, the high total weight of honey gathered may be counterbalanced by other faults; the extra management time demanded may render the colony less economic than other stocks which gathered smaller amounts of honey, or it may be bad-tempered or succumb next winter to acarine disease.

The fact is that honey productivity (like many other attributes such as temper) is not a single inheritable character but a complex of many component characters and interacting environmental circumstances. We need to propagate bees which possess the components, even if in a particular year they did not gather much honey; and we need to cull those colonies which lack them, even if in a particular year they were our "best" colonies. Thus we are gradually building up strains of bee which will give consistently good results, not ones which may give the occasional brilliant result. We also need to be able to separate genetic from environmental factors; otherwise our whole breeding programme will be founded on illusory data.

Management for evaluation

A significant part of the environment of the bees is the management system (or lack of it) to which the beekeeper subjects them. There are two sides to this, namely standardisation between colonies, and the masking effects of certain manipulations.

When one reaches the stage of comparing the hive records of different colonies, it is important to know whether they have been given roughly the same management and whether, therefore, one is really comparing like with like . As far as is practicable, all colonies should be kept in the same type and size of broodbox, fed at the same time with similar amounts of syrup, supered at the same time, and generally dealt with in a comparable manner. Of course it is not always possible or even desirable, for other reasons, to do this. In such cases one must be sure to record carefully on the record card all deviations from the common standard of management, so that they may be discounted at the stage of comparison and selection. In the same way, the name of the apiary and details of weather conditions should always be noted, as these too are important environmental factors.

Several manipulations and techniques as commonly practised, and even widely taught in textbooks, make evaluation of particular characters difficult or impossible by ironing out or masking real differences between stocks. Particularly to be avoided are practices which lead to admixture of bees. What we are trying to achieve is the evaluation of the offspring of the queen heading the hive. Anything which introduces the offspring of another queen (other than her own daughter, in queenright supersedure) into the hive makes the whole operation pointless. It takes only a few "followy" or "jumpy" workers from another stock to transform a colony in appearance and seriously falsify its records. Workers from a swarmy strain will cause a colony to swarm when it might otherwise have superseded, whereas the converse is rarely true. The peak number of queencells which the bees will build is especially susceptible to admixture with bees of another strain. Many other characters are affected to a small but often significant degree.

Beekeepers often deliberately mix bees. "Equalising" stocks in spring by transferring brood with or without young bees from strong to weak colonies is a common culprit. Switching fliers in order to boost the foraging force of particular stocks, uniting colonies, running swarms together or into occupied hives, shaking bees from several colonies into nuclei, and even requeening all result in periods of admixture.

Accidental admixture through drifting is common where hives are set out in rows all facing the same way. This is especially prevalent at the heather. Apart from its masking effect on evaluation it leads to robbing and the spread of disease, and so is undesirable from the management point of view as well. Another by-product of admixture is the introduction of unwanted drones into colonies.

Multiple mating of queens with different drones, natural requeening and the joining up of swarms all lead to admixture through natural causes. The bee breeder should try to avoid adding to these by his own management, and when he cannot, must record his manipulations carefully.

A big environmental influence when evaluating bees is the use of smoke. In selecting bees for docility, one has to make an assessment in a number of stages. The first stage is "no smoke". A commercial beekeeper has to go through his colonies quickly, so he puffs smoke automatically before inspecting each hive. The breeder should make a point of going through all his colonies, at least in spring and early summer, without even lighting the smoker, as smoke drifting from a smoker placed on the ground may inadvertently affect the bees. Any colony showing signs of bad temper may subsequently be smoked, and if that does not have the desired effect, the bees can be sprayed with water. Careful recording of the results will often reveal striking differences between colonies which, if routinely smoked before examination, would seem to be very similar from the point of view of temper.

Many of the manipulations often advocated for the prevention or control of swarming can ruin the evaluation of the bees' behaviour. Cutting out of queen cups and queencells as a routine measure prevents one from counting the peak number of cells and spoils the bees' chances of superseding or tearing down the cells themselves. Giving extra room to, taking frames from, or requeening colonies believed to be preparing to swarm may likewise distort their underlying behaviour patterns and is even more misleading if not applied to all colonies simultaneously.

Record keeping

A. Physical characters

Many morphological variations of the honeybee have been discussed in detail in the literature and need not be gone into here. One can easily imagine many useful measurements, both anatomical and physiological, which could be made as a regular part of colony assessment. Most of these would involve sending off samples of bees to suitably equipped laboratories which at the time of writing are not accessible to beekeepers generally.

1. COLOUR. The two columns "black colour" on the record card (Pl. 41) are intended for entering the estimated percentage of worker and drone bees which are arbitrarily defined as "black". Blackness effectively means in this context absence of yellow or unpigmented bands across the dorsal side of the abdomen, a character readily noticeable in the individual bee and not difficult to estimate on a percentage basis with a little practice.

A separate box is provided for the colour, shape (and size) of the queen. Carefully made, these notes can serve at a pinch as a substitute for queen marking and are a useful fallback should the queen's mark rub off. The information is of interest in tracing the history of a strain and involves so little work that the time and effort involved can hardly be begrudged.

Other physical characters such as colour of ventral side or body hairs, or shape of drones, can be entered in the "peculiarities" box if time permits.

The ecological significance of colour has been discussed in Chapter 3. It is also of use as a genetic marker. When working with uniform strains, a sudden jump in the percentage of black or yellow can alert one to the possibility of a new queen in the colony, of outcrossing or of multiple mating. Often it is accompanied by an increase in prolificacy and followed in the next generation by a deterioration in temper. If workers are of mixed colour, but the drones are all black or all yellow, one may suspect that the current queen has mated with drones not of her own strain, but that her mother mated "within-strain", so that the current drones are still "pure" and perfectly suitable for one generation of within-strain mating. Mixed drones in a colony suggest outcrossing further back.

On many occasions I have found the colour percentage of bees in a swarm to be an accurate guide to the stock or group of stocks from which the swarm had emerged, thus saving management time by not having to go through stocks unnecessarily.

2. DISCOIDAL INDEX. An earlier version of the record card had a space for discoidal index rating. At the time I was offering an examination service of samples of 30 bees from the same stock. The technique is not beyond the determined amateur and might usefully be undertaken by associations as a service to their members. The results could be entered in the "peculiarities" box.

Comparisons of wing shape based on discoidal index proved to be of value in a) distinguishing strains of bee from each other; b) recognising degrees of hybridisation between strains; c) pointing out mixtures of strains, and occasionally; d) where big changes in rating occur from season to season, indicating multiple mating by a queen with different strains of drone.

Briefly, counts with a high proportion of negative ratings are the long-winged bees (British, Irish, French and other West European types); those with high positive ratings are the broad-winged bees (Italian, Caucasian and Carniolan types). Hybrids generally have some of each rating, with the majority in the zero category; mixtures, and unstable and often bad tempered hybrids, may show a wide scatter of readings, the better types for breeding generally showing a high proportion in one or, at most, two categories.

Following German work, studies in France on samples of bees from that and other Mediterranean countries have also shown the value of the discoidal index in distinguishing clearly between different strains'.

3. CUBITAL INDEX. At the same time as the discoidal index, the cubital index can be determined. A low index of 1.5 to 2.0 is diagnostic of typical native bees, most *non-mellifera* foreign strains averaging over 2.0.

B. Handling characters

1. SUBDUABILITY (Boxes C6-8, column D3.) The need for and response to subduing treatment varies enormously between stocks, and has an

important hereditary component. It obviously needs to be considered together with "temper", which as will be described varies with both genetic and environmental factors. The character can be a very important one to the beekeeper, determining to a large degree the time taken in inspection and manipulation and often deciding whether the colony is opened up at all. It can have an indirect influence on breeding, as when a colony that is impossible to subdue is left alone and so produces its own queens, drones and swarms unhindered.

Subduability may be divided into a) the "natural" temperament of the bees the moment the hive is opened; b) the "cool air temperament" after the warm air in the hive has had the chance to rise in a bubble after a few minutes, being replaced by cool air from below. With some strains, including those exhibiting "cool air clustering" (see below), this causes a marked improvement in temper as the bees chill slightly. Often this rising of warm air is all that is needed to subdue a colony which was somewhat sharp-tempered on opening; and c) temperament on the application of smoke or other subduant.

Most beekeepers use smoke as a subduing agent, often quite unnecessarily; or even counter-productively, as some strains of bee are infuriated by smoke. The common practice of smoking a colony fairly heavily before opening is unhelpful from the point of view of breeding as it obscures the distinction between those stocks which require smoking and those which do not. It is better to wait until after the warm air has risen to see whether subduing is called for. The queen of a colony which regularly continues to sting badly after this treatment followed by smoking should normally be culled.

Other methods of subduing in use are spraying with water or thin syrup, and drumming on the hive, skep or comb. They are preferred to smoking or used together with it by some beekeepers. Again it is important to note the response of different colonies to such treatment. The same goes for chemical subduants.

2. COOL AIR CLUSTERING (Box CIO, column D5.) This is a behaviour pattern which helps numbers of bees to keep warm in cool air. It is easily observed when lifting combs from a hive at air temperatures up to 50 degrees F in still air or 55 degrees in a wind. There are noticeable differences between colonies in respect of this character, very little of it being seen in Italian strains. This is a component of ease of handling, as the clusters of bees forming on the combs, particularly on their lower edges, and falling into the hive, confuse the eye and can hide queens, queencells and other things which are being looked for. However it is valuable when wax is being secreted for comb building or capping of brood or honey, and is a great asset in comb honey production.

Young bees noticeably respond to cool air in this way, perhaps because they are the normal wax secreters, and less agile and able to keep themselves warm. This tendency is less marked in older bees.

3. RUNNING (Column D5.) Cool air clustering is not easy at first to distinguish from running. The latter, however, is done in warm weather as well as cold, and is usually provoked by smoking, rough handling, shaking or drumming on the hive.

A form of this character is "night running", observed particularly when hives are being moved at night. It is a response to movement, and particularly to artificial light shining through a screenboard or hive entrance. If not confined, bees of some colonies will pour out of the hives and run over the ground and the beekeeper, while others, not showing this character, will be perfectly quiet.

Running is a nuisance during examinations for the same reasons as cool air clustering, and like it may lead to the survival of queens which should be culled but cannot be found among the scurrying workers. On the other hand running bees are easily driven out of supers or broodboxes. The skeppists' practice of "driving" bees had the effect of selecting for this character, which is still common in some areas where driving was a normal part of skep beekeeping.

4. TEMPER. Bad temper in honeybees has several aspects. All are undesirable on social grounds, and all make the handling of bees slower. The beginner cannot tolerate bad temper, and may be put off beekeeping for life by it. To some extent it may confer a selective advantage against marauders, and there are times when one may suspect a relationship with good foraging ability. But clearly it is not essential to high honey yield, since there are many strains where reasonable docility accompanies high productivity. One of the tasks of the breeder should therefore be to try to produce manageably docile bees of good vigour and honey-producing behaviour.

Three aspects of bad temper are not hard to distinguish. Being aware of their distinctness is a must for everyone hoping to breed for good behaviour, for all three are inherited independently as far as we can see. The three are "stinginess", "jumpiness" and "following".

a) STINGINESS (Column D6) is a propensity to sting people when no good reason is apparent. The bee which stings when it gets up one's sleeve probably has no option if one's clothing squeezes it. But the one which stings without apparent provocation, despite reasonable use of smoke and gentle handling, is clearly not in this category.

In order to get a standard assessment of stinginess one must apply a standard treatment, and supply a standard target to receive the stings. The standard treatment is "going through" the broodbox (examining every comb). The standard target is the ungloved hands of the operator. If gloves are worn, obviously the target is very different: one tends to crush bees and provoke stinginess, but stinging clothes is not a satisfactory alternative, as bees that are clothes-stingers are not always hand-stingers.

The gentleness and deliberateness of handling influences the likelihood of receiving stings. A gentle handler would deduct 5% from 100 for each sting received, unless the bee was crushed and the sting provoked. A rough handler might deduct only 2 or 3% per sting to achieve the same marking for the same stock. Equally, a smoked stock will often be less likely to be marked down for stinging than an unsmoked one. Here one does not alter the evaluation, but annotates the "no smoke used" column, so that the reader can discount the docility column appropriately.

Where low markings are given, and the cause is obvious (see below), this can be recorded in the "notes" column, again so that the reader may apply a correction factor.

Experiments I have conducted, supported by the observations of other beekeepers, suggest that the inheritance of stinginess operates in an indirect manner. The workers may not be reacting sharply or quickly because of their own inheritance, but because of the inheritance of the queen which heads their colony. It is almost as if the queen sets the pattern of tranquillity in the colony, or goads the workers into stinginess.

In 1962 I removed three queens from sharpish stocks and in their place introduced three sister queens from docile ones. Within 24 hours of introduction one could handle these formerly sharp stocks as easily as the docile ones, yet not a bee in any of these hives was the progeny of the "docile" queen. In another case, the queen of a sharp-tempered stock was removed and a ripe queencell introduced. Three days later, when the virgin queen had hatched, that stock had metamorphosed into a quiet one. She did not begin laying for three weeks and all the bees around her were the progeny of the "sharp" queen.

The "sharp" queens removed were put into nuclei, and their bees continued to be sharp. Later, two were introduced to docile stocks whose queens were being used for propagation purposes. Within two days these "docile" stocks had become as sharp as the other "sharp" colonies in the apiary.

In 1970 I dequeened a very stingy colony and united it to a docile one. Two days later the bees were removed to a new hive without being smoked, and all were perfect-tempered. In the same year a collaborator caged a queen of mine from a very stingy colony over a docile queenright stock. The following day the colony became bad-tempered, despite a honeyflow, and remained so until the caged queen was removed.

These and similar experiences suggest that the behaviour of the workers, in part at least, is stimulated by some pheromone which is passed on from the queen and spread around among the workers[2].

How does temper inheritance operate? Here again recorded observation may provide a clue. My docile North Yorkshire strain, when crossed with a docile yellow Italian strain, produces in the first generation vigorous worker bees of largely Italian characteristics, which are usually hard workers with good temper. Let us see what happens if a queen of the dark strain is paired in the yellow apiary. Her offspring are hybrids, dark on the mother's side, yellow on the father's. The queen is black but the sperm within her is of the yellow character. In other words the queen is providing the colony with the pheromone of the black docile type, and the fact that she has paired with yellow drones does not enter into it. Although hybrids, the workers are reacting to the black pheromone, and are docile.

Let us see what the next generation may provide. This next queen is herself a yellow x black hybrid, irrespective of what drones she has paired with, and her workers may have more of the one type or the other according to these pairings. But sharp temper can almost be guaranteed at this stage. The sharpness seems to arise from the hybridity of the queen, and not that of the workers. If the breeder wishes to eliminate the bad temper, he must eliminate not only this queen but also her mother and sisters, unless he wishes to be sorting out the resulting mixture for many years.

Going through my records for some years I found numerous exceptions to the above. Later I looked at these more closely, using morphological characteristics other than colour as guides. The ones where bad temper was shown in the apparent first generation from the cross now had every appearance of being the result of the parent generation having itself been a cross, but not showing it through colour. In other words, what I had assumed to be a first generation cross was in fact the second generation from the cross, and the bees were responding to the pheromone from a hybrid queen parent and not a pure queen inseminated from an incompatible strain.

It would seem possible that a "second generation hybrid" queen (i.e. the first true hybrid queen) gives out two pheromone messages - one from each parent line - and the workers are upset by this double pheromone message, reacting with incoherent or unbalanced behaviour and stinginess.

b) JUMPINESS (Column D8): this is where on opening the hive, bees surge to the top of the combs and may tend to dart at the operator, usually returning immediately to the hive entrance. If one stands to the side of the hive the bees dart to that side; if one stands behind, they dart behind. The stimulus to jump may be a shadow, as of a fast-moved hand, or a physical knock as caused by a comb being prised away, brace comb being snapped off, or a comb top being scraped.

When a hive is being opened without smoke, as in springtime, jumpiness is common until the warm air rises and bees have filled themselves with nectar. Many jumpy bees make a characteristic sound when they are in a jumpy mood, and the bees all look one way - towards the source of alarm - and run towards it before taking off. They may not sting, they may not follow, or they may do either or both. One needs to smoke such bees frequently and so waste time.

Jumpiness appears to be a character of the worker. After uniting to a non-jumper, the stock continues to show jumpiness till the old bees have died off.

c) FOLLOWING (Column D7) is a propensity for bees to circle round one's person during manipulation, or fly around others nearby, or around neighbours in the next garden, or chase the postman down the road. Followers are the bees that get through the hole in one's veil, or have a go at us the moment we take our veil off in the seclusion of our car.

A special adaptation of extreme following is "clinging", dingers are those bees which run over one (as in night running) and push up one's sleeves, down one's neck, and inside one's veil.

There is possibly a link between following and a well-developed "searching sense" (see below), though I would regard this as unproven.

Here again, following may accompany jumping or stinging, or it may not. It is following, more than any other aspect of temper, that alarms the general public - who promptly wave their arms about and get stung - and it is fear of getting stung which so alarms most people. In my experience it is only "followy" stocks which get vandalised, presumably as a form of revenge.

A peculiarity of following is that it sometimes appears as if spontaneously in a strain. I suspect that this is the result of the queen's having crossed with a different type of bee. At least, I have noticed following as commonly occurring in first crosses between strains, neither of which appeared usually to display this failing. Unlike stinginess it is a character shown by the workers which they retain whichever queen is introduced into their colony and which does not disappear until they have died off.

I have been struck by the localised nature of apiaries containing strongly following bees. Occasionally, whole districts may show following, while in other parts it may be a rarity. South-West England, for example, is generally bad for following, while the East Midlands are largely free of it. More often, a few follower stocks occur in apiaries composed largely of non-followers. Once a follower hive has been opened, the bees follow the operator from hive to hive. It becomes impossible to tell whether the bees of a particular stock (after the first) are followers or not. To sort this out, one must open hives in a different order at each examination. When any hive is found to be a follower, it is automatically placed at the bottom of the list for future examination. Even better, move it to a distant out-apiary, where it cannot confuse the issue.

When such stocks are moved, the rest are often found to be non-followers, or only such slight followers that they give little trouble. In 1966, on holiday in the Isle of Man, I was introduced to Mr. P.R. Foulkes-Roberts who had several large apiaries on the Island. Although followers were a prominent feature of one apiary we visited (and stingers too, in the same lot of bees), I expressed the opinion that such hives would almost certainly be in the minority. He was very dubious. Later he wrote as follows:

"I had to visit Ballaghennie on two separate jobs ... I started at one end and no followers appeared until having passed hive 47 I came to 46 when followers became a nuisance. Three days later I went there again ... I started at the opposite end, passed hive 46 and the followers became a nuisance at

47; and so it seems reasonable to suppose that perhaps there is only one really troublesome hive, i.e. 46 or 47. Incidentally I remember that it was at roughly this very spot that bees attacked Mr. Basnett when he was here ... It is true, however, that I have often been stung immediately I got inside the gate, which is far enough from 46 and 47!"

Following is not always apparent. When pollen in spring, or nectar at any time is abundant, the foragers are occupied and there is little following to be seen. When weather is bad or food scarce, following is likely to be at its maximum. But even when bees are fully occupied, there is usually, in a follower stock, the odd bee to bother one; and if this is jotted down on the record card, one knows what to expect in abundance later in the year, when bees are more numerous and less occupied. Like stinging, following is scored by deducting a standard mark - say 5% - per single bee showing the trait.

d) ENVIRONMENTAL FACTORS. Besides the genetic disposition discussed above, temper is closely influenced by a wide range of environmental factors, some of which are in turn genetically influenced, in that different strains respond differently to the same factor.

i) Quantity and quality of forage have long been known to have a major influence on temper in many strains of bee. When a strong honeyflow comes to an abrupt end, the bees are frequently bad-tempered for some days before settling down again. The same effect can often be observed when hives are moved and the bees turn bad-tempered for a day or two until they locate new sources of nectar.

A shortage of pollen can have a similar effect, at least in spring and early summer. In an article in *Bee Craft* Terry Theaker described a striking case of bad temper among pollen-starved stocks on a "pollination" contract, which cleared up as soon as the bees were relocated in apiaries with abundant pollen. In bean pollination experiments conducted by my department in 1972, hives with pollen traps became bad-tempered before hives without them, and comb inspection showed that the hives with traps during the bad-tempered period were almost devoid of stored pollen, though broodrearing had continued unabated.

Particular nectar-yielding plants are often blamed for inducing bad temper in bees working them. There is a genetic effect here, as bees have inherited likes and dislikes over food sources, no doubt correlated with chemical peculiarities of their digestion or makeup. Some beekeepers have found that their bees become bad-tempered on oilseed rape, turnipseed, swede seed, charlock and other brassica crops; perhaps the nectar contains something which upsets their digestive or hormone system, or perhaps it is merely a longing for a previous food which is no longer available[3].

Heather is said to have a similar effect, though in good weather I have not noticed this. In my experience, sharp colonies become very sharp at the heather, but docile ones remain docile. Rhododendron has also been blamed. On one occasion, described in a *Bee Craft* article, I attributed bad temper during a pollination move to the bees' working a lush growth of chickweed within the orchard[4].

One point to watch when hives are moved to rape or heather is that if they are placed in rows, drifting may easily introduce followers or stingers from one hive into another; and it does not take many of these to make the colony seem bad-tempered when its own bees are in fact docile.

Another possibility is that the effect may be caused not so much by the particular crop as by the fact that it is the sole source of nectar available to the bees. The position with bees may be akin to that of many "polyphagous" or mixed-feeding animals and birds. Because they eat poisonous or irritant items in only very small amounts of each, no harm accrues, but they would be poisoned if the proportion from toxic sources was increased. "Monosource" forage working is likely to increase with many modern trends in farming which involve the removal of weeds, hedgerows and other plants not wanted in agriculture.

ii) Meteorological factors can also be important. Some normally docile strains become bad followers and stingers in thundery weather or when placed under high tension power cables. Others are bad-tempered during the summer or in very hot weather (particularly when confined[5]), but perfectly docile in spring and autumn - probably a temperature effect. When bees are clustering, or beginning to, in spring or autumn or in a cold spell, following behaviour is not apparent. Very bad followers may appear quite docile and can be seriously misjudged under such conditions.

The onset of rain can sometimes bring on bad temper. Some stocks are much more manageable early in the morning than in the evening; perhaps a meteorological effect.

iii) The effects of queenlessness on temper have been discussed in Chapter 4. Both following and stinginess normally increase in queenless bees.

iv) Other factors leading to bad temper include robbing, acarine disease, midges biting the bees, physical disturbance of the hive, strong smells and pesticide poisoning. Any factor which leads to a high proportion of old bees in a colony may worsen temper, such as a queen which has gone off lay for a long period.

Finally, the placidity or otherwise of the operator can have its effect. I have known several people who received more stings at times when they were under mental stress, near to a nervous breakdown or overtired through lack of sleep. Probably their movements were less controlled and incited the bees to jump at them.

C. Nest characters

1. PROPOLIS (Column D9.) Strains vary greatly in their liking for propolis. Some native strains work very hard to get it and go crazy over it even to the point of neglecting honey and pollen for it. Other strains, particularly from Southern Europe, only gather it in moderation. Bees on

average show most interest in it after midsummer and in hot weather, but some strains work it and possibly even collect it very early in the season.

Propolis is generally thought to be a nuisance by beekeepers, and on the BIBBA record card "non-propolising" is conventionally regarded as a virtue. Its disadvantages are obvious: it makes manipulating combs very slow and unpleasant, is transferred from hands, gloves and hive tools onto clothing and all sorts of unwanted surfaces, and can cause serious misjudgement of hive weights in winter "hefting". (Bees of one strain I have kept filled the cells of whole combs with propolis.) A hive heavily gummed up with propolis can be impossible to manipulate, and the beekeeper's efforts to wrench out combs can provoke uncharacteristic bad temper in the bees.

There are however many advantages to the colony from using propolis, and the conventional "virtue" should be regarded as an optimal amount, not a complete absence of propolis. The bees use it to make a eutectic mix with wax (i.e. a mixture solidifying uniformly at a low temperature) to strengthen their combs; the mixture shrinks and cracks less readily than wax alone. Many British, French and Dutch strains build their own propolis mouseguards across the hive entrances in autumn and break them down in April, and the plugging of smaller gaps helps to exclude moths, wasps, earwigs and robber bees. Propolis helps to give each colony its distinctive odour, useful in defence and recognition.

Experience suggests that propolis, which contains natural antibiotics, is of value in combatting disease, particularly nosema, amoeba and chalk brood, probably also moulds and American foulbrood. This is especially so when propolis collection is combined with the habit of "varnishing", or spreading a thin layer of propolis over all hive surfaces. The varnish is most noticeable over the wood of frames, especially top bars and side bars, but it is spread everywhere: combs, cell walls and even foundation. Varnishing is particularly seen on the underside of a glass quilt which then takes on a yellowish tint. It is not only the housewife who gains a temporary advantage from sweeping the dirt under the carpet when mother-in-law is coming; varnishing may confer long term behavioural resistance to disease. Materials varnished over may include nosema spores, amoeba cysts, excreta, mouldy pollen, dead larvae, chalk mummies, AFB scales, eggs, pupae and larvae of wax moths and braula, and other refuse. Probably both the antibiotic action and the physical blanketing combine to reduce or destroy the effects of these harmful things.

Nosema and amoeba in particular are normally transmitted by bees licking up moisture in winter or cleaning combs in spring and so ingesting spores and cysts. I have noticed that varnishers, like "comb scrapers", tend to suffer less from these diseases; the effect was particularly noticeable in 1976-7 when colonies wintered on honeydew and direct sap collection from plant and tree tissues. 1976 was a bonanza year for propolis collection also, and comb varnishers showed much less nosema and amoeba infection in 1977 than did stocks without the character.

2. COMB CAPPING (Column D10.) This has been discussed in Chapter 3. Apart from the selective advantages in severe winters of convex cappings, they also make comb honey more saleable.

3. COMB CLEANING (Column Dll.) This is the readiness to remove from the combs larvae or pupae which are dead or infected from whatever cause; also mouldy pollen, wax moth and spiders' webs and all other refuse. Studies by Rothenbuhler on resistance to AFB have shown that readiness to uncap dead pupae and readiness to remove them are separately inherited[6]. A combination of the two characters confers a high degree of behavioural resistance to the disease. A standard test has been devised for measuring the two traits[7].

A colony with "clean" combs will be given a high mark in this column, whereas one with many dead larvae etc. will be marked down, even though its individual bees may be physiologically no less resistant to disease.

A character which could be scored in the same column is "comb stripping", i.e. the readiness to break down old comb to the midrib, or completely, and to rebuild it. Strains vary greatly in this character, which in my experience can confer a powerful degree of resistance to nosema. Old excreta-stained combs from nosema-infected stocks can be given to the best comb-strippers, who will make a wonderful job of rebuilding them without showing infection subsequently. This character was also prominent in Margaret Logan's AFB resistant strains, which stripped away comb, foulbrood scales and all and later showed recovery from the disease.

4. POLLEN STORES (Column D12.) Pollen gathering has been discussed in Chapter 3. Strains vary greatly in their appetite for pollen[8]. Scoring a colony for pollen stores is difficult, because the amount of pollen available to the bees in the field varies according to the flora and the weather, and at times when pollen collection is impossible there may be no difference apparent in the hives between good and poor pollen collectors. After a prolonged pollen dearth or spell of bad weather one would expect any colony to have used up its stored pollen. What one is looking for is the ratio of stores in a given colony to those in other colonies in the same apiary. The marking is somewhat subjective but well worth making, since a strong urge to collect pollen at certain times of year is one of the chief characteristics of native bees. Observing pollen gatherers at the hive entrance is of little value in assessing overall pollen gathering, as different stocks may gather pollen at different times of day.

As a rough guide, other things being equal a suggested scale of marking is as follows: a) no pollen or only a light scatter, score 0-20; b) Substantial amounts on the outside frames but little on the broodcombs, score 20-40; c) pollen in outer frames and in an arc up to 4 cells wide above brood in brood frames, score 40-60, d) ditto, but an arc 5 or more cells wide, score 60-80, e) ditto, with pollen among and below the brood, score 80-100.

Colonies can scarcely have too much pollen in conditions prevailing in the

British Isles. "Pollen-clogged combs", to use the rather derogatory term applied by beekeepers favouring strains which store less pollen, are extremely useful for giving to nuclei, to stocks building up in spring, and to queen- and drone-raising colonies, even if they may seem to be surplus to the requirements of the donor colony. In fact a large reserve of pollen in spring conserves the effort which would otherwise be expended in foraging for it.

5. BROODNEST SHAPE (Column D13.) This has also been discussed in Chapter 3. We may usefully distinguish one nest shape, as observable on the face of a comb from the centre of the broodnest, common to most strains early in spring, and four different nest shapes at the peak of brood production in about early June. The early season pattern is roughly spherical or triangular, with the apex pointing upwards. At brood peak, the shape may be spherical or "normal", tall (i.e. up to one and a half times as tall as broad), very tall (over one and a half times as tall as broad), or broad (broader than tall). Broodnests which are exaggeratedly broad are seldom found in the British Isles, even in imported strains.

The queen excluder, though it may curtail the upward spread of brood, does not prevent one from spotting a taller-than-broad pattern. If the bees favour a tall broodnest and there is not room for it in the broodchamber, they will at first leave an area in the supers free of honey and pollen where they would like to have brood. In a prolonged honeyflow this space may eventually get filled up.

The pattern of brood cells within the broodnest area is also of interest. The keeper of Italian bees likes to see a "nice frame of brood" filled to the edges with a slab of brood of similar age. This is the product of a fast-laying, often prolific queen. Native queens who lay more slowly and temper their rate of laying in the nectar dearth will create a concentric pattern of brood of different ages, often dotted about with enclosed pollen cells. A small degree of "pepperpot" brood can be tolerated in a native queen, though taken to excess it can indicate inbreeding depression, brood disease or an aged queen.

6. FRAMES OF BROOD (Column D14.) The amount of brood in a stock is an index partly of the compactness of the broodnest, but mainly of prolificacy. Perhaps their relative non-prolificacy is the most important single characteristic of native-type bees (see Chapter 3). This column on the record card, then, is a very important one. It can also help one to gauge speed of buildup, which is another character very useful in determining nativeness, as most native strains build up slowly, particularly in early spring. Speed of buildup is also important for management, as it affects the strain's usefulness in early or late-season honeyflows, and in pollination work.

Ideally we would like to be able to relate quantity of brood to numbers of adult bees, and thus to make the important distinction between "populousness" and "prolificacy". A colony which is populous has a high ratio of adult bees to brood. Components of populousness include longevity (usually the genetic converse of prolificacy), ability to minimise chilling or other losses outside the hive, resistance to diseases likely to cause premature ageing or loss, and good wintering ability which may give a vigorous spring buildup.

A colony which is prolific has a large ratio of brood to bees. Some prolific strains from warmer climates form very large colonies in terms of adult bees, but the shorter life of the bees and the greater relative amount of brood to feed may result in their storing less surplus in British Isles conditions than more "populous" colonies with fewer adult bees and much less brood.

The relative weighting of populousness to prolificacy varies with time of year even within a given colony. Almost all North European bees are populous in winter, whether strong or weak in total numbers, and have their greatest prolificacy when building up in spring (for an old queen) or in late summer and autumn (for a young queen). Long-lived strains are more populous throughout the season than are shorter-lived strains. Populousness is not necessarily the converse of prolificacy: a colony may be both prolific and populous, or neither (say if it has nosema causing shortened adult life), or one or the other.

Estimation of the number of adult bees in a colony is beset with difficulties and I know of no practicable field method of doing this, though there is nothing to prevent one from noting down the observation that a colony seems to have many or few bees relative to its brood. Many schemes have been devised for measuring or estimating the amount of brood, but most seem too time-consuming for everyday use. The simple counting of the number of frames containing brood (scoring a half for a shallow frame) though crude, has proved extremely useful. As a refinement one may count half-frames (i.e. sides) containing brood.

D. Queen replacement and colony reproduction characters

These characters have mostly been discussed in Chapters 3, 4 and 5. Careful filling in of columns D15-D20, and of summary boxes B1-B24 and C11 is essential if the processes of queen replacement and colony reproduction are to be properly recorded.

The entry in box C11, "queen longevity", is an indirect means of gauging the length of life of the workers, since the two quantities will be proportional.

Column D19, "amount of drones" is rather like D12 "pollen stores" in that a subjective assessment must be made of numbers of drones relative to the time of year and to other colonies in the apiary. The amount of drone comb available in the stock should also be borne in mind. Most native strains start rearing drones early but in small numbers, and are very ready to expel them, even as early as May, in dearth conditions. Sometimes they retain a few drones over the winter. Thus although drones are available most of the time in case of need for mating, their numbers are not allowed to get out of hand.

E. **Health characters**

There are big differences in resistance to disease between strains, which apply among strains of both native and foreign origin. Resistance or susceptibility may be conferred by many different physiological and behavioural traits, some of which have already been referred to. Thus a fluctuating broodnest temperature confers susceptibility to chalk brood, heavy use of propolis confers resistance to nosema and amoeba. In my experience hybridity between certain strains, particularly between some native and some Italian strains, confers susceptibility to acarine.

That some bees are resistant to AFB is well known from American work. The late Margaret Logan conducted many experiments on AFB resistance in Scotland. I was able to follow some of these in the days when this was legally permissible, and verified her results. Some of her colonies were capable of surviving being hived onto a complete set of AFB-infected combs, which they would strip to the midrib and rebuild, eliminating all AFB symptoms. This recovery process was sometimes aided by sulphathiazole treatment, which brings up a point that I have often made in my professional work: chemical or other treatment of disease is much more effective and inexpensive when applied to organisms that are already partially resistant to the disease in question.

The presence of a disease should be noted by the appropriate abbreviation, with a number 1, 2 or 3 denoting light, medium or heavy infestation.

Individual stock record cards

In my early days I kept a notebook, with one page per stock. I made the mistake of numbering the hive, instead of the queen. When I realised how variable stocks were, it took a very long time tracing from one queen to her relatives, and from one apiary to another, to discern what was inherited and what was due to the location, the season, or my management. And the discursive style of a notebook did not lend itself to picking out the significant information free from my likes or dislikes, or interesting but irrelevant happenings of no importance in years to come. Having a bad memory for detail, and the scientific training that warned that even small differences could be significant, it was apparent that I had to design a card which could be scored very quickly, was easy to read back later, and had a high degree of precision and versatility.

Several sources of inspiration were available. The idea of rapid scoring of records on cards was not new. Major Harold Hitchin, in Norfolk about 1948, showed me how rapidly he could complete his entries on 3" x 5" cards after examining a hive. I was sceptical at first, but found that his system worked, though its mere ticking of boxes was too imprecise for many of the things a breeder needed to do. Harold Hitchin regarded everything in terms of black and white, or right and wrong. To most of us, life is one of balancing tones of grey, and breeding is no exception. I designed my own system with generalised terms of degree such as nil, few, many and very many; this was better, but still far from adequate. I have recently been surprised to see an Apimondia card with the four categories: unsatisfactory, satisfactory, good and exceptional as the measurable criteria. It is not difficult to improve on this.

My own work in the measurement of pest damage and the establishment and growth of crops showed the need for greater precision in assessment with, wherever possible, actual counting as the basis for assessment. Where counting is impossible, a type of assessment had to be followed which would minimise personal preferences and reduce subjective bias. To do so, assessors needed to be trained to adopt like standards and criteria. The notes of guidance needed to be supplemented by actual training in the field, so that different people would evaluate the same material in the same way. Personal preferences may be applied in the later interpretation of the scorings, but should not bias the scorings themselves.

Another step forward came from Terence Theaker, in Lincolnshire in the 1950s. He was a clear-eyed naturalist well able to make his own judgements on facts as he observed them, and not as the books said. His observation that peak queencell number is inherited and that management practices involving mixing bees hide the genetical state of affairs made a big contribution to breeding evaluation.

I have visited a good many commercial honey-producing establishments and enquired about their record-keeping. Their enterprises have to be geared to maximising production and minimising capital and labour requirements. In the main, their records are inadequate, even for their own limited objectives, and their contribution to our card has been minimal. By concentrating fully on the management side, they are missing the opportunities afforded by breeding. But the swing of the pendulum is inevitable, and we are happy to see an improvement in the situation coming along. The "productivity" column of record card RC1 originated from the suggestions of John Ashton of the Northumberland College of Agriculture in 1963, the year before VBBA was founded. It was the need for a more precise system of record keeping that led, among other things, to the formation of what is now BIBBA.

The record card has gained from seeing the records of some of our French, Belgian and German colleagues. Their needs differ somewhat from ours, but there is a considerable area of commonality. We have chosen those items that are most valid in our British and Irish strains of bee. Their omission of the anti-social character of "following" as a fault surprised us. That there are big inherited variations in this character is clear from our studies, but no-one but BIBBA seems to be recording it. Perhaps the Germans will take it more seriously if they can be transformed into adherents of the magazine hive instead of the bee house. Perhaps in hotter and more thundery climates environmental stimuli towards following are more pressing.

The RC1 record card has been improved over its predecessor by incorporating a double section B, to allow supersedure to be tracked more conspicuously. If supersedure is to be more assiduously sought, the place to begin is in the hive records. We also provide a box for details of the father as well as the mother. This will specially interest those who are practising artificial insemination of queens, but can also, by inference and in retrospect, help those of us who use natural mating methods, but wish to measure introgression of other characters into our monostrain area.

Composite stock record cards

The composite card, RC2, was designed in 1967 at the request of John Oxenham of the Wiltshire College of Agriculture, to expedite strain comparison in a joint group apiary. It has been largely used by bee farmers for quickly scoring stocks in out-apiaries. It has the major advantage that the scoring of a stock on a particular occasion is not influenced by the scores at previous inspections. We liked the method we saw at Bures-sur-Yvette, France, where standard hive observations were tape recorded by the working apiarist and subsequently carded up by a clerk in the cloistered sanctity of the laboratory. No loss of time in the field, no honey or propolis on the card! The composite record card performs the same function as the tape recording. Carrying individual cards into the apiary takes up time in sorting, and risks loss or damage by rain and propolis.

Ready reference

It is necessary to be absolutely clear that an individual record card refers to a particular queen, not a hive or colony. The double line in section B allows for continuation with reference to a daughter queen if desired. This will often be convenient when a queen is replaced in a colony. The reference number of the queen is attached to the outside of the hive box she is in, on something which is durable yet easily removable, such as embossed plastic tape secured by a drawing pin. If she is transferred to a different hive or a different part of the same hive, this number must accompany her. A rough sketch plan of each apiary on an A5-sized card provides a useful check on the layout of the hives and the numbers of the queens within them. There is nothing to prevent hive numbers being used in addition to queen numbers, if desired.

Queen marking

The record card loses most of its breeding value if each queen cannot be individually identified. It is possible to do this by a written description, perhaps devising one's own personal code system. This demands care and precision, but can be done successfully. It is not bad training in observation, and has the advantage of eliminating all risks attendant on the handling of queens.

There are various systems of marking and/or clipping queens described in the literature, and every bee breeder will doubtless adopt whichever he finds most convenient. I used to clip all my queens, saving the clipped-off wings for venation studies, but gave up the practice in the face of evidence that mated queens sometimes take flights from the hive, particularly in early spring. My own system is to stick a small numbered disc of the type readily available from appliance dealers onto the thorax, using as adhesive not the spirit gum provided but coloured paint. Thus if the disc falls off, all means of identification is not lost.

I try to ensure that a queen is marked with a colour different from that of the previous queen or any other queen or queens present or thought to be present in that hive. If feasible I try to have as many different colours in use in the apiary as possible. This I prefer to the method of marking according to the year, as widely advocated. As well as aiding in the detection of supersedure, my system means that when a swarm is found, the colour of the queen's mark often indicates which hive she has come from. Bees which are biennial swarmers, for example, will tend to swarm all in the same year, and under the "colour of the year" system all will bear the same mark. With proper record keeping the age of a queen should not be in doubt anyway. Another merit is that for management reasons in autumn or before a honeyflow I may wish to join together quickly two bad-tempered stocks. It is time-consuming and painful to search for one queen and remove her, but not to unite them with newspaper. If the mark colours are different I can next year continue the card of the victor. Again, it is not unknown for queens to fly out and return to the wrong hive, particularly when mating but even at other times. Sometimes they are accepted, and without proper identification the record card would be worthless.

My method of marking the queen is to pick her up from behind with my right hand (I am right handed). The comb she was on is lowered back into the hive with the top bar sloping so that the far lug rests in the hive rebate but at the near end the bottom corner of the frame rests on the runner. This is done easily and quickly with the left hand. The queen is then transferred to the left hand where I hold her by the sides of the thorax with the thumb and middle finger. A little paint is squeezed out of the tube with the right hand and applied to the queen's thorax with the non-business end of a matchstick. More paint is dabbed onto the underside of a disc (laid out in advance) which is then lifted onto the thorax with a pin. After two or three minutes' drying time, she is put back onto the frame from which she was taken.

Queen marking is not without its risks. It is difficult to do in the rain, as the paint does not stick properly on a wet queen. Occasionally the queen may get blown away or fly off. In very hot weather I have had queens attacked by the workers on returning them to the hive, perhaps because of the volatility of the paint. Some beekeepers believe that marked queens are more likely to be replaced by the bees. On the whole, I have found all such losses to be an insignificant proportion of the total number of queens marked over the years. My own losses are attributable to carelessness, very hot weather or to marking when robbing was in progress.

Record keeping in the apiary

Quick scoring of columns on card RC2 or into a tape recorder following the same headings need hardly slow up one's work. Many beginners are unnecessarily put off by thinking that they have to score all the columns on every occasion. At first only two or three columns, perhaps those of management relevance, need be scored. As confidence and interest grow, more entries can be made, but a given breeder might never use all the columns. It is important to realise that any accurate and correctly recorded information is better than none, even if it does not cover the whole of one's beekeeping activities.

Column entries must be made quickly, and must be intelligible to oneself and preferably to others at a later date. To these ends a standard abbreviation guide has been produced by BIBBA. Again it is not intended that the user should commit the whole of this to memory. Probably no one beekeeper would use more than a fraction of all its items.

The scoring of entries numerically or by standard abbreviations by no means precludes the writing of more discursive notes across the card. The two forms of record - standard abbreviations and notes - will reinforce one another to give a better picture than either alone.

The principle of column entry is that where possible, an actual count is recorded. Non-countable items are scored on an estimated percentage basis, where the virtue (or an agreed convention) scores 100 and the complete absence of that virtue scores 0. In columns 4, 17, 21 and 22 the actual count is given; a description in columns 2, 13, 15, 16 and 20, and the weight in 23-26. Intermediate scores between 100 and 0 can give great precision of assessment, but there is need to set one's sights first by receiving tuition from someone who has already mastered the variability available for scoring. Until one knows the range of variability amongst and between several strains it is not easy to set one's criteria appropriately for columns 3, 5-12 and boxes C6-8.

Entries on individual cards

Entries may be transcribed onto individual cards RC1 at leisure when time allows. Section D is provided for this purpose, giving space for up to sixteen or more hive inspections. Section A is a key index unit, its most important box being A3 which holds the queen's reference number. This also goes into boxes B2 and B23. Section B is the queen description unit, with one line for the first queen, and one for her daughter (Fl) queen. Some of these boxes will not be filled in till later (if at all), as a summary drawn from the entries in section D. The same goes for section C, which is intended as a summary of the first queen's value as a breeder.

CHAPTER NINE

Selection

A. **Implications of evaluation**

A particular hive inspection and its corresponding record card entry refer to the state of the colony at one particular stage in its history. To illustrate the state of affairs, genealogically speaking, at succeeding stages, we have drawn up Pl. 38 (bottom). This shows succeeding stages, numbered 1, 2 and 3, on the assumption that between each stage and the previous one there has been a turnover of one generation in each case (queen, drone and worker). Of course in real life there may be an overlap between stages resulting from natural or artificial queen replacement in the recent past. The diagram assumes no admixture of bees from other stocks, and would be complicated, though not changed in essentials, by admixture through multiple mating.

At a given stage there may be present in the hive a queen; drones which genetically speaking are the same "generation" as she (and the same as the workers of the previous stage); and workers of one generation further on. (We leave aside two-queen hives for the present purpose.)

In assessing a colony for possible selection in or culling from a breeding programme, we must be clear exactly what genetic material it is that we are evaluating: 1. Environmental factors apart, the characters of the colony will be largely the product of the genetic makeup of the workers, as determined by their inheritance from their mother the queen and from the drone or drones she mated with. Such characters will include subduability, colour, followiness, jumpiness, use of propolis, comb capping and cleaning, peak queencell number and inclination to swarm.

2. Another group of characters will be determined partly by the workers, partly by the queen their mother. These include number of frames of brood (i.e. degree of prolificacy), amount of drones, and tendency to ball crossbred queens.

3. The influence of the queen is predominant in a few characters: longevity of the queen herself, degree of aggressiveness towards other queens and disposition to pipe (characters affecting supersedure), and the stinginess of the colony. In evaluating these characters we are evaluating the queen rather than the workers, and hence the genetics of the drones she mated with are irrelevant.

4. Drone characters, including colour and shape, flight temperature, tendency to drift and disposition to local or assembly types of mating are determined by the ancestry of the drones themselves; here again the drones with whom the queen mated are not relevant.

It follows from the above that a colony with serious faults may yet be valuable in a breeding programme. If the faults are worker-related and caused by cross-mating of the queen (herself pure-bred), the drones will be quite unaffected and may be perfectly suitable for mating purposes. The characters they will transmit are those handed down from their mother's parents only.

For example, characters possessed by a queen, such as non-aggressiveness encouraging supersedure, will be passed on to her drones and onward to the next generation, even though her hybrid worker offspring may be swarmy and her hybrid queen offspring may be aggressive towards other queens, through genetic dominance. Thus although the colony may be sure to swarm rather than supersede, the components of supersedure can still be passed on by the drones. A wisecrack heard on the BBC programme "The Archers" runs, "Insanity is hereditary: you get it from your children!": obviously absurd, but no more so than the widespread notion that a stock's inherited characters are carried by the drones raised in that colony. The drones' characters are in fact those shown by the preceding generation: the workers produced by the grandmother queen. Realisation of this fact can greatly aid the bee breeder in promoting and maintaining valuable characters which happen to be recessive in expression, and which at first sight might seem to have been lost.

B. Strain creation

The bee breeder will normally have as his first aim the creation of one or more identifiable strains of bee. Let us first of all define what we mean by the term "strain".

A strain is a group of colonies which may be defined largely in terms of a comparison with the whole bee population of the area at large, viz. 1. Its colonies are known or believed to be related to one another, perhaps quite closely, whereas relationship of colonies within the general population is not known. 2. The colonies of the strain show uniform or fairly uniform characters on proper evaluation. Put another way, their range of variation is less, usually much less, than that of the overall population or a random sample of it. 3. The strain breeds "true to type". The range of variation among the offspring colonies will be no greater than that among the parents, and the characters of parents and offspring are generally similar. (This does not preclude deliberate attempts to alter the characters of the strain over time.)

Having created his strain or strains, the breeder now has several options, including: 1. Maintaining the strain as it is. 2. Attempting to improve the strain by selective breeding. 3. Crossing strains repeatedly to produce F1 hybrid offspring. 4. Crossing strains to produce a new combined strain. 5. Getting rid of the strain and substituting another, better one.

Bee breeding is at best a lengthy and complex process, attended by real and apparent setbacks. Anything which saves time and minimises the complexity is welcome to the breeder. The fastest and surest method of creating a strain will usually be to base it on a single stock. If this method is chosen, years of selection work may be saved by starting with good bees. By "good" we mean bees which not only possess good qualities in themselves, but are suitable to the area in and the purposes for which they are to be kept, and are themselves preferably from an established strain or local ecotype. By selection one can only enhance characteristics already present in the bees. It is well nigh impossible to breed a non-swarming bee from a very swarmy type or an acarine-resistant strain from a susceptible one. Somewhere in the parentage the genes for the desired characteristics should be present.

W. W. Smith used to say, "The best bees are in your own apiary." If not, they are probably within a few miles of it.

What characters are important?

No two beekeepers will completely agree as to what exactly they require from a strain of bee. Yet one must have a plan to work to if one is to progress. The plan should not be too rigid, as variety is necessary if any population is to remain vigorous. It should concentrate on a wide range of small characteristics rather than a few big ones. Ability to gather a large honey surplus is largely the result of a great many interacting circumstances, and is by no means number one point of importance to the breeder, even though it is the obvious ultimate aim of every honey producer. The lesser goals of a hard working nature, ability to winter on little food, little desire to turn a honeyflow into slabs of brood, and a reduced swarming proclivity, along with resistance to disease and ease of handling, are much more important attributes: ones which should contribute, under good management, to a high honey surplus.

Prolificacy

There is much confused thought among beekeepers as to the real value of prolificacy. There is no argument that, within a given strain of bee, a well-populated stock can harvest more honey than a less-populated one. From this, authors generally deduce that it is always necessary to produce an abundance of bees by appropriate management and use of the most prolific strains available.

The flaw in the argument is that, in fact, a given number of bees of a non-prolific but otherwise healthy and vigorous strain will usually yield considerably more honey than will the same strength of bees of a more prolific strain. In a great many districts, the less prolific bee will produce more surplus honey per stock in the poor and average season (when demand for honey exceeds supply), although it may be behind the prolific bee in the relatively uncommon specially good season, perhaps one year in five, when supply is good and prices are depressed. In these days of productivity drives, this fact should appeal to the beekeeper who is pressed for time.

The small colony bee is preferable for pollination work and for migratory beekeeping; for carrying into and out of tall crops or over rough ground;

and even for lifting over fences when one finds the gate padlocked or a usual route blocked. Many beekeepers, who in their youth favoured large and prolific stocks, have later discovered that less prolific ones are easier to handle and often just as productive. And while native bees should provide an answer to the middle-aged beekeeper's less energetic years, they can also save time and effort for the younger operator, and so increase the productivity of his beekeeping effort.

Longevity

Closely related to the small colony character and to non-swarming is longevity. I have good evidence of a queen still effective in her seventh year, but superseded in that year; of another still laying well in her ninth year; and of a third queen which, given away as "too old" at two years of age, headed a productive colony for several years and was still laying, though only just, in her tenth year. It may be worthwhile to keep an extra special queen ticking over in a small colony so that one may study her progeny over many years while still breeding from her. Longevity is thus a most useful tool to the bee breeder. Since long-lived queens will usually beget long-lived workers, it is also of value to the honey-producer.

Some very long-lived strains are slow to build up in their first year, and unless one is aware of this propensity, they may get culled before they can show their paces. If this character is known, and the beekeeper's patience can be curbed, these queens are often wonderful honey-producers in their second and subsequent seasons.

The character of longevity may theoretically be disadvantageous in bees that are susceptible to nosema or acarine disease, but may equally be advantageous in resistant stocks. On balance the advantages to the breeder are such as to make him wish to increase this valuable propensity.

Activity in cool or damp weather

It is an undoubted fact that some strains of bee will work strongly for pollen, nectar or water at several degrees lower temperature than other strains. This was first brought to our attention some years ago in a cloverseed field in Lincolnshire where stocks of a black strain hired from one beekeeper worked much more strongly early in the morning and on cool days than did those of a yellow strain hired from another beekeeper, and set in the same field alongside. On warm days there was no noticeable difference in activity, and examination of the broodnests and stores position gave no clue to a husbandry explanation.

In 1950 a big fruit grower in the Wisbech area of Cambridgeshire asked me to look at some hives of bees he had hired for apple pollination purposes. Ten stocks hired from one man were working well, but twenty from another were doing less. Could I advise whether someone was not giving value for money, sufficient for him to withold payment of the hire fee? The day

I went to see the bees, it was 46 degrees F on my arrival, and 48 degrees when I left, with a brilliant cloudless sky but a cool wind off the North Sea. All the hives were queenright, and all had plenty of brood and bees. The dark Norfolk native bees were clearly working strongly on the apples for pollen at 46-48 degrees, but the others were of a strain which evidently needed a higher temperature to work for pollen. In fact, the hives which were not doing their stuff averaged ten combs of brood and clearly had many more bees than the harder workers, which averaged six combs of brood and looked distinctly less populous on the combs.

I pointed out that all the stocks were of reasonable strength, and that the farmer had no case against the beekeeper with the idle bees. In fact, when hot weather ensued, he would get even better service from the prolific bees than from the hard-working ones. He was not impressed. "Do you know, young man," he pointed out, "that in the years of hot weather at blossom time, the bees cost us good money, not earn it. Too much blossom sets, we have a heavy June drop, and the smaller fruit fetch rock-bottom price, because everyone has fruit that year. Without bees I'd have had fewer but bigger fruit, and the price would have been better." I suppose that nowadays he would have remedied this with blossom-thinning or fruit-thinning sprays, but that was not then his practice.

"Out of three seasons," he went on, "we generally get one that is warm at blossom time. The second season we do a little better as a result of hiring bees, and make enough to cover the costs of hiring and the nuisance of having to misplace our spraying so as not to harm the bees unduly. But in the third year the bees pay hands down. It is this year that makes the whole exercise worthwhile. This year we have fruit and good fruit when many of our neighbours have little. This is the 'off' year with minimum blossom and cool weather throughout blossom time. I want bees that will work even when it is cool." Since then, when visiting large fruit growers, I have made a point of going into the finances of hiring bees for apple and pear pollination. And the above state of affairs has not altered. Most modern pear and apple varieties are pollinated by pollen-gatherers, not by bees visiting the flowers for nectar. If the hire fee of the high-temperature bees - that is, those which need hot weather if they are to do a full day's work of pollen-gathering - were £1 per colony, then the low-temperature bees could well be worth £6 a colony to the fruit grower. This would be a very much more realistic figure than one of somewhere near £3 a stock for any type of bee.

The same factors apply in blackcurrant growing. It is the bees which will show an interest in this unattractive crop which earn their keep in the cool spring. Those who grow fruit on contract to processors manage to avoid the price fluctuations, but the prices today need a full crop to make them pay. And in the cool spring it is the placing of bees in the plantations which most increases the yield of fruit. At such times more distant sources of nectar and pollen are less accessible, and a greater proportion of the colony effort is directed to nearby, if less attractive, blackcurrants.

The same early spring climate affects crops like cherry, greengage and other plums which need cross-fertilisation, and some gooseberry varieties. In the East Midlands, spring flowering brassica seed crops, like kaleseed, winter rape and turnipseed come under this head. Although one gets the most honey in a warm period, low-temperature strains of bee will fill a super or two even in a cool season.

As an example, in 1952, when I was working at the Kirton, Lincolnshire NAAS Laboratory, I had 12 stocks on the edge of a field of turnipseed. Six were of the local Lincs native bee, a black but rather prolific bee, early to build up (and to swarm). The other six were the Buckfast strain of that era. Both would start work early on a bright morning, but by ten to eleven o'clock the blacks would be working hard while the yellows would be sitting around on the crop chilled by the strong off-sea wind. Day after day the temperature would rise to 44-49 degrees F and the local bee would profit by it. The native colonies each had one to two full supers by the end of the turnip flow - but the Buckfasts had consumed most of what they brought in, and had done many fewer hours of work, even in the brightest of sunny weather. Clearly they were not an East Coast bee. My friends who used them told me that the very different-looking Buckfast-Israeli bees of later years suffered from the same dislike of wind in springtime.

Yet another example. In June 1964, a friend of mine in Northamptonshire imported a large number of American package bees, and installed them in hives with full quotas of syrup to build them up. At that time we were doing some NAAS studies on field bean pollination, so I kept an eye on the apiaries during subsequent weeks. Shortly after installing the packages, we had three weeks of predominantly dull overcast weather with cool north-east winds. Near to these apiaries were crops of field beans. Twice I walked these crops making counts of bees working the beans. On both occasions certain colonies only were bringing in appreciable loads of grey bean pollen. The temperatures were 48 degrees F one day, and 51 degrees the second, and one needed a coat in the brisk wind. The only hives which were repaying the farmer for providing the apiary site were the native bees, the "Northamptonshire mongrels" as my friend called them. None were the hives of American bees. The low-temperature characteristics, pollen storage behaviour and other features labelled the bean pollinators clearly as natives. So, even in late June and early July, it can be an asset to have low-temperature bees. One could argue that the above merely represents a management effect, the package bees having a larger area of brood to keep warm relative to the available workers, and hence inability to spare as many foragers as the old-established stocks of natives. Partly so. But other evidence shows that the imported strain is genetically a very different bee, unable to work in such cool weather as our darker bees manage to work and even gather surplus in.

This distinction is also observable at the heather. Here another environmental factor comes into play, but the temperature factor plays its part. High-temperature bees tend to sit at home at temperatures when native types are strongly working the heather. More than this. Those strains which breed late into the summer turn much of what they do gather into brood, instead of storing it as honey. In this case, abundance of high-temperature bees may be effective in a heat wave, but is a liability in even moderately good weather; the lower threshold temperature strains do well even in moderately poor weather, and it takes an exceptionally poor season for them not to fill even the brood box.

The commercial beekeeper may only be interested in total crop; but many of us eat (and, if we could get it, sell) roughly the same amount of honey year by year. A wonderful crop one year is no special advantage - it has to be stored free from fermentation till the years of scarcity. Many of us would willingly forgo the topmost peak years if we had a bee which would do better in the average summer. That, indeed, is one of the main reasons for use of the native low-temperature bee.

In many parts of Britain there is another factor: the effect of intensive cereal production. It was always said that our main honey crop came from white clover. Yet clover could only yield surplus because our bees built up on the many early pollen and nectar sources of springtime. We have only to think of willow, sloe, dandelion, deadnettle and charlock. With hedge grubbing, ditch clearance, ploughing of grassland, and spraying out of existence of so much bee forage in this land, many formerly wonderful areas have been lost to beekeeping. The trend is noticeable even in Ireland, Scotland and Wales. Where our bees had food on their doorstep they now have to fly long distances. This cuts down the days on which they can work effectively, because it is well known that they are loth to go far in dull or chancy weather. So the temperature effect is more marked today than it was only a few years ago.

Cool-tolerance, however, may not always be conducive to high honey yield. Bees that conserve their energies for the real honeyflow may yet earn more honey. In other words, the ideal pollination bee is not necessarily the ideal honey-producing bee. Nor are cool-tolerant bees the best for late season pollination work. From July onwards native strains slacken off their desire to collect pollen rather sooner than do strains from southern or continental climates. Italian and Carniolan strains carry on breeding later in the summer, and bring in appreciably more pollen per hive at this season. This is specially advantageous for the pollination of scarlet runner bean and red cloverseed crops.

Winter hardiness

One of the most treasured characteristics of the native bee is its winter hardiness and ability to winter on little stores. We may deduce that in part this is related to its ability to survive as a relatively small colony; in part to its fat-wintering (pollen wintering) habit; and in part to its early cessation of brood rearing in autumn. The chief fault to many people of Italian, Carniolan and Caucasian bees is their appetite between late July and the New Year, making them economic only in the best honey-producing areas. It is only in exceptionally hard or damp winters, or after a poor summer when bees have not been fed and have gathered pollen late, that serious winter losses occur among native bees. It is important that native bee strains shall be hardy enough to withstand such adverse weather under conditions of through ventilation, and to excel over other types of bee without "mollycoddling".

Sedateness

Several authors object to the "runnable" nature of some native bees, which herd about and ball up when smoked or manipulated. While some do have this unhelpful characteristic, it is by no means general; nor is it confined to natives. Some natives are the most sedate bees obtainable, and can never have been handled by the authors concerned.

Runners take longer to examine, and brood is more easily chilled in cool weather through the bees rushing off the comb. Although severe running is no drawback to the let-alone beekeeper - it may even be advantageous in clearing supers quickly - it is a serious time-waster to anyone who wishes to find the queen. Sedate bees can be little disadvantage to the let-alone beekeeper, while runners are an abomination to the precise beekeeper. Native bees must be selected for sedateness and freedom from any tendency to run. Drivable bees are not wanted in these days of movable comb hives.

Docility

While stingy lots of bees can be productive if left alone, or if one is thick-skinned or heavily armoured, they are an undoubted hazard to neighbours, children and livestock, and a real menace if many stocks are kept. They are slower to work with, and therefore more costly in time and labour. Since stingy bees discourage close inspection, the beekeeper is less likely to make precise observations and keep records, and disease is more likely to pass unnoticed among them. It is clear that native bees must be rigorously selected for non-stinginess.

Following, while only a minor annoyance to the experienced beekeeper, does undoubtedly slow up his activities, and when near a building it may lead to unpleasantness with non-beekeeping neighbours, who may misinterpret the bees' intentions and eventually get stung by swiping at them. When the following habit is accompanied by stinginess, the bees may become real chasers and a menace to the whole neighbourhood, livestock included.

Docility is a must in native bees if they are to be acceptable to amateurs and town beekeepers.

Supersedure and non-swarming characters

A great deal of the time in beekeeping is devoted to queen and queencell hunting and swarm prevention. The Ministry of Agriculture Bulletin *Swarming of Bees* states, "With a [bee farming] enterprise of this kind the limit to the number of stocks that can be run is set by the work involved in swarm control." Much of this labour can be eliminated by utilising bees that are relatively infrequent swarmers, and possess well-developed supersedure characteristics. These two characters may occur together or independently. Let-alone beekeeping becomes practicable with such bees. With them, the beekeeper who is a keen gardener or motorist or tennis player, or has a job that allows little time in summer for manipulation, may still be a successful honey producer. They certainly eliminate much of the drudgery from summer beekeeping, since hive division, as a means of queen rearing, is so much easier than the more complex, though perhaps more exciting methods which have to be used with swarming types of bee. Against this must be weighed the undoubted difficulty of persuading some highly inbred superseders to raise queencells when dequeened. Many strains of native bee must be selected for supersedure and non-swarming characteristics. For certain types of husbandry, swarming is indeed desirable. In heather areas, the early swarm will usually build up to give the most productive heather unit. For red cloverseed pollination in August, the developing colony with the young queen is the most assiduous pollen collector. Some native bee strains must be swarmers, though preferably only moderate swarmers, raising say 8-10 queencells.

Disease resistance

Along with characteristics that assist in obtaining high honey yield and ease of management are those which confer resistance to disease and climate. In both animal and plant breeding, these latter have had to go hand-in-hand with selection for management and yield attributes, or else there has to be great retracing of steps at a later date when the short-sightedness of omitting to do so has become apparent.

It is not generally realised that acarine resistance is widespread in these Islands today, and though most stocks are only moderately resistant, a few may be very susceptible. Even in resistant strains, the occasional susceptible stock may turn up. There is little doubt that several resistance-conferring mechanisms exist, and until we know more about them it would be wise to propagate only from the more resistant stocks. One point to watch: two moderately resistant strains we know in Lincolnshire yield very susceptible offspring when hybridised.

Another form of resistance to look for is nosema resistance. One behaviour pattern we have observed seems to confer a degree of resistance on its possessors. Most bees seem loth to clean up winter excreta spots from hive, comb and frame surfaces, as if they had a disagreeable taste. But some stocks in springtime set to work to polish their homes with enthusiasm, and in so doing must become infected by the disease. As the season progresses, diseased bees get fewer or less infected, and little re-infection can take place from hive furniture the following winter; with the susceptible, but poor house-cleaning strains, re-infection from old excreta occurs in winter when the bees lick cold surfaces to collect water for brood rearing. Given a dry hive with through draught in winter and sufficient shelter to allow of occasional cleansing flights, a good house-cleaning strain can eliminate the infection in a couple of seasons without recourse to drugs or antibiotics. And where drugs are fed, it would seem reasonable to expect less recurrence where the bees are good house cleaners.

Other characters conferring a degree of nosema resistance are comb varnishing and comb stripping, already referred to. Less prolific types probably consume less food during a mild autumn or winter, and so tend to drop less excreta in the hive after prolonged confinement. Some strains collect and devour especially large amounts of pollen in autumn, apparently for the oils and fats in them, voiding the waste before the onset of hard weather, and presumably wintering to a great extent on their fatty body stores; whereas Italian bees seem to rely more on honey and fed sugar and possibly suffer more from surplus water in the cluster.

A character making for susceptibility is found in excitable strains prone to excrete in the hive during manipulation, or when shut in for migration or crop-spraying avoidance.

Patient work in the USA. over many years has brought to light several types of undoubted inherited resistance to American foulbrood. That such resistance exists in at least some native bees was confirmed by the late Margaret Logan in Scotland, in the days when such work was legal. It would be highly advantageous to incorporate this characteristic in as many native strains as possible. The Americans have shown, however, the great inherent complexity of such work, and legislation prohibits such studies from being conducted by other than official bodies in the United Kingdom.

European foulbrood is another story. Until new information indicates otherwise, it would be wise to assume that all strains are susceptible to EFB. Although the disease has certainly been found on many occasions in native bees, it has just as often been spread in other bees when these have emanated from those parts of the country where the disease is indigenous. In the USA it is mainly the yellow types of bee that have been severely affected by EFB. The same difficulties apply as in AFB, preventing unofficial bodies from carrying out disease resistance testing.

It has been said that Italian bees are generally more resistant than natives to chalk brood disease. Certainly some strains of natives, as well as "Italian hybrids", are very susceptible. Fairly mild outbreaks of the disease occurring after very cold nights may be the result of a fluctuating broodnest temperature, itself a useful survival character, and should not be regarded too seriously. Some native strains are such good house-cleaners that even in a wet season or damp apiary site they will refuse to let the disease build up, but will completely clean up and raise brood in severely diseased combs presented to them. Diseased larvae and pupae are eliminated before they produce infective spores.

Other bees seem to find the diseased "mummies" distasteful and will not clear them out until absolutely forced to by lack of room for brood raising or storage. Susceptibility to the disease is undoubtedly inherited, and inbreeding susceptible stocks seems to worsen the tendency. Very susceptible stocks should not be used as breeding material.

Some strains are particularly tolerant of attack by wax moths. While the use of strong colonies, modern hive and good combs usually eliminates the small wax moth, some bees appear to be repelled by the webbing or cocoons, and make a poor job of clearing it out. The large wax moth is even more difficult to dislodge, and few native strains of bee make a complete job of it. If larvae are tolerated in strong colonies with otherwise good combs, it is time to commence culling.

Inbreeding

Many people are afraid of inbreeding. They know that an inbred population is liable to throw up defective types, and are afraid of a progressive degeneration of the stock. Failings such as addled brood and susceptibility to chalk brood can build up in inbred apiaries. In the peculiar case of the honeybee, they are also afraid of obtaining an excessive proportion of diploid drone instead of worker brood.

In fact inbreeding is a wonderful tool in the hands of a breeder, as has been abundantly proved by plant and animal breeders for many years. The fact that defective types are produced in the early stages of an inbreeding programme is actually a big advantage of the method, as it enables these types to be quickly identified and culled from the programme. Such types are usually homozygous for recessive genes which would be masked for much longer in a non-inbred programme. By the same token, recessive genes which are useful to the beekeeper, such as many of those involved in supersedure, can be quickly identified and earmarked for retention in the programme. After the initial phase of culling, an inbred population will then be found to "settle down" to produce uniform types with predictable regularity, and (if culling has been rigorous enough) with a low or negligible proportion of defective stocks.

The general loss of vigour in inbred offspring when compared with many hybrids will often be an acceptable price to pay for increased uniformity and predictability. If it is not, then hybrid vigour can easily be recaptured by crossing inbred lines repeatedly to produce F1 hybrids: a much more productive approach than breeding hybrids among themselves. This procedure is also usually effective in eliminating at a stroke the "diploid drone" phenomenon, a degree of which may be tolerable in inbred strains where they are being used for producing F1 hybrid offspring.

Mass selection

When one's strain has been multiplied up to form a fairly large apiary, there is sufficient variety among the types to avoid inbreeding troubles almost indefinitely by adopting the mass selection method. Instead of multiplying a very few selected stocks, progeny are kept from large numbers, merely culling those that fall below certain standards laid down in advance. It is worth tolerating old and failing queens which are known to have been good in their younger days. Although this method may appear slow, it has much to commend it, and it should not be beyond any observant beekeeper. The important point is to raise many more queens than one at first sight appears to need, so as to have plenty of leeway for heavy culling.

Introducing new blood

This has been widely advocated, but as practised by most beekeepers is of rather doubtful advantage. Unless one's present strain is clearly faulty, it is better to hang on to what one has than try to maintain other strains in the same apiary alongside. If one wishes to hybridise with another stock, one should raise queens in one's home apiary and pair them in another apiary (one's own or another beekeeper's). If the cross is not a success, one has not by then spoilt one's original strain. If it is, one can repeat the process till the whole strain is altered. I have several times seen two excellent strains spoilt by putting them together in the same apiary, under the compulsion to "introduce new blood", when both would have continued quite satisfactorily in their own apiaries. Because you have addled brood or bad temper or some other grave fault repeatedly cropping up is good reason to replace the whole strain - not dilute the faults with a modicum of "new blood".

Culling

The removal of stocks showing distinct faults from breeding and mating apiaries requires considerable thought, observation and determination. The very best honey-producing stock, if it shows a severe undesirable trait, must be culled from the breeding programme. In fact the success of bee breeding depends on having the resolve and single-mindedness to cull, even when honey is coming in or stocks are saleable, and to cull heavily enough to be effective. Too little and too late is the most likely cause of failure in most attempts at bee breeding. High priority (not last resort status) must be given to culling. F1 and later hybrids, however, may show such a wide range of variation and temper that it is often worth tolerating these faults for a generation or two, in the hope that their progeny may show a recurrence of many of the recessive desirable characters.

In the early stages of a breeding programme almost any fault may be tolerated if the bees have other desirable characters not available elsewhere; at the same time, it probably is worth eliminating stocks showing any severe fault or disease susceptibility, as these have a way of worsening with inbreeding and are difficult to eliminate at a later date when all the stocks in an apiary suffer from them. In this category can be placed serious acarine susceptibility, and tolerance of heavy attacks of addled brood or chalk brood. Really bad temper and bad house-cleaning ability also come into this category.

At a later date, when one has a good deal of material to choose from, one can eliminate over-swarminess, lack of sedateness on the comb, over-collection of propolis and so forth, but to begin with such variants can be tolerated in the breeding strain. As a general rule, a virtue should be allowed to outweigh a fault, unless the fault is a really serious one.

Culling, in the sense of eliminating queens from a breeding programme, need only mean refraining from raising queens from eggs laid in the colonies to be culled. This is, however, not sufficient to prevent these colonies from influencing the future makeup of the strain. Colonies not culled will send out drones, as will any swarms from them which lodge in the wild or in empty hives. Another consideration is that genetically unwanted colonies take up valuable space, equipment and management time which might be better devoted to the propagation and evaluation of the desired types. There are various methods of culling in the sense of drone elimination:

1. Killing. Colonies may be killed with petrol or by shaking bees onto frost or snow on the ground. Killing is more useful as a method of culling for management reasons, such as to provide combs and food for a more productive stock; to do away with laying workers; to save time in disposing of a queenless nucleus which is hardly worth saving; to eliminate vicious bees quickly; to remove bees from a chimney or other unwanted place; or because of disease. Because of the economic loss, one has to be very strong-minded, or very pressed for time, to do this for breeding reasons.

2. Starvation. This is an easy method of culling bees suspected of being over-prolific in periods of dearth or over the winter. The colonies are simply not fed, and any which do not in fact die may be forgiven. An exception must be made for small nuclei at times of year when such small colonies are unnatural.

3. Removal from the area. One can often combine management and breeding aims here, as there can be good management reasons for moving colonies. Removal of queens to a distant monostrain area is the converse procedure which achieves the same end. As colonies to be culled may be perfectly good honey producers, it often makes sense to have special apiaries devoted to "honey cull" colonies. It is, however, important not to take bees where they will spoil someone else's monostrain area, or to take disease into another district.

4. Dequeening and uniting. This can be a good autumn procedure which

reduces the number of stocks to be fed, and may be used to obtain strong colonies in early spring for propagation, pollination or catching an early honeyflow, while ensuring that no drones of the undesirable strain will appear in the spring. In late autumn, however, the queen of the desirable strain is often killed, particularly if of a very different strain to the workers of the other colony or when the dequeened stock is a vicious one. The technique can also be practised in summer, but drones are not then eliminated for some time.

5. Dequeening and using the same stock to propagate the preferred strain. This technique tends to lose little honey under ideal conditions, and feeding may help it to succeed. But a yellow bee used to propagate a black one in this way seems to result in an undue proportion of matings with yellow drones - at least, this has been my experience and that of some of my collaborators. Could the feeding by workers of a different strain affect the queen's sex attractant and influence their choice of mates? Or could the workers play a part in directing the queens towards drone assemblies?

6. As 5, but combined with removal of drones. One way of doing this is to remove the brood with adhering workers and drones after flight has ceased, and use the drone-free bees in the supers to raise a new queen. This is more likely to result in desired matings, but is more troublesome.

7. Culling drones. There are various ways of doing this. Probably the most effective is removal of drone brood and its replacement with drone brood from desirable stocks, as already described. The drones may be caught in drone traps, filtered out through queen excluder by various methods, or sealed drone brood may be uncapped, and drones may even be picked out of small nuclei by hand. Mating nuclei to be sent to monostrain apiaries must be drone-free and can well be stocked from the bees in supers, or by other methods described in Bernhard Mobus's *Mating in Miniature.* Otherwise, most methods apart from withdrawal of frames of drone brood are tedious and usually far from 100% effective.

CHAPTER TEN

Propagation and Mating

Queen raising

Queen raising techniques have been well described in many publications, including several by BIBBA, so that it is not necessary to describe them in detail here. From the breeding angle it is simply necessary to stress two points: the need to overpropagate, and the effect the system of propagation itself may have on the strain of bee.

Systems of queen raising may be divided broadly into two types: slow and fast. Slow systems rely on some form of division or dequeening of colonies which are of normal size or perhaps boosted somewhat for the purpose, or on the use of naturally occurring swarm, supersedure or emergency cells. Excellent queens may be produced by these methods, often at little cost in time and effort, so that they need to be part of the armoury of every bee breeder. There are a number of difficulties with these methods, however, including:

1. Slow methods may not produce enough queens, particularly in the early years of a breeding programme, to satisfy the real need to overpropagate.

2. Many superseding, infrequently swarming, and low peak queencell-number strains are very reluctant to produce cells to order. Only around midsummer can they usually be guaranteed to do so, and even then they may build a disappointingly low number. The breeder must guard against the temptation to see something "wrong" with these strains and to raise queens from colonies which will build cells more readily.

3. Use of naturally occurring cells can easily lead to the maintenance of swarminess in the strain. Inveterate swarmers build cells the most readily, and in the largest numbers. Any breeding programme which relies on the use of natural cells will tend to include an unduly large proportion of such strains unless the breeder is unusually astute and watchful. This is one of the big disadvantages of systems based on some form of artificial swarming. Another disadvantage is that the use of natural cells from a colony prevents the observation of what the bees would otherwise have done with them.

When a strain has become established, and its character is reasonably predictable, slow methods of queen raising come into their own in breeding for strain maintenance.

Fast methods generally involve the preparation of special extra-populous cell-raising colonies, and the presentation to them of large numbers of young larvae by some such technique as grafting or cell punching. Completed cells or hatched virgins must then be removed for mating in separate colonies, usually small nuclei. The great advantage of such methods is that large numbers of queens may be produced: indeed the bottleneck now becomes the shortage of bees to stock the colonies which these queens are to head. Purchase of colonies, dequeening of stocks whose queens are earmarked for culling, and the capture of swarms may all help out with this problem, as long as one remembers to allow for admixture of bees for a time in one's evaluation. Although they can demand considerable skill, time, care and equipment, these methods should repay all this extra investment by cutting years off the breeding programme, particularly in its early stages. They also provide a good use for colonies of a high peak queencell number or high degree of swarminess which can be pressed into service as cell-raisers.

Drone raising

The genetic contribution of drones to the breeding programme and the strain of bee is of equal importance to that of queens. Most queen raisers and would-be bee breeders fail to take adequate cognisance of this fact, and rely rather vaguely on "flooding the apiary" with drones and on a hoped-for geographical isolation. Apart from such matters, to be discussed below, the breeder can easily take steps to propagate large numbers of drones of the required type in the course of his management.

1. Strong colonies will raise more drones, and raise them earlier, than small ones. Stocks to be used for drone-raising can well be prepared the previous autumn by uniting, perhaps wintering on two boxes.

2. Ample pollen is essential for abundant drone raising. Stocks put down for winter should be well provided with pollen, transferred if necessary from other stocks. Carefully stored frames of pollen can be given in early spring.

3. Early feeding of warm syrup in small quantities ("trickle feeding") from a contact feeder encourages early drone production. It can start as early as mid-February.

4. The provision of a frame of drone comb in each broodbox, as mentioned in Chapter 6 as a useful management dodge, is a very valuable tool in breeding. An apiary containing stocks of variable quality may easily be "drone monostrained" by this means. The technique is to remove drone brood from undesirable colonies and replace it with combs of drone brood from the desirable ones, which are then given more drone comb. The process can be repeated through the season as required. It is as well to feed the good colonies slowly in bad weather or early in the year to keep their queens in full lay. The good stocks should be up to strength for their strain. Combs of reject drone brood can be removed to cull apiaries or honey-producing apiaries, or left outside for tits and starlings to destroy the brood. Because they have whole frames of drone comb to lay in, the undesirable colonies will produce few or no drone cells outside these combs.

Obtaining isolation

Complete geographical isolation is hardly ever possible; purest matings seem to be obtained in hives placed in extensive woodland situated in valley bottoms. Mismatings are commonest at high altitudes and in open treeless and hedgeless places, even though "miles from the nearest hive". Presumably queens and drones in such locations seek and set up assemblies more readily. The vicinity of known drone assemblies should be avoided in the weather conditions and at the time of year when these are likely to be in operation, though at other times they may be disregarded. Close woodland with hives in quite dense shade seems to provide the best conditions of mating isolation, though quite unsuitable for honey production. Clearings in woods, and deep quarries also seem quite good.

Early queen mating

Ecological isolation through early mating is a natural mechanism which the breeder may encourage with much greater hope of effectiveness than geographical isolation. The steps described above for early drone raising should be taken, and queen raising may commence as early as mid-April if the weather is at all reasonable. Mating success may well be low, but there will be strong selection for low-temperature flying ability.

Late queen mating

Some superseding strains, instead of raising queens early, habitually raise them late, in late August or early September. At this time the drones of many swarmy colonies have been thrown out and drone assemblies are less in evidence. Within-strain mating is more likely than at the height of summer, though much less likely than in early spring. There may still be plenty of drones about, and rejected drones from swarmy colonies may have found their way into the superseding colonies. Nevertheless the mechanism appears to be effective in some circumstances. It can be simulated by the breeder by holding desirable colonies queenless in September, so that they will retain their drones after queenright colonies have thrown theirs out. Bad weather and the presence of refugee drones often upset this out-of-season mating, but it has advantages for the beekeeper who is otherwise occupied earlier in the year.

Monostraining

Regardless of isolation, whether geographical or ecological, a determined effort to build a monostrain zone usually pays handsome dividends. This begins by monostraining the mating apiary. If six or more strong drone-producing stocks are present in it, a useful proportion of within-strain mating will nearly always be achieved. It is well worth the beekeeper raising large numbers of queens to supply to other apiaries in the district. Drones come and go from hive to hive, and fly from apiary to apiary over quite a wide area, so that if outgoing drones are balanced by incoming drones of equally desirable qualities there will be a minimum of mismatings. First-generation mismated queens whose workers show undesirable qualities may be perfectly good for heading drone-producing colonies; this is often an excellent use for them.

Unfortunately, many beekeepers are deeply wedded to their own favourite strain of bee, and it often needs great patience and diplomacy to get the few who will not cooperate in an area to appreciate that they are delaying beekeeping progress by their attitude. For this reason, it is important to base the breeding programme on the local strains of bee rather than on more recent introductions which are minimally selected for the local conditions of climate, flora and style of beekeeping.

Mininucs

Overpropagation of queens places a strain on the supply of bees for stocking nuclei, especially as large numbers will also be needed in cell-raising stocks. Package bees can help here, provided that careful precautions taken to keep their drones out of mating apiaries. The mininuc or miniature mating nucleus, with its very small requirement for bees and its ease of transportation and inspection, has a big potential in breeding programmes. The reader is referred to Bernhard Mobus's *Mating in Miniature* for full details of this interesting technique, developed by BIBBA members under inspiration from German-speaking countries.

APPENDIX ONE

The Inaugural Meeting of VBBA

Minutes of the Inaugural Meeting of the Village Bee Breeders' Group held at the apiary of Terence Theaker, Leadenham, Lines., at 2.30 p.m. on Saturday July 27th, 1963.

PRESENT Miss.I. Jaques (Weston, Notts) and Messrs G. Arblaster (Killamarsh, Sheffield), B.A. Cooper (Shardlow, Derby), Harold Inglesent (Manchester), T.F. Theaker (Leadenham) and D.E. Wakeling (Leasingham, Lincs.).

APOLOGIES for absence were received from Messrs W.A. Barratt (Sleights, Whitby, Yorks.), G. Crossley (Sowerby Bridge, Yorks), G. Gardner (Leicester), Dr.D. Lipp (Beighton, Sheffield), and G. Sommerville (Derby).

PREAMBLE It being a delightful afternoon, some time was spent in examining and opening up several of Mr. Theaker's hives, their gentleness of habit, non-following behaviour, small coloniness and other virtues being very apparent. Smoke was not used in looking at even the strongest hive of these black or near-black bees. Mr. Theaker explained that he had two strains, kept in different apiaries, a "black" strain and a "brown" strain. The latter made slightly larger colonies, and yielded slightly more per hive, but both had virtues, and hybrids between the two were gentle and did especially well. He had a strong proportion of non-swarming (infrequent swarming) stocks, and supersedure after a long life was characteristic, but kept a proportion of normal swarming stocks, partly to assist in raising larger queen cell numbers for propagation purposes or partly appearing by accident from crosses with the rather more swarmy bees of that district. A less attractive characteristic was that when yellow hybrids turned up as progeny of black queens, these frequently showed a tendency to bad temper, and it was therefore his policy to eliminate them. Fortunately a neighbour who favoured Italian bees had now given up the craft. The visitors were duly impressed, and loth to move on to the business meeting.

FORMATION OF THE GROUP After considering whether such an organisation could be viable, and what lines it should take, it was agreed unanimously that such a group should be convened. At present it had no constitution, no funds and no official support, but it was hoped to collect together sufficient people to produce a workable policy beneficial to British apiculture.

AIMS It was agreed to follow the policy set out in the document prepared by Mr. Cooper: *Improving British Honeybee Strains - Suggestions for Co-operative Work* (now VBBA Leaflet 2) which was a practical application of his earlier lecture handout *Bee Breeding - Suggestions for Upgrading Local Strains* (now VBBA Leaflet 1) The principal aim should be the maintenance, if not the selection and improvement, of non-prolific bees, with low-temperature working ability, some strains of which should have the supersedure characteristic well developed, and which should be good honey producers under average British (or Irish) conditions. The group should admit assistance from those willing to submit to these requirements, but if volunteers wished to go in another direction, they should form their own breeding group.

It was felt that such a bee would undoubtedly be more costly to produce than the commercial article sold in these Islands or overseas, but that, if queens cost 20/- each more than the commercial article, this was only a matter of 20 lbs of sugar or 5 lbs of honey - a fraction of the saving which its use could lead to. Small colony bees are good larder managers, showing a definite capacity for limiting their brood raising according to the stores available and incoming flow; conversely, they were slow and difficult to stimulate to breed as a result of feeding.

IMMEDIATE NEEDS The main need at present was (1) to prepare a standard record card for scoring the abilities of breeding material, and to act as a hive record card incidentally. Mr. Cooper agreed to prepare a design and to submit a draft to those at this meeting. (2) To interest more people in the various facets of work which the Group would have to engage in, and to enrol more helpers to share out the jobs involved. (3) To each make plans for the main breeding lines to be followed up, and the subsidiary investigations that must back up the more obvious aims.

The meeting closed at 7.30 p.m. with a vote of thanks to our host for the interesting day he had provided, and the excellent tea which had kept everyone in a state of physical wellbeing.

APPENDIX TWO

A Note on Terence Theaker

Terence F. Theaker, Terry to his friends, died suddenly on May 10th 1972, shortly after moving ten colonies of bees to a crop of turnipseed for pollination, while in his 59th year. He was not known to a wide circle of beekeepers, despite having been County Secretary of Lincolnshire Beekeepers' Association for eleven years. He rarely wrote to beekeeping magazines. Yet his remarkable powers of observation of honeybee colonies, and recognition of the importance to honey production and ease of management of many significant and inheritable behaviour traits found in different stocks, singled him out as a leader of beekeeping thought. Of his warm, if lonely, character we will say little here, except our belief that it is by his deep love of nature, of his birds and his garden, of music and poetry, that he will be remembered in his home village of Leadenham, nestling amidst trees below the escarpment of the Lincolnshire limestone.

His grandmother had kept skeps of the local Vale of Belvoir black bee from at least the 1860s, when it was the custom to feed them on "ale and brown sugar". They were taken over by his father and kept through the "Isle of Wight disease" era without losing a single stock. In 1936 the local gamekeeper acquired some Italian bees from his brother in Essex, which started to cross with the natives to give swarmy and bad-tempered hybrids. This upset the incumbent of the village church, Canon Shorton from Cork, Ireland, who with the local schoolmaster had already become interested in breeding for non-swarming. Terry's response was to confine his virgin queens and drones in mating apiaries until evening, and then release them in the hope of achieving within-strain mating. In combination with heavy culling, this technique was successful in maintaining a long-lived, superseding bee. Three queens bred on embarkation leave in 1941 were still alive when he was invalided out of the RAF in 1945, and from them he built up his apiaries again.

Because of ill-health, which dogged most of his life, he found himself unable to lift heavy weights. He therefore devoted himself to maintaining his one-broodbox strain of bee, but it had to work hard and get him as much honey as did other people's larger broodboxes or multiple broodbox strains. In this he was entirely successful. He found longevity and supersedure to be better servants than prolificacy in his relatively bleak area, a requirement which is becoming even more pronounced in present-day weed-free, tree-free, hedge-free arable East Midland counties.

After the war he tried several other types of bee in comparison with the local one. A "brown" strain from Ayrshire which had also come unscathed through the "Isle of Wight disease" years proved very similar - indeed slightly superior for his purposes - and for many years he maintained it in a separate apiary. F1 crosses between it and the local black bee were especially productive. Some Swiss "Nigra" bees of *A. m. mellifera* type again proved to be very similar except for their tendency to build up several weeks earlier in spring. An experiment involving local bees, Italians and Carniolans has been mentioned in Chapter 1. He set up five colonies of local bees and five Italian colonies in the same apiary without sugar feeding or honey removal in another experiment which was intended to last five years; but by the beginning of the third year, the native stocks were in excellent condition while the Italians were all dead! He tried queens of Buckfast, and Hastings and other Caucasian strains and their crosses, and found them all wanting.

The native strains he developed were essentially single-broodbox bees, wintering happily on ten British standard combs with minimal feeding. Slow to build up in early spring, their small broodnests in National boxes were easily moved for the pollination work he regularly undertook in May. At this time the stocks were just starting to expand; their big appetite for pollen and cool-flying ability made them a good pollination type for early fruit crops.

In June and July they formed populous colonies notable for their "searching sense" and far-ranging ability, though this did seem to entail a great propensity for robbing. They were not taken to the heather. Swarming was at a level of about 10%, mostly in late June and July, and steady from year to year without marked fluctuations. Swarmy colonies were used for raising cells in propagation work. Queenright supersedure was normal, with queens very long-lived. Most colonies were extremely docile, smoke not usually being used at all before 1962.

Initially because of ill-health, but later because he found it rewarding, he would crouch for hours in his apiary, watching the hive entrances and studying the behaviour of the colonies. When he had a virgin queen ready to mate he would sit for long periods peering through field glasses timing the duration of her flights and the behaviour of drones flying in his apiary, until he saw her return triumphant with the mating sign. Time which others would have spent in management, he devoted to observation and careful thought, enabling him to make penetrating contributions on subjects like queen mating, inbreeding and outcrossing, and identification of inherited traits.

It was in studying the problems of supersedure beekeeping, and putting this trait to profitable use, that Terry was so far ahead of other beekeepers of his time. When I first met him I was frankly sceptical of his stories of natural two-queen hives, supersedure in spring or early summer for generation after generation, and no steps to curtail swarming or reduce hive congestion. Experience was to prove my tutors at fault, and not Terry. Superseding strains of bee are different from swarmers in so many ways that to apply a system that suits a swarming strain is the best way to eliminate supersedure, and vice versa. Terry had learned the hard way, by trial and error, and preferred his own findings to the dogmatic statements of the pundits. Swarming systems were all very well for those that liked them - but his health could not stand the heavy toll involved. So he optimised supersedure rather than swarming, and found it possible to make a rewarding, if frugal, living in a way the books said could not be done.

It was his unwillingness to accept the teachings of the "do as I tell you" fraternity, rather numerous in his area, and his excitable nature when his health was playing him up, that lost him some support locally; but to his intimates he was a sincere and imaginative character, always to be listened to with open mind, and if some of his conclusions at first seemed a trifle impractical, it was wise to put away one's preconceived notions in order to grasp why they were in reality both sound and worthwhile.

APPENDIX THREE

A Note on Queen Balling

Balling of queens seems to be relatively common in some strains of bee. Some authors (e.g. Clark, page 74) regard it as an ever-present danger at certain times of year, and Terry Theaker often witnessed it. In other strains it appears to be very rare. In my own bees I have witnessed it only two or three times, despite handling closely of many dozen stocks per year. I have no evidence on the question of whether native and imported bees differ in respect of queen balling, but it may be of interest to set down the circumstances in which the phenomenon is said to occur in the British Isles.

1. Balling a virgin. One beekeeper has described to me how he found a tight ball of bees formed around a virgin queen on opening a hive. The bees in the ball were quiet and the ball was already formed when the hive was opened. Later, the virgin mated and became a normal laying queen with no recurrence of balling.

2. Balling of a newly mated queen. Terry Theaker observed many cases of this, and in nearly all of them the queen was thought to be crossbred; i.e. from parents of dissimilar strains. I have mentioned in Chapter 4 the possibility of this being a mechanism for encouraging within-strain mating. Sometimes the queen was balled immediately on returning to the hive or alighting board; sometimes up to a week later. The weather was typically very warm, and the time of year late June or July. [I have observed this in a superseding colony in the presence of the old queen. (Ed.)]

3. Balling after queen marking. Several beekeepers have described this to me. I have had queens lost or attacked after marking, but with no evidence of balling as such. Some authors would describe such losses as "supersedure", which seems best avoided in these circumstances.

4. Balling after introduction. An introduced queen will sometimes be accepted for some days or weeks but then be balled. I have had this happen with a queen which had been tethered to a balloon in drone assembly experiments.

5. Balling an "unsatisfactory" queen. I have received some reports of queens which were very old, or had imperfectly mated, being balled and replaced by the bees.

6. Balling on hive inspection. In some cases, whatever the ultimate cause, balling only begins after the hive has been opened. The exposure to light of an observation hive, with no jarring or other disturbance, has also been known to trigger off balling.

7. Balling after overheating. I have described a case of queen balling I experienced in Nottinghamshire native bees after they had been moved and

showed signs of overheating. On opening the hive after the move, the queen was found to be in the middle of a ball of excited, rapidly vibrating bees. I rescued her, wetted her in water and returned her to the hive. Twelve days later she was laying normally, though there were eight capped queencells in the hive (another known reaction to overheating).

8. Balling in swarms. I have observed several queens being balled simultaneously when multiple swarms were being run together up a sloping board into a hive at the late Albert Hind's apiary in County Durham.

9. Balling in the presence of strange bees. Terry Theaker once found the queen being balled in an excited colony, which was later discovered to have been invaded by queenless bees from an adjacent nucleus.

10. Cold weather balling. Although I have neither seen this nor heard an eyewitness description of it, many authors refer to it. It must be very difficult to witness, as one rarely opens a hive under such conditions, and then only for a short time. Could the cold air cause queen pheromone components to separate out and the queen to "taste" different from usual? Or is balling merely assumed to be the cause of unexplained queen losses?

The common factor in many of the above instances is that there seems to be something "wrong" with the queen, most likely in the quality or quantity of her queen substance. Opening the hive may render some of the workers more sensitive to such anomalies.

APPENDIX FOUR

A First Introduction to Bees and Beekeeping

In the course of conversation with Professor Kenneth Mellanby about the publication of this work, he suggested that the book would be of interest to some who are not familiar with the honeybee and its husbandry. However, for such readers to appreciate its content, some elementary knowledge is clearly necessary and to that end I have prepared this very brief outline. The emphasis is on brevity and the aim is to make Beowulf Cooper's book a little more self-contained than it otherwise would be. For those who feel this note is too brief and who require more details, there are innumerable introductory books on beekeeping. For those who wish in a few minutes reading to obtain an initial appreciation of the subject, I hope it will be of assistance.

Honeybees are social insects living in colonies which during the summer months can consist of 40,000 to 50,000 individuals. The vast majority of these individuals are workers who genetically are females but do not under normal circumstances lay eggs. The egg laying individual in the colony is the queen and in most circumstances only one queen is present (although in superseding strains mother and daughter queens can co-exist for a time). Both the workers and the queen are diploid. The respective roles, appearance and behaviour of workers and queens are not determined genetically but by the food which the insect receives during its larval stage. The sexual characteristics are only developed fully if the larva is fed on copious quantities of a brood food described as "royal jelly". The third member of the colony is the drone or male of which there may be several hundred during the spring and summer. The drone is haploid, developing from an unfertilised egg. Therefore the drone receives no genetic material from the drones with whom its mother has mated but only from the mother herself. Thus the drones and workers are not full brothers and sisters as they only have one parent in common.

The queen mates on the wing in the early days of her life. Mating can take place with a number of drones on such occasions. The spermatozoa which will fertilise the eggs produced by the queen are stored in a sac (the spermatheca) within her body. The numbers and survival of spermatozoa are such that they provide for the fertilisation, as they are laid, of all the eggs produced during the life of the queen.

Whilst the continued replacement of individuals in the colony is the role of the fertilised queen, the day to day maintenance of the colony is carried out by the workers. It is the workers who gather the nectar from which the honey is produced and the pollen which provides the protein source for the colony; it is the workers who defend the colony, regulate the environment in the hive, secrete the wax, build the combs and care for the developing larvae.

Eggs are laid in the cells of the comb and hatch to pass through the stages of larva and pupa in the same cell. There are differences in appearance between the cells in which queen, drone and worker are raised. The total period of development from egg to adult worker is some 21 days; the development period for a queen is 16 days and for a drone 24 days.

Unlike the bumble bee, honeybees pass the winter as a colony, the bees clustering in a compact mass within the hive and consuming during the winter months food stored during the more favourable part of the year. This is the time of year when the survival of the colony itself is most at risk from a variety of causes. Death of a colony may occur, however, in any season and a mechanism is required whereby colonies themselves can reproduce as well as the individual bees within them. Swarming is the means by which this reproduction is brought about.

In Britain the swarming season normally extends from early May until July. The process is characterised by the production in a hive of several queencells. When the young developing queens have reached a certain stage of development, the old queen will fly from the hive accompanied by a large number of workers. This prime swarm emerges from the hive as a cloud of bees and they settle for a time on a nearby object before moving off again to a new home. The first of the virgin queens to hatch (usually a few days later) may leave the hive with a second swarm (known as a cast). Further casts can emerge with subsequent queens. Alternatively the first emerging virgin can head the colony, the remaining queens being destroyed. In either event the hive gains a new queen.

The queen may, however, be replaced by a process of supersedure whereby only one queen is raised and she assumes the role of queen to the colony without swarming taking place.

Swarming presents a serious problem in modern beekeeping and much of the work of the beekeeper is often directed during the swarming season towards the prevention of or the control of swarming.

Prior to the late nineteenth century the straw skep was the most widely used beehive in this country. The combs were fixed in such hives and had to be cut from the hive to harvest the honey with the consequent disruption to the bees. Indeed to achieve this the bees were either killed by fumigation or driven from the skeps. The beekeeper relied heavily on the swarming propensity of the bees to restock the skeps the following spring.

The invention of the movable frame hive in 1851 opened the way for the development of the modern hive as we know it today. The combs are held in wooden frames which can be lifted from the hive for ready inspection of adult bees and brood. There are two areas in the hive - a lower deep box or boxes which make up the brood chamber in which the young bees are reared and the upper shallow boxes or supers in which honey is stored. The supers are separated from the brood chamber by a perforated or slatted screen, the queen excluder, which confines the queen to the brood chamber but allows the workers to pass.

When inspecting his colonies, the beekeeper wears protective clothing which includes a veil and may include gloves. He uses a smoker with which smoke is puffed into the hive to subdue the bees. The purpose of routine inspections of the colonies is to ensure that a queen is present and laying, brood and adult bees are healthy, stores (i.e. honey and pollen) are adequate, the colony is not preparing to swarm and to assess the general character of the bees. Swarm prevention/control by some intensive management methods can involve inspections every eight days.

The periods when nectar is plentiful (i.e. when there is a honey flow) in Britain occur between May when fruit trees and oil seed rape are flowering and August when heather is in bloom on the uplands. Since the arrival of oil seed rape it has become customary for the beekeeper to remove two honey crops each year. The first is at the end of the May or beginning of June and the second is towards the end of the summer when the last honey flow of the season has ended.

Honey removal consists of clearing the bees from the supers by means of mechanical devices or driving the bees using a repellent chemical. The supers are then removed and each comb prepared for honey extraction by cutting off with a heated knife the wax cappings which enclose the honey in the cells. The combs are then placed in a centrifuge or extractor and spun to remove the honey from the comb. The empty combs may be returned to the hive and the extracted honey filtered and stored prior to bottling.

From the above account it can perhaps be seen why only limited progress has been made in bee breeding. The lack of control over mating, the need for a long term programme and the other demands on the time of a busy beekeeper all conspire against the potential bee breeder. Most beekeepers would regard the taking of a honey crop as the main objective of their beekeeping enterprise rather than bee breeding. On the other hand the person who wishes to work in the field of selective breeding would not make bees his first choice as experimental material. Beowulf Cooper in his work attempted to establish bee breeding and the improvement of honey bee strains as major objectives in the beekeeping world.

ROBERT PRICE
Chairman, Executive Committee of BIBBA
March 1985

Notes to Chapters 1-10

Chapter 1

1. See Appendix 2.
2. See Appendix 1.
3. See the works by R. Delperee and Father Reginald in the Bibliography.
4. See Bibliography.
5. See Mobus & Van Praagh.

Chapter 2

1. See Berry, Ford, Kettlewell.
2. The subject is summarised by Berry and Ford, who give further references.

Chapter 3

1. See Kettlewell.
2. See Cena & Clark.
3. See Bibliography.
4. See Dews, Louis.
5. For a debunking of the Isle of Wight disease theory, see Bailey, and for the opposite point of view, Brother Adam and Couston. I have myself very occasionally observed mass crawling in bees heavily infected with acarine, and some evidence suggests that this behaviour was formerly commoner among native bees, but was self-eliminating. I would not agree completely with Bailey, but find most of his arguments convincing.

Chapter 4

1. See Simpson, page 3; Snelgrove, page 136.
2. See Sutton.
3. See Woods, 1959. Some large-scale trials supported his contentions, but others did not.
4. [My observations confirm the reluctance to build queen cells even in favourable circumstances, and the non-development of laying workers for over six months in certain superseding strains. Compare also Clark, page 107. (Ed.)]
5. [I have experienced repeated balling of successive young mated queens on opening up a superseding colony. The old queen, present and laying throughout, was not molested. (Ed.)]
6. [See "Mac". I have observed this in March. (Ed.)]
7. Eddie Woods described a test for detecting a virgin by crushing a queen

cell with a finger. The finger is then held near where the virgin is suspected to be, and piping is listened for. It could also be used to test for readiness to pipe. See Woods, 1983.

8. [Some beekeepers maintain that supersedure cells are distinguished by the hollowing out of the comb behind the cell and opposite it on the adjacent frame. (Ed.)]

Chapter 5

1. For an excellent bibliography on the subject, see Tribe. Also relevant are Fraser, Hayden and Van Praagh.
2. See Wadey, page 23—4.
3. [Dare one suggest that mating could even take place within the hive? For circumstantial evidence of this, see Anonymous, *The Scottish Beekeeper,* August 1984. (Ed.)]
4. See Met. Office, and Wallington.
5. See Bibliography.
6. See White.
7. See Jefferies, page 387.

Chapter 6

1. For metric/imperial drawings of this hive, see Walsh.
2. See Mobley.

Chapter 8

1. See Dews, Louis.
2. For other examples see Anonymous, *The Scottish Beekeeper,* August 1984, Asquith, Cox, Rattray.
3. See "Mac" (September 1982), Tonsley.
4. See Cooper, May 1965.
5. [Bees which are released after being moved can be very aggressive at first. If the hive is opened and the warm air allowed to escape, they may become docile within a few minutes. (Ed.)]
6. Referred to in Berry, page 412.
7. See Taber.
8. See Louveaux, 1963.

Glossary

ADAS. The Agricultural Development and Advisory Service of the Ministry of Agriculture.
Admixture. The existence, in the same colony, of bees of different parentage.
Alleles. Different versions of a given gene, giving rise to differences in the characters controlled by that gene.
Anabatic wind. Wind blowing up a valley in conditions of warm sunshine.
BIBBA. British Isles Bee Breeders' Association (formerly VBBA).
Breeding. The attempt to control the genetic makeup of a population by propagation, mating, evaluation, selection and culling.
Cast. A swarm subsequent to the prime swarm, usually containing a virgin queen.
Character. Some measurable aspect of a creature's physical form, physiology or behaviour.
Chromosome. A minute, elongated body in a living cell which carries genes.
Cline. A gradual and progressive change in a character over a certain geographical distance within a population.
Compressibility. The ability of a colony to occupy a small broodbox without undue tendency to swarm.
Crossbred, a) Raised from parents of different type or strain; or b) Heterozygous.
Cubital index. A measurement of the ratio between two sections of the veins on a bee's wing (see Pl. 38).
Culling. The elimination of individuals from a breeding population; whether natural or artificial. The converse of "selection".
Diastase. An enzyme found in honey.
DIB. Initials of the West German Beekeepers' Association.
Diploid. Possessing two sets of chromosomes. Diploid drones are killed by the workers at the egg stage.
Discoidal index. A measurement of the relative position of two points on a bee's wing (see Pl. 38). May be positive, negative or zero.
Dominance. The ability of an allele to mask or override the effects of another allele of the same gene.
Dorsal. Relating to the upperside or back of the bee.
Drone assembly. Congregation of drones awaiting queens to mate with; place where such congregations occur.
Drone comet. A compact formation of flying drones seeking or chasing virgin queens.
Ecology. The relations between living organisms and their environment.

Ecological genetics. The genetics of wild or semi-wild populations.
Electrophoresis. A technique for detecting different proteins in organic material.
Evaluation. The objective recording in standard form, of certain characters displayed by honeybee colonies.
Extensive management. Management system aimed at maximising honey production per man-hour.
Fl. Refers to individuals and colonies of the next generation on from an arbitrary starting generation (P1). The following generation is F2, and so on.
Fitness. The ability of an individual to survive and reproduce in a given environment. In the honeybee, the worker's fitness is expressed by the reproductive success of the queens and drones related to her.
Following; followiness. Tendency of the workers of a colony to fly towards, buzz around and pursue people or livestock, either when a hive is opened or at other times. Distinct from "jumping".
Gene. A small particle sited at a particular spot on a chromosome, which controls or influences one or several characters of the individual creature as it grows.
Genetic drift. Change in allele frequencies due to extremely small population size.
Glass quilt. Hive inner cover consisting of a framed single sheet of glass.
Haploid. Possessing only one set of chromosomes (as in the drone honeybee) instead of the more usual two sets (as in the worker and queen).
Hefting. Estimating the weight of stores in a hive by lifting.
Hemi-queen. A queen raised from a desirable mother, but which may have mated with undesirable drones.
Heterozygous; heterozygote. Possessing two dissimilar alleles of the same gene.
Homozygous; homozygote. Possessing two similar alleles of the same gene.
Hybrid. An Fl cross between bees distinct in one or more characters.
Inbreeding. The pairing of an individual with a mate more or less closely related to it. The converse of "outcrossing".
Intensive management. Management system aimed at maximising honey production per hive.
Introgression. The successful introduction of new alleles and their characters into a given population.
Jumping; jumpiness. Tendency of the workers of a colony to dart at the operator when a hive is opened.
Management. General term to denote all aspects of the practical running of a honeybee enterprise. Distinct from the science of bee culture, and from breeding.
Mendelian. The system of inheritance whereby individual characters are associated with separate genes, developed from the work of Gregor Mendel.

Melanism. The occurrence of dark-coloured or black forms of a species.
Mininuc. Miniature nucleus hive for queen mating.
Mongrel. An imprecise term best avoided in the context of bee breeding.
Monostraining. Converting all the colonies of an area or apiary to the same strain, so that all their drones are of similar type.
Morphology. The anatomy and physical form of an organism, including its size and colour.
Mutation. The spontaneous changing of one allele into a different one.
Natural selection. The effect of the environment in determining the proportions of different alleles in a population. It operates because the individuals bearing the alleles have different degrees of "fitness" in that environment.
Nucleus. A hive smaller than that normally used in honey production, and its colony.
Orphanage. Loss or serious deficiency of a queen, leading to the production of "emergency" queencells.
Outcrossing. The pairing of an individual with a mate not related, or only very distantly related, to itself. The converse of "inbreeding".
Peak queencell number. The number of queencells constructed during swarming, supersedure or orphanage by a colony of full strength around midsummer.
Pheromone. A chemical given off by an individual of which the function is to act as a signal or message to others of the same species.
Polymorphism. "The occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation." (Ford.)
Population. A number of individuals of the same species who are potential mates for one another (sex and age permitting).
Populousness. A high ratio of adult bees to brood in a colony.
Progeny testing. Evaluation of queens or drones by recording the colony characters of their queen and drone offspring.
Prolificacy. A high ratio of brood to adult bees in a colony.
Propagation. Queen raising and drone raising by the beekeeper.
Pure; pure-bred, a) Raised from parents of the same type or strain; or b) Homozygous.
Queen substance. A pheromone or group of pheromones produced by the queen which influences the behaviour of other bees.
Queenright supersedure. The production and retention of a mated laying queen in a colony in the presence of her mother, who does not depart with a prime swarm.
Recessiveness. The ability of an allele to have its effects overridden or masked by those of another allele of the same gene.
Segregation. The process whereby variations in a character separate out in successive generations along with the alleles controlling them.

Selection. The retention of individuals in a breeding population, whether natural or artificial. The converse of "culling".

Stinging; stinginess. The tendency of the workers of a colony to sting people or livestock at any time, independently of "following" and "jumping".

Strain. A group of related bee colonies with uniform characters and the tendency to breed "true to type".

Supersedure. (See "queenright supersedure".)

Taxonomy. The classification of organisms into groups such as genera, species, subspecies etc.

Temper; temperament. A combination of "stinginess", "followiness" and "jumpiness".

Tergite. The back plate of a segment of the bee's abdomen.

Thermal. A bubble of air which is lighter than the air surrounding it by virtue of greater warmth or humidity (or both), and which therefore rises.

Tomenta. The bands of short hair on the tergites of the bee's abdomen (singular, "tomentum").

Variation. The measurable differences between individuals in a population.

VBBA. Village Bee Breeders' Association (later BIBBA).

Ventral. Referring to the underside of the bee.

Vortex. A rising, twisting column of air, usually at the convergence of two or more airstreams.

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