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ECTD_187

TITLE: Honeybees.

SOURCE: Chapter in: *Evolution of domesticated animals*,
Ch. 65, pp. 403-415 ed. I.L. Mason. London:
Longman Group

DATE: 1984

(1984)

187

Evolution of domesticated animals

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Longman
London and New York

Honeybees

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Introduction

Definitions and nomenclature

The domestication of bees is in a somewhat different category from that of animals whose mating can be arranged for and witnessed by the farmer. In 1610, John Guillim expressed it thus, in *A Display of Heraldry*: 'The Bee I may well reckon a domestick Insect, being so pliable to the Benefit of the Keeper.'

In this chapter domesticated colonies of bees are defined as those living in man-made hives, and wild colonies as those living in natural sites (or adventitiously in man-made structures not intended to house bees, such as the roof spaces in buildings). Many wild (feral) colonies start as a swarm from a domesticated colony.

The main species involved is the European honeybee, *Apis mellifera*, which is the source of most of the honey produced in the world, some 800 000 tonnes a year. In Asia a similar but somewhat smaller species, *A. cerana*, is kept similarly in hives. Both these species build a nest of parallel wax combs in a dark cavity. The other two *Apis*

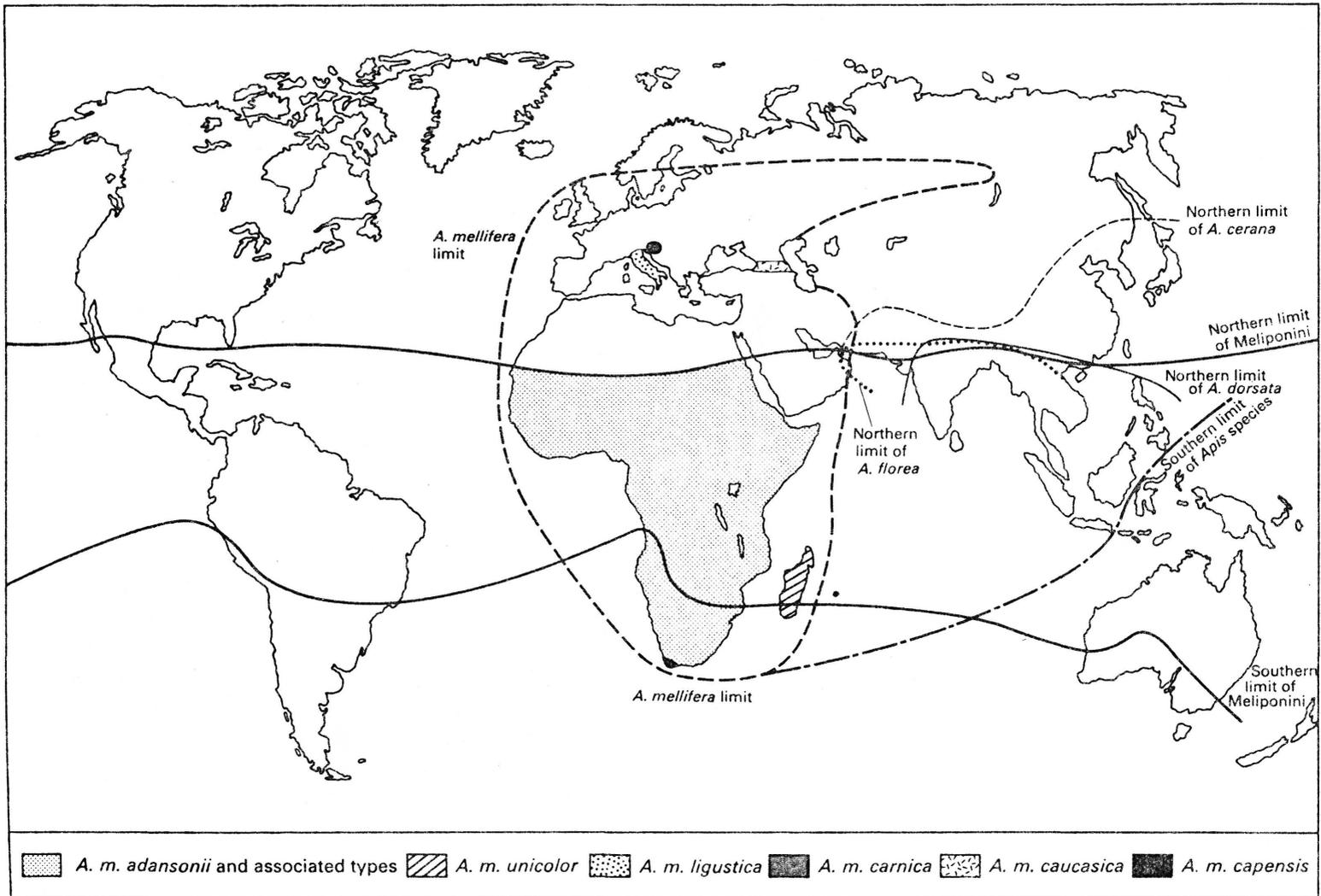


Fig. 65.1 The natural distribution of the four honeybee species (*Apis*) and of the stingless bees (Meliponini)

species, *A. dorsata* and *A. florea*, build a single comb in the open, and therefore cannot be hived in the same way, but honey and wax are nevertheless harvested from them.

In the tropics various species of Meliponini have been domesticated; like the Apini, whose only genus is *Apis*, these form permanent colonies and therefore store honey that they consume in dearth periods. Bumble bees (*Bombus*) have been 'kept' occasionally for their honey, and some of the larger species for pollination purposes. Other bees that nest gregariously, although not socially, can be domesticated, and species effective as pollinators of specific crops have actively been sought in the past few decades.

Natural geographical distribution of *Apis* species

Fig. 65.1 summarizes the known natural distribution of the honeybees. They are an Old World genus, originally tropical (Crane 1978). *Apis florea*, the smallest and the most primitive, is distributed throughout most of tropical Asia and as far west as southern Iran, and also Oman – the only place where its domestication has been recorded. It does not live higher than 500 m. A colony contains up to 30 000 bees, which produce a few hundred grams of honey a year, but – perhaps because the yield is low – the honey has commonly been prized as a medicine, and commands a high price.

The distribution of *A. dorsata* is closely restricted to the full tropics, and does not extend north of the Himalayas. This bee is, however, found up to 1200 m, occasionally up to 2000 m. Its workers have the largest body-size of all the *Apis*, about 18–19 mm long. The single comb may be up to 2 m × 1 m, and the honey yield up to 30 kg. In India more honey is harvested each year from the wild nests of *A. dorsata* than from the 650 000 colonies of *A. cerana* in hives.

Apis cerana is indigenous throughout tropical Asia and also farther north: in Himalayan valleys with a temperate climate such as Kashmir, and as far west as Afghanistan; in the east throughout mainland China and as far north as Korea, Japan and the Far Eastern province of the Soviet Union. It can live up to at least 2500 m. Different races or ecotypes have evolved in the regions outside the tropics.

Apis mellifera, the most highly advanced of the four species, presumably evolved from stock that originated in the tropics. Its natural distribution

extends from Scandinavia to the southern tip of Africa, and from Portugal to the Ural and Caucasus mountains, and to Turkey and Iran. It has three main divisions, each consisting of many subspecies/races/ecotypes, in tropical Africa, in North Africa and the Middle East, and in Europe. Until after A.D. 1600 honeybees were confined to the Old World. Their spread throughout the New World is described later.

Several races of *A. mellifera* evolved in areas that remained isolated after the end of the last Ice Age, and some of these have been especially important in bee breeding (see Ruttner 1973). Cut off from the north by the Alps, Italian bees (*A. m. ligustica*) developed in a region with a long brood-rearing season and rich food resources. They have a great capacity to rear brood, which is advantageous in other areas with similar conditions, but not where food sources are uncertain. Carniolan bees (*A. m. carnica*), from a much harsher region in the eastern Alps, are more frugal in brood rearing and consumption of stores, and in recent decades they have been gaining in popularity in northern climates. Caucasian bees (*A. m. caucasica*), from the mountain range that stretches between the Black Sea and Caspian Sea, are rather gentle, conservative bees that have a longer tongue than most, and so are good pollinators of red clover with its deep corolla. But some Caucasian bees use so much propolis in the hive that it hampers beekeeping operations.

We do not yet have a very clear picture of the races of *A. mellifera* in tropical Africa, and the same is true of *A. cerana* in Asia. We know still less about races of *A. dorsata* and *A. florea*, but different ecotypes certainly exist.

General biology

All the honeybees live in permanent colonies, normally consisting of one female reproductive (queen) and many sterile females (workers), with a smaller number of males (drones) during the reproductive season. All species have the same haploid chromosome number, 16. A nest consists of one or more vertical combs of bees-wax, which is secreted from abdominal wax glands. The cells of the comb are hexagonal, and in them brood is reared and food stored. All species reproduce by swarming, and all defend their nests by stinging an attacker. The colonies are permanent, and the food stored provides a

Table 65.1 Summary of age-linked stages in the life of a worker bee in summer (The ages entered for the adult bee are examples only. All are flexible in normal colony conditions, and highly flexible in abnormal conditions; an individual bee may show several different behaviour patterns on the same day.)

Age (days)	Stage	Food required	Other conditions	Behaviour
Brood Stage: Day 0 = Day Egg is Laid				
0-3	Egg	None	Temp. c. 34 °C	None
3-8	Larva	Bee milk, then pollen + honey	Temp. c. 34 °C	Eats, moves in open cell
8-9	Larva	None	Temp. c. 34 °C	Spins cocoon in sealed cell
9-21	Prepupa, pupa	None	Near 34 °C	None
Adult Stage:				
Day 0 = Day 21 of Brood Stage = Day of Emergence from Cell				
0-20 'House bee'* subdivided as follows:				
0-5	'Young bee'	Pollen + honey		Cleans cells
5-10	'Nurse bee'	Honey/nectar	Hypopharyngeal glands secrete bee milk	Feeds larvae
10-15	'Building bee'	Honey/nectar	Wax glands developed	Builds comb, caps cells
15-20	'Guard bee'	Honey/nectar	Venom glands developed	Guards hive (a few days only, or not at all)
20-30	'Honey-making bee'	Honey/nectar	Hypopharyngeal glands secrete invertase	Elaborates nectar, etc. into honey
20-35+ to death	'Field bee'	Honey/nectar	Flight muscles developed; attracted to light, not darkness	After short orientation flights, forages for pollen, nectar, etc., also (some bees) for water, or for propolis (and works with propolis in hive)

* remaining in the hive; preferring darkness to light. From Crane (1980a)

reserve for consumption during the next dearth period. Food is collected by foraging on plant resources within a few kilometres of the nest (less for the smaller species than for the larger ones) (see Table 65.1)

Carbohydrates are provided mainly by flower nectars, but also by extrafloral nectars, and honeydew excreted by Hemiptera. Protein is provided by pollen, which is also the bees' main source of minerals, vitamins and other trace substances. In *A. mellifera*, and probably in the other species, collection of pollen by a colony is intimately connected with its brood rearing: after a dearth period substantial brood rearing is usually initiated by the availability of new pollen, and pollen collection is stimulated by the pres-

ence in the nest of unsealed brood, i.e. larvae that need feeding. Pollen is not normally stored in large amounts. On the other hand, nectar and other energy foods may be collected greatly in excess of requirements, and collection can be stimulated by a large amount of empty storage space in the nest. The world's honey industry is based on this behaviour characteristic.

The dearth period, for which the food store is needed, is caused by drought or excessive rainfall in the tropics, and by cold in the temperate zones. The single-comb builders, *A. florea* and *A. dorsata*, cannot survive a cold winter, nor can the southern races of *A. cerana* or the tropical races of *A. mellifera*. These bees can, however, survive the relatively short warm dearth periods experi-

enced in their native regions. In some regions *A. dorsata* colonies regularly migrate between two areas, each of which provides food resources for part of the year. The same is true of *A. mellifera* in parts of tropical Africa, for instance between the top and bottom of the Rift valley. *Apis florea* may also migrate through short distances, and *A. cerana* shows a similar tendency, but to a less pronounced degree.

As well as this migration, although not always easily distinguishable from it, the tropical honeybees may abandon their nests if subjected to various types of disturbance; this is often referred to as absconding. An *A. florea* colony may return to the nest a short time afterwards.

The ecotypes of *A. cerana* that colonized regions north of the eastern end of the Himalayas, and in the Himalayan valleys, are able to survive a cold winter by forming a cluster within the nest and regulating the temperature inside it. This characteristic is more highly developed in European ecotypes of *A. mellifera*, although not in its tropical ecotypes in Africa.

Colony reproduction in all honeybees is by swarming, in which the colony divides into two viable units. Unlike migrating and absconding swarms, reproductive swarms consist of only part of the adult population, the other part remaining in the parent nest with a substantial amount of brood. This brood includes several queens, each in a specially constructed elongated cell. One of the queens will remain to head the colony in the original nest, the others being either killed by her or leaving (unmated) with small 'after-swarms' or casts. A few days after emergence from her cell, the surviving queen flies out and mates with a number of drones and soon starts egg-laying.

The 'prime' swarm that leaves the nest includes the mated queen that headed the colony; she has been slimmed down by reduced feeding and is thus able to fly – for the first time since her own mating flight. The swarm clusters on some support not far from the nest, often quite high above the ground, and finally (usually on the same day) flies off to a new nesting cavity that has been found by scout bees from the swarm. The modern beekeeper aims to manipulate his colonies to prevent swarming or, if swarming does occur, to 'take' the clustered swarm and hive it, and prevent after-swarms by destroying queen cells.

The issue of a swarm represents an econ-

omic loss, the season's honey yield for the parent colony being approximately halved. Some earlier systems of management, for instance the skep beekeeping of northern Europe where heather (*Calluna*, *Erica*) provided a late honey harvest, encouraged swarming. One spring colony might produce a progeny of four or even more swarms in the course of the summer, each of which might produce a small honey harvest. One or two of these were left with some honey for winter consumption, and the rest killed off when the honey was taken.

The above refers to *A. mellifera*; there are some differences with the other species which there is not space to describe here. All *Apis* species mate in flight. The sex pheromone that attracts drones to a nubile queen (9-oxodecenoic acid) is the same in all species, and this presents problems when one species is introduced into the territory of another.

An account has been given elsewhere (Crane 1980a) of the foraging behaviour of honeybees, and of their production of honey from the materials collected. Table 65.1, from that source, summarizes the chronology of the individual worker bee's life and activities.

Wild bees and their exploitation

Exploiting wild nests of honeybees (*Apis*)

The following rough time-scale shows the antiquity of bees and honey compared with that of man (Crane 1975):

For 150–100 million years	Flowering plants have existed and produced nectar and pollen
For 50–25 million years	Solitary bees have existed, also early primates (monkeys)
For 20–10 million years	Social bees have produced and stored honey
For a few million years	Man has existed and has eaten honey
For ten thousand years	Records have survived of man's exploitation of honey

The nests of the social bees were certainly

raided by animals throughout the 10–20 million years of their existence. This would have been especially true of honeybee nests, which contain the most honey, and we can get an idea of the methods used through observation of similar animal marauders today. In general they seem willing to suffer many stings to get at the honey, but certain primates, including baboons, try to get the honey free from bees. Chimpanzees have been observed poking a long twig into a hole leading to a nest and withdrawing it coated with honey. This is one method used by primitive man, whose honey hunting was thus a continuation of much earlier animal behaviour: robbing bees' nests using a tool to extract the honey from them, and trying to avoid at least some stings.

The earliest known records of honey hunting by man are rock paintings in eastern Spain, made soon after the end of the Ice Age, probably around 7000 B.C. Ladders are a feature of most such paintings, so many of the nests must have been under a rock overhang on a cliff face or in a similar position; I do not know of any painting that shows a nest in a tree. Bees and their nests are shown in about eighty Bushman rock paintings in southern Africa, and in one a man is using a smoker when raiding a nest. The dates of these paintings are not known.

In the Middle Ages there was intense exploitation of honeybees in the forest areas of northern Europe, where the bees nested in hollow trees. This developed into a sort of beekeeping (Galton 1971), in which each bee tree would be owned by a beekeeper and marked with his sign. Felling of bee trees was prohibited, whether they had bees in them or only empty holes that might be used later by a swarm. Honey and beeswax were harvested through a door cut in the side of the tree, and marketed through a vast trade network; Novgorod was a great centre, and wax was sent down the Danube to Bohemia, down the Dnieper to Byzantium, and down the Volga to the Orient.

This tree beekeeping led to the development of beekeeping proper, when logs containing bees' nests were cut from the tree and removed to some convenient place (an apiary) where they could be tended and guarded. Beekeeping had also developed separately, several thousand years earlier, in the Middle East, whence it spread throughout Africa, Europe south of the Alps, and into Asia. Before following the course of these two developments of beekeeping with honeybees, the

exploitation of other bees must be mentioned. The honeys from the four *Apis* species, and from the bees mentioned below, have been discussed elsewhere (Crane 1975).

Exploited nests of non-*Apis* bees

Stingless bees. The most important group of domesticated bees after the honeybees is the tropical Meliponini or stingless bees; their distribution is shown in Fig. 65.1 (p. 404). The two main genera are *Trigona* and *Melipona*, the latter being the larger bees. Most known sources of information on their biology and exploitation have been recorded (Crane 1978). The nests usually contain an irregular collection of central brood cells and peripheral honey pots, somewhat like nests of bumble bees (*Bombus*). Stingless bees have been most extensively domesticated in Central America (Schwarz 1948), being kept in logs, gourds, pots and other containers, and also in wooden hives designed appropriately for the species concerned (Nogueira-Neto 1970). Meliponiculture has also been promoted in parts of Africa, e.g. Angola, but not to any extent in Asia or Australia, where the bees also occur.

Honey yields vary from species to species, being often 1 kg or less each year, more rarely 10–20 kg. The honey is usually pressed out from the comb.

These stingless bees were the only source of honey and beeswax in Central and South America until honeybees were introduced in the 1800s. They must therefore have produced the large amounts of beeswax used by American Indians – notably in Colombia – in making the golden ornaments which were cast by the 'cire perdue' (lost wax) method.

Honey hunting must certainly have preceded beekeeping with stingless bees, and an account of honey hunting by the Guayaki Indians in Paraguay published in 1939 (see Crane 1975) shows the important part played by honey in the life of these people.

Bumble bees These social bees (*Bombus* species) are widely distributed in the northern hemisphere, where the queens overwinter alone and found colonies in spring that last through the next summer. (In the tropics there are species that form permanent colonies.) Honey from wild colonies has been collected and eaten in many

areas, although the yield is small, since no stores are needed for overwintering. I know of only one record of the domestication of bumble bees for their honey, in Transylvania (Romania/Hungary), where villagers set up clay pots as hives (Crane 1975).

In the last few decades the domestication of bumble bees has been intensively studied in some areas, especially in northern Europe, because of their value as pollinators. The large species fly at lower temperatures than honeybees, and are thus useful pollinators of fruit blossom in spring. Also, some have much longer tongues than honeybees; these bees can collect nectar from flowers with a long corolla, and pollinate flowers such as tetraploid red clover (*Trifolium pratense*). Apart from direct domestication, populations of wild colonies can be usefully increased by locating red clover seed plots near land with many suitable nesting sites, and by leaving land round the plots uncultivated. This method has proved very effective in Finland, for example.

Apart from social bees, two species that are highly gregarious have been domesticated; both for pollination of alfalfa (lucerne, *Medicago sativa*). Pre-emergence conditions are adjusted so that adults are flying when the alfalfa blooms. *Megachile rotundata* (Hobbs 1972) nests in hollow stems, and will accept drinking straws of the right size, or similar hollows drilled in wood. Banks of the (horizontal) nest sites are set up under a shelter on alfalfa plots, together with trays containing overwintered immature bees on the point of emergence. The females use the nest sites provided, forage on the alfalfa, and pollinate it efficiently. *Nomia melanderi* (Bohart 1972) nests in alkaline soils, so artificial 'bee beds' are set up close to the alfalfa plots, and stocked with the prepupae; if necessary the beds are warmed. The most notable developments with both species have been in the northwest of North America, on both sides of the U.S.A.–Canada border.

Other candidates for similar domestication include species of *Osmia*, *Xylocopa*, *Anthophora*, and other *Megachile*.

The development of beekeeping

Traditional hives

The earliest known evidence of the use of hives

is in Egypt. It consists of paintings or engravings that ornament a temple dating from 2400 B.C., two tombs from about 1450 B.C. and one from 600 B.C. These scenes are sufficiently similar to show that beekeeping did not change very much in the 1800 years spanned. It appears in 2400 B.C. as a well-developed craft, and we do not know its earlier history or chronology. (See Crane 1983).

Hives of much the same shape made of mud, cow-dung and straw are still used in the high mountains of Simen, Ethiopia. At the appropriate time of year (after the flowering season) the beekeeper takes the honey, and this may well be the only occasion on which he opens the hives. These are on the ground, not stacked up, and the beekeeper lies so that he faces the back of the hive, which he breaks off, and puffs smoke in from a primitive open smoker. The smoke drives the bees to the front end of the hive where their flight hole is, and induces many of them to leave it. The beekeeper can then, without too many stings, cut out the combs near the back of the hive that contain honey. The combs near the flight entrance are likely to contain the brood nest, and if the beekeeper is sufficiently enlightened he will leave them intact; with luck the queen will be unharmed, and the colony will survive. The beekeeper may strain the honey, or may eat it as it is – honey, pollen, wax, and any brood that is present. The pollen and brood provide protein and other nutrients; the wax is not digested by mammalian species.

This type of beekeeping, in long horizontal hives, was the norm in the ancient world, in Egypt, Crete, Greece and Rome. It remains so today where traditional beekeeping is practised in these regions, throughout Africa and the Middle East, in parts of southwestern Asia (Iran, Afghanistan, Turkey, Kashmir) and in some areas farther east. (In much of the rest of Asia, honey hunting was not replaced by beekeeping until development programmes were set up after the Second World War.)

All the ancient Greek hives found in excavations have one end open, with a circular closure, but no flight hole at the other end, so the beekeeper could not drive the bees through and out of the hive. The Greek hives are made of baked clay, as are most traditional hives today in the Middle East (except in Egypt where Nile mud is still used); they are usually stacked, and most have an opening at each end. In Egypt nowadays

a stack contains 400 hives or more – mud cylinders about 120 cm long and only 8 cm in diameter. In tropical Africa, to which cultural practices were transmitted along the Nile valley, most of the cylindrical hives are made of log or bark, and are hung in trees to protect them from the many enemies that are present. I have measured such hives from widely scattered areas, and found that many are about 90 cm long, 15–20 cm longer than an arm's reach, so that a beekeeper taking honey from one end would be likely to leave the last four combs behind. I do not think this happened by chance. There are many variants in hive shape, in material (woven wicker and coiled straw are common), and in flight entrance position.

The other basic type of early traditional hive, the upright log of the forests in northern Europe, spread as far south as Spain and Portugal, but there the much lighter bark of the cork oak (*Quercus suber*) is used. If an upright hive is open at the bottom, the honey can be taken by turning it over and cutting out accessible honey comb from the bottom. In many forest areas, instead, a door was cut in the side of the log (as in the living tree) to give the beekeeper access to the combs, and the log was closed at both top and bottom.

A log large enough to house a colony of bees is heavy, and at some time – probably in late centuries B.C. – a tall wicker basket came to be used as a hive. It stood upright, its open mouth on a stand of wood or stone, and the bees flying out from a gap at the bottom edge. The beekeeper could gain access to the combs only from the open mouth, which presented him with maximal exposure to the bees, and in this aspect the wicker skep would seem to be a retrograde step. There is no evidence of clothing that protected the face against stings until about A.D. 1400.

These wicker hives cost less effort to make (and to move) than log hives. They spread as far south as the Pyrenees, as far east as Romania and Novgorod, and as far west as Britain, where their last recorded use was in Herefordshire in the 1920s. The use of upright hives hardly crossed the Alps – the horizontal hives deriving ultimately from ancient Egypt occupied all the territory beyond.

In due course, as agriculture developed, coiled-straw work was used for baskets, and these

provided a more weather-tight container for bees. The wicker skeps had to be coated (cloomed), usually with a mixture of mud and cow-dung. Straw skeps were probably first used in north Germany, somewhere west of the Elbe, and they gradually replaced the wicker skep over most of its range.

The spread of honeybees into unoccupied territories

In the story of the domestication of honeybees so far, their distribution has been confined to the Old World, and their management has consisted of little more than cutting out combs of honey once a year. The 1600s were to change both these situations, and to initiate an explosive development that in the 1800s revolutionized the exploitation and domestication of bees.

The earliest likely record that has come to light of hives of bees making the Atlantic crossing is in 1621. The hives taken to North America were almost certainly straw skeps, but most records of early hives there are of upright logs (known as bee gums) or tall hives made of wooden boards; wood was generally plentiful.

In many of the places to which the bees were taken, they prospered sufficiently to yield honey for their owners, and to throw swarms, which spread across the country in advance of the settlers. The European honeybee had probably become fairly common throughout the eastern part of North America by 1800. Pellett (1938) gives details. Hives were taken to the west both overland and by sea; they were in California by 1853, and from there the first hives reached British Columbia in 1858. Honeybees were already in Florida by 1763, when they were taken thence to Cuba. They reached South America surprisingly late; e.g. the earliest known record for Brazil is 1839, and for Chile and Peru probably 1857.

Honeybees were first landed in Australia in 1810, in New Zealand in 1839, in Hawaii in 1857, and in other Pacific islands much more recently, e.g. Papua New Guinea in the 1940s.

All this expansion was into territory with no indigenous *Apis* species, and therefore no competition from them. But except in some Pacific islands, there were other indigenous bees, and also indigenous plants that produced pollen and nectar and were pollinated by bees. Many parts

of the New World offered very rich forage to the adaptable honeybee, and even today the average honey yield per hive there is three times as high as in the Old World.

All the importations of honeybees into new territories (except the Pacific) were made before the start of modern beekeeping, which is the next phase in the history of the domestication of bees.

Modern hives

We shall shortly consider the complications and limitations to breeding and selection of honeybees. These are on quite a different scale from those encountered with domesticated mammals and birds; on the other hand a breakthrough was made in the last century in the effective *management* of bees for honey production, which increased the potential yield by a factor of 10 or 20 per hive and by a factor of several hundreds per beekeeper. This, rather than breeding, is what differentiates modern from traditional beekeeping.

The crucial advance was made by the Rev. L. L. Langstroth in Philadelphia, U.S.A., in 1851: he used vertical-sided boxes, with appropriately separated wooden frames (for combs) supported like files in a suspension system. Provided that the ends of the frames were similarly distanced from the hive walls, the bees would 'respect' the space and not build comb across it. The whole frame was removable.

In 1853 Langstroth set out his ideas and achievements in *The Hive and the Honeybee*, and the book played a seminal role in spreading the use of the movable-frame hives throughout the world. This in turn led to the invention of embossed beeswax comb 'foundation' to fit into the frame; the centrifugal extractor that spun the honey out of the strengthened framed combs, leaving them ready for re-use; and the queen excluder, a grid penetrable by workers but not by the queen, used to separate the brood chamber from the honey chamber.

What Langstroth's development makes possible is the manipulation of a colony of bees so that it achieves a high population – 50 000 adults or more, as well as brood – which can produce honey greatly in excess of the colony's requirements; it has stores for the winter, and the beekeeper gets his harvest as well. Each spring, honey cham-

bers (supers) are superimposed on the brood chamber(s) in which the colony wintered, more being added as the colony expands, so that the colony continues to grow but is never crowded enough to swarm. More brood space is provided as necessary, kept separate from the honey store by a queen excluder. Reproduction of the colony by swarming is prevented, and excess honey is produced instead.

Bee breeding

Honeybee genetics and sex determination

The genetic mechanism of inheritance in social insects is very different from that in most animals considered in this book. Some background information is therefore needed before the practicalities of breeding and selection of honeybees can be considered. Both silkworms and honeybees have been discussed briefly by Hoy (1976).

Honeybees (*Apis* species) reproduce by a haplo-diploid system. The queen and worker castes are female; they develop from fertilized eggs, and have the diploid number of chromosomes (32). Differentiation between queen and worker – which includes both body characteristics and behaviour – is not genetic; it results from differences in the food of the larva during the first 3 days after hatching from the egg. Larvae become workers (non-reproductive) except for a few which are given richer food, and more of it; these become queens (reproductives). The critical factor that triggers the rate of food intake by the larva appears to be the sugar content (Beetsma 1979). The drone is male, produced by arrhenotoky from an unfertilized egg, and has the haploid number of chromosomes (16).

In the queen's reproductive system meiosis of the oocytes proceeds in the usual way, resulting in gametes with 16 chromosomes. In the drone's reproductive system, the first meiotic division in spermatogenesis is abortive, producing a cytoplasmic bud; the second meiotic division is modified so that only one spermatozoon is formed, and it contains all 16 chromosomes from each spermatocyte. According to one commonly accepted theory of sex determination (Whiting 1945) there is a single sex locus (X), with multiple alleles, and sex is determined thus: individuals that are heterozygous for the sex alleles (diploid)

become females, and those that are hemizygous (haploid) become males. An individual developing from a fertilized egg that is homozygous at the sex locus is a diploid male. No diploid males are reared in nature, because the workers eat them soon after they hatch from the egg. In a long series of experiments Woyke (1978) has succeeded in rearing diploid drones to maturity, and triploid queens and workers were produced by 1980, but this work has not (yet) impinged on practical bee breeding. Another theory, the genic balance theory, has been proposed by Kerr and his co-workers (see Kerr 1974).

Mutations that are useful as markers for genetic studies have been produced, and where possible maintained; thirty-five are listed by Rothenbuhler (1975), but none of these is directly useful in practical bee breeding.

Every haploid drone inherits all his genes from one individual, the queen that is his mother. Female progeny of a single queen inherit genes from their mother, and from one of a number of drones that mated with her in flight – the donor of the spermatozoon fertilizing the egg in question. The only exception occurs if the queen is instrumentally inseminated with semen from a single drone (see below).

Natural mating

The young queen honeybee mates in flight, with a number of drones in quick succession. The drones may have flown more than 5 km from their colonies, and queens nearly as far. In tests with genetically marked bees (the cordovan mutation, in which black colouration is replaced by brown), 25 per cent of queens mated with drones from 16 km away. So, however carefully the genetic make-up of a queen is controlled, that of her worker offspring cannot be assured so long as there are any adventitious colonies containing drones within, say, 20 km of the queen's colony. Sites used for mating stations in different countries are: desert oases (excellent); small islands (often windy, but satisfactory if well off shore); deep valleys with high mountains on either side to give protection (but very few such bee-free valleys are available).

The difficulties in ensuring 'pure' mating were appreciated long before details of the mating itself had been elucidated. But it was not understood until 1954 that queens normally mate with a number of drones (commonly 6–10), on a single

flight. In 1963 it was shown that drones are not attracted to a virgin queen unless she is flying higher than a critical distance above the ground, which can vary from about 5 to 40 m, for reasons still not fully understood. The workers' flight space is below that of the reproductives, and this helps drones to locate a queen in the air.

Attempts have been made in Zimbabwe to predetermine the drones mating with a queen by using a flight cage up to 11 m high, but only occasional successes have been reported.

Instrumental insemination

An inviting approach to breeding is insemination of the queen in the laboratory. A technique was first devised in the United States by L. R. Watson in 1927, and this has been improved by many others since, in the United States and elsewhere. During the past decade the procedure has been a routine one, and many thousands of queens are instrumentally inseminated each year in bee-breeding programmes.

The queen is anaesthetized with carbon dioxide and immobilized in a tube, from which the tip of her abdomen protrudes, in the field of a binocular microscope. A specially designed syringe is mounted appropriately, and is charged with semen from several drones, which is then injected into the queen's vagina, beyond the valvelfold which is held out of way by a hook (Laidlaw 1977).

Changes in honeybees under selection

Social bees were producing honey for 10–20 million years before man existed. In the course of natural selection, the honeybees that survived had genetic characters enabling colonies to store enough honey to last them through the dearth periods they encountered, to defend their nest against enemies (many mammals and birds will eat the contents of a bees' nest), and to resist hazards of climate, disease and predation.

When and where man persistently took honey, and disrupted the bees' nests in doing so, there was also selection in favour of bees that were best able to defend their nest (were more 'aggressive'). In traditional African beekeeping, empty hives were populated by swarms. This was also true in early European beekeeping; the beekeeper 'took' the clustered swarm and put it into a hive. There was thus selection towards swarming tendency, and also towards swarming early in the

active season, because early swarms had the best chance of building up population and stores before the dearth period. ('A swarm of bees in May/Is worth a load of hay . . . A swarm in July /Isn't worth a fly.')

In modern beekeeping, queens are reared from eggs that are the progeny of a selected (breeder) queen. They do not originate in a colony preparing to swarm, but in a colony chosen by the beekeeper for the purpose. By judicious choice of breeder queens for colony characteristics such as those listed below, progress in selection through the female line can be made (Rothenbuhler 1980). Selection can include the male line if newly reared queens are put into (small) colonies in a completely isolated mating apiary, with other chosen colonies organized to rear many drones. But such progress in selection is not *permanent* unless this procedure is repeated for every queen reared. Normally drones of unknown ancestry are present (in other colonies) within flying reach of the young queen's flight range, and will contribute their genes to the queen's female progeny, in a way and to an extent that the bee breeder cannot know.

Selection became much more effective when queens could be inseminated instrumentally with semen from drones of specified ancestry, and selection for characteristics 8 and 10 below was not possible before this could be done. Different bee breeders have selected *Apis mellifera* for one or other of the following characteristics, according to their requirements. Queen-rearers, in general, will continuously aim for characteristics 1-4; 9 and 10 are specializations, and so is 8. at present, although its importance will increase.

1. Improved honey production.
2. Populous colonies with a low tendency to swarm (in earlier management based on use of swarms, selection had the opposite aim).
3. Gentleness, bees remaining on the combs when colonies are inspected - as they must be with modern management - and not flying off and stinging the operator.
4. Other colony characteristics such as overwintering, compact brood nest, early spring development.
5. Light (golden) colour of queens, which has found inordinate favour especially in North America, and whose only merit is that a queen is easy to spot on the comb.

6. Resistance to brood diseases, e.g. American foul brood (*Bacillus larvae*), European foul brood (a complex of bacterial pathogens), chalk brood (*Ascosphaera apis*). For American foul brood the mechanism(s) could be: resistance of honeybee larvae to *Bacillus larvae*; antibiotic content of the food fed to them by workers; or hygienic behaviour of the workers in cleaning-out infected brood cells.
7. Resistance to adult bee diseases, e.g. acarine disease (*Acarapis woodi*), 'hairless-black syndrome' (viral).
8. Low variability in colony performance, which allows all colonies in an apiary to be given the same treatment at the same time.
9. Heavy early brood rearing, needed for package bee production.
10. Effectiveness in pollinating a difficult crop, notably alfalfa.

Selected characteristics cannot be maintained in subsequent generations through natural matings, unless these occur in isolated areas. Moreover, bee breeding can impose a heavy burden in the maintenance of colonies with the required genetic characteristics. Some advances have, however, been made with storage of frozen drone semen.

The idea of crossing different strains of honeybees to exploit hybrid vigour is attractive, and heterotic effects have been well studied (e.g. Cale and Gowen 1956). Experiments have been done with inter-racial crosses, e.g. in France (Fresnaye and Lavie 1977) and in the Soviet Union (e.g. Mel'nichenko and Trishina 1977). In the United States, hybrids have been produced as a commercial operation since 1949 (Witherell 1976). In this system four inbred lines A, B, C, D, are produced from colonies selected after several years of evaluation and breeding. These lines are crossed in pairs whose characteristics complement each other (e.g. AB, CD), and the resultant hybrids are themselves crossed to give a 'double hybrid' (AB × CD). Two such double hybrids have been developed by Dadant and Sons, and are now sold by Genetic Systems, Inc. They are known as Starline (from all Italian stock) and Midnite (from Carniolan and Caucasian stocks).

The beekeeper who buys these hybrid queens in spring, and replaces ordinary Italian and Caucasian with them, can get up to twice as much honey from the colonies concerned. But only F₁

hybrids benefit from heterosis, and in subsequent generations deterioration is very rapid, so the beekeeper must buy new queens as necessary, usually each year, if he is to maintain the high yields. There are no improved, fixed hybrid races or strains in honeybees, because of the mating behaviour of these insects.

Present situation and future prospects

Today the domestication of bees results in the annual production of around 800 000 tonnes of honey, of which 75 per cent is consumed in the country of origin and 25 per cent sold on the world market. The largest producers are all large countries; the United States Department of Agriculture estimates for 1979 are: United States 98 000 tonnes, Chinese People's Republic 85 000, Soviet Union 80 000. Of these, only China is a major net exporter, and indeed it is becoming the world's largest honey exporter. Mexico and Argentina export most of their production, which is 56 000 and 28 000 tonnes respectively. The same is true of various other countries of Latin America that together produce some 35 000 tonnes. Australia and New Zealand between them produce 24 000 tonnes and export 6000. Other countries producing 10 000 tonnes or more are as follows. In Europe: France, West Germany, Greece, Spain; in Asia: India, Turkey; in Africa: Angola, Ethiopia, Madagascar. Most consume all or most of their production, and France and West Germany also import honey. West Germany is the largest importer, followed by Japan and the United Kingdom, for which 1978 figures were 57 000, 24 000 and 17 000 tonnes respectively. Most of the honey on the world market is imported into countries of Western Europe. A high per caput consumption of honey tends to be linked with a strong beekeeping tradition in past centuries, either directly as in northern Europe, or indirectly as in New World countries populated from northern Europe: United States, Canada, Australia, New Zealand. Japan's relatively high honey consumption started only after the Second World War, and was part of a change in eating habits brought about by American influence.

Prospects for increasing world honey produc-

tion in the future depend mostly on events in those regions of the tropics and subtropics where beekeeping has a large undeveloped potential. Few dramatic gains can be expected in temperate zones, except perhaps in the intensive short-summer growth regions in northern Canada and eastern Siberia, where it will depend on crops being grown that are good honey plants. In the tropics there is a wealth of honey plants, but the honey can be harvested only if there are more hives, better management systems, better roads, and suitable vehicles to carry the hives from one honey flow to another.

Beeswax is most easily produced in the tropics where temperatures are high, and the beeswax harvest could be increased greatly by paying proper attention to its production and collection. Whether or not the harvesting of other hive products – pollen, royal jelly, propolis and bee venom – will increase appreciably depends on future demand for them at attractive prices. Methods have been developed for harvesting all of them commercially (Crane 1980b).

The breeding of honeybees for honey production, and for other more specialized purposes, will continue. It is likely to increase yields in areas with good food resources for bees and a suitable climate, and where sophisticated systems of bee management are used. But it does not provide the same cost-effective pathway to increasing yields as with mammals, because of the instability of any lines or strains bred.

One type of beekeeping that will surely increase greatly is the provision of colonies of honeybees – and of other bees – for pollinating crops (Free 1970, McGregor 1976). In small-scale agriculture, scattered colonies often provide enough pollination to ensure good seed and fruit set in entomophilous plants. In large-scale agriculture, which will become more and more the norm, it is essential to move pollinators to certain crops in order to obtain maximum yields. The most versatile pollinators are the honeybees, and hives of honeybees can easily be transported to provide a large number of pollinators where required. Where an insect other than a honeybee is especially effective, it is almost always another species of bee, and methods will be devised for domesticating it, when and where the demand arises.

References

- Beetsma, J.** (1979) The process of queen-worker differentiation in the honeybee. *Bee World*, **60** (1): 24-39
- Bohart, G. E.** (1972) Management of wild bees for the pollination of crops. *Annual Review of Entomology*, **17**: 287-312
- Cale, G. H., Jr and Gowen, J. W.** (1956) Heterosis in the honey bee (*Apis mellifera* L.). *Genetics*, **41** (2): 292-303
- Crane, E.** (ed.) (1975) *Honey: a comprehensive survey*. Heinemann and International Bee Research Association: London
- Crane, E.** (1978) *Bibliography of Tropical Apiculture; also Satellite Bibliographies*. International Bee Research Association: London
- Crane, E.** (1980a) *A Book of Honey*. Oxford University Press: Oxford
- Crane, E.** (1980b) Apiculture. In: *Perspective in World Agriculture*, pp. 260-94. Commonwealth Agricultural Bureaux: Farnham Royal, Bucks, England
- Crane, E.** (1983) *The Archaeology of Beekeeping*. Duckworth: London
- Free, J. B.** (1970) *Insect Pollination of Crops*. Academic Press: London and New York
- Fresnaye, J. and Lavie, P.** (1977) Selection and cross-breeding of bees in France (*Apis mellifica* L.) In: *Genetics, Selection and Reproduction of the Honey Bee*, pp. 212-18. Apimondia Publishing House: Bucharest
- Galton, D.** (1971) *Survey of a Thousand Years of Beekeeping in Russia*. Bee Research Association: London
- Hobbs, G. A.** (1972) Beekeeping with alfalfa leafcutter bees in Canada. *Bee World*, **53**: 167-73
- Hoy, M. A.** (1976) Genetic improvement of insects: fact or fantasy? *Environmental Entomology*, **5**(5): 833-9
- Kerr, W. E.** (1974) Advances in cytology and genetics of bees. *Annual Review of Entomology*, **19**: 253-68
- Laidlaw, H. H.** (1977) *Instrumental Insemination of Honey Bee Queens*. Dadant: Hamilton, Illinois, U.S.A.
- McGregor, S. E.** (1976) Insect pollination of cultivated crop plants. *Agricultural Handbook, United States Department of Agriculture*, No. 496. Washington, D.C.
- Mel'nichenko, A. N. and Trishina, A. S.** (1977) Ecological and genetical bases of the heterosis in the honey bee (*Apis mellifera* L.) In: *Genetics, Selection and Reproduction of the Honey Bee*, pp. 203-9. Apimondia Publishing House: Bucharest
- Nogueira-Neto, P.** (1970) *A Criação de Abelhas Indígenas sem Ferrão (Meliponinae)* (2nd ed). Chacaras e Quintais: São Paulo
- Pellett, F. C.** (1938) *History of American Beekeeping*. Collegiate Press: Ames, Iowa
- Rothenbuhler, W. C.** (1975) The honey bee, *Apis mellifera*. In: *Handbook of Genetics*, ed. R. C. King, Vol. 3: *Invertebrates of genetic interest*. Plenum Publishing: New York
- Rothenbuhler, W. C.** (1980) Necessary links in the chain of honey bee stock improvement. *American Bee Journal*, **120**: 223-5, 304-5
- Ruttner, F.** (1973) [*Techniques for the Rearing and Selection of Honeybees*]. Ehrenwirth Verlag: Munich. (In German)
- Schwarz, H. F.** (1948) Stingless bees (Meliponidae) of the western hemisphere. *Bulletin of the American Museum of Natural History* No. 90: 1-546
- Whiting, P. W.** (1945) The evolution of male haploidy. *Quarterly Review of Biology*, **20**: 231-60
- Witherell, P. C.** (1976) A story of success - the Starline and Midnite hybrid bee breeding programs. *American Bee Journal*, **116** (2): 63-4, 82
- Woyke, J.** (1978) Biology of reproduction and genetics of the honeybee (E21-ENT-28). Final technical report (1971-78). Agricultural University of Warsaw