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PHILANTHUS TRIANGULUM AND ITS RECENT ERUPTION AS A PREDATOR OF HONEYBEES IN AN EGYPTIAN OASIS

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Philanthus triangulum

The genus *Philanthus* (Hymenoptera, Sphecidae) or digger wasps contains about 135 species and is well represented in the Ethiopian, Palearctic and Nearctic regions. Small numbers are Oriental and Neotropical; the genus is not known from Australia and South America.

Philanthus species prey on numerous solitary bees in the Halictidae, Andrenidae and Colletidae, as well as on social bees (Apidae), in providing food for their offspring. The single species under discussion here is *Philanthus triangulum* (Fabricius, 1781), commonly known as the bee wolf, which hunts exclusively on the honeybee, *Apis mellifera*[2,3].

P. triangulum is widely distributed and occurs from central Europe as far south as South Africa, and from the Atlantic coast of Europe into western Asia. Lepeletier was under the impression that a different species occurred in North Africa, which he called *P. abdelcader*[10]. Subsequent taxonomists realized that the difference is merely a variation in colour, and that *abdelcader* and *triangulum* are identical[6]. So only the name *triangulum* will be used here.

P. triangulum is about 16 mm long, with a black head and a thorax with yellow markings. The female can be recognized easily by the characteristic yellow V on the front of her head, whereas the male has three divergent lines (Fig. 1). Colour of the abdomen of the female varies: in Europe it is yellow with a black triangle on each segment, whereas in Asia and Africa it is completely yellow.

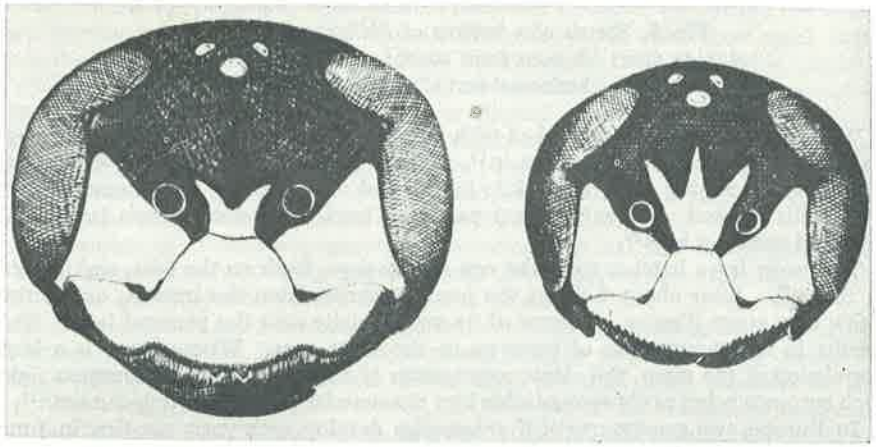

Fig. 1. *Philanthus triangulum*, head in frontal view: *left* female; *right* male

Life history

P. triangulum is a solitary wasp, each individual—whether male or female—occupying a burrow of its own[17]. The male digs a shallow hole, merely to sleep in, but the female spends much time digging a deep burrow with cells on both sides of the horizontal part of the main burrow, and in these the eggs are laid (Fig. 2). The female captures honeybees on flowers and paralyses them by a sting between the first pair of legs[14]. Some of the bees are carried to the burrow and provide food for the offspring, and the rest are used by the female herself; she squeezes the honey sac and licks up the contents.

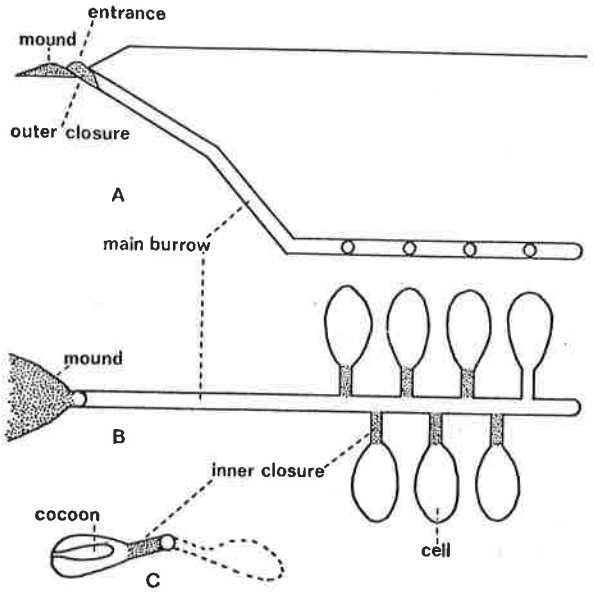

Fig. 2. Sketch of a burrow of *Philanthus triangulum*.
A. side view; *B*. seen from above; *C*. cross-section through horizontal part of main burrow

When a cell is sufficiently stocked with paralysed bees, the female deposits an egg on the bee most recently brought in[19]. Some eggs are fertilized and others unfertilized, developing respectively into female and male wasps. Males emerge from small cells stocked with only 1 or 2 paralysed bees, and females from larger cells provided with 3-6 bees[23].

The wasp larva hatches from the egg in two days, feeds on the bees, and pupates in the cell. After about 4 weeks the imago emerges from the burrow, and within a few days starts digging a burrow of its own, usually near the parental hole. This results in a concentration of burrows in the same area. Where there is a large population of the wasp, this dense aggregation of entrance holes is a common sight, each entrance being easily recognizable by a characteristic mound of dug-out sand[17].

In Europe, two generations of *P. triangulum* develop each year, the first in June/July and the second about a month later[17].

Damage caused

One female may catch up to ten honeybees a day[17]. In Europe a *P. triangulum* population of 3000 in an area is no exception, and it is able to capture 30 000 honeybees daily—the number in an average colony.

Nearly half the adult bees in a colony are foragers, and it is these that are attacked by *P. triangulum*. When the colony finally has too few foragers to collect enough food for the colony, it dies of starvation. In Europe, there are many examples of flourishing bee industries that have been destroyed by *P. triangulum,* which has been a serious pest at different times and at various places. Well known outbreaks occurred in Germany in Oldenburg in 1850[8] and in the Rhine Valley in 1905[12], and a disastrous outbreak occurred in the Werra Valley around 1932[20]. At the same time it was a pest in the Netherlands[22], and more recently in Belgium[18].

The Dakhla oasis

In North Africa beekeeping is locally a major industry. When in 1972 one of the largest oases, Dakhla in central Egypt, suffered heavy losses in honey production, this caused much concern. After it transpired that the cause was in all probability an outbreak of *P. triangulum,* one of us (RTS) paid a brief visit to the area at the request of the Egyptian government, in August 1976. Extensive research was done subsequently by both authors in the oasis, from 16 November 1976 to 19 January 1977 and from 2 November 1977 to 13 January 1978.

The primary aim of the research was to study the pest in greater detail, in order to formulate possible control measures. A secondary aim was the mass collection of female *P. triangulum* on behalf of the Pharmacological Laboratory of the University of Amsterdam, where research is carried out on the mechanism of action, and the chemical structure, of the venom of paralysing wasps. Since *P. triangulum* can become a pest to honeybees, most work has been done with the venom of this species, which paralyses the muscles of the legs and wings, but leaves the muscles of the heart and gut unaffected[13].

History of beekeeping

Colonies of the Egyptian bee, *Apis mellifera lamarckii* Cockerell (=*fasciata* Latreille), were introduced into the Dakhla oasis in 1928, and were used there until 1960, when the government of the so-called New Valley (which includes Dakhla) decided to take advantage of the unique isolation of the oasis to breed bees less 'aggressive' than the Egyptian bee. The latter were eradicated as far as possible in October 1960, and the bees introduced were descendants of Carniolan bees from Czechoslovakia, *Apis mellifera carnica* Pollmann. They interbred with the remaining Egyptian bees, and from the progeny a new strain, called Queen Wadi, was selected; these bees are easy to handle and are also very industrious workers.

The number of colonies was increased satisfactorily to 300, and honey production to 8000 kg per annum, yielding approximately 2400 Egyptian pounds, and then in 1972 honey production suddenly dropped to practically zero. In the same year wasps, later identified as *Philanthus triangulum,* were seen to attack the bees. Whether the sharp decline in the honey production was actually and exclusively caused by these wasps cannot be established. From 1972 onwards, large numbers of the wasp were caught in apiaries, as a control measure, but honey production recovered only slowly: in 1973 to 1977 it was 13, 486, 644, 1000, 1200 kg respectively. There-

fore in 1976 beekeeping in the oasis was mainly directed towards producing Queen Wadi queens, which are in demand throughout Egypt and in neighbouring countries. From the experimental station Mariot, near Alexandria, queens were sold to Libya and Iraq. But in 1976 the revenue from 240 queens amounted to only 360 Egyptian pounds, by no means enough to compensate for the reduction in honey production.

Some additional details

The Dakhla oasis lies in the Sahara Desert, about 500 km south of the Mediteranean coast and roughly 300 km west of the Nile. It forms a section of the 'New Valley', being up to 10 km wide and about 80 km long, bounded on one side by a steep cliff. It contains 22 villages with a total population of about 46 000. Beekeeping is solely a governmental matter; there are no private beekeepers. Most of the data concerning *A. m. carnica* and *P. triangulum* have been provided by the Agricultural Officer Mr. Hassan Omran (in charge of bee management) and by the Director of Agriculture Mr. Mohammed Raffet Abdul Mumin.

The bees were kept in five apiaries dispersed over the oasis (Fig. 3, no. 2, 3, 4, 6, 8 with, respectively, 8, 108, 91, 53, 42 hives). Each apiary consisted of a palm-leaf

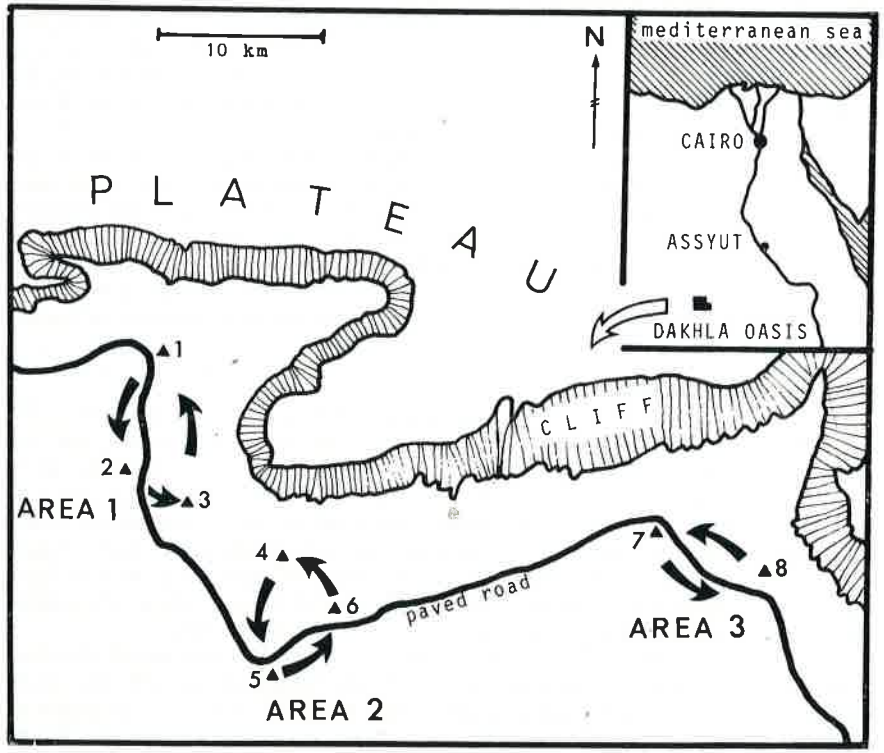

Fig. 3. Map of the Dakhla oasis (23° 30′, 29°) about 500 km south of the Mediterranean and about 300 km west of the Nile. Triangles indicate apiaries: (1) Ezeb-el-Kassr, (2) Budkhula, (3) Rashda 3, (4) Ewina, (5) Mut, (6) Sheik Waley, (7) Balat, (8) Balat 7. In each of the three areas arrows indicate the directions in which hives should be moved when *P. triangulum* becomes a nuisance.

roof over several rows of hives, and three palm-leaf protective walls. All were situated between agricultural and semi-desert areas. Only no. 6 (Sheik Waley) was very shady, with *Casuarina* trees. In winter the colonies covered 1-3 combs in a 10-frame hive.

The numbers of bees entering and leaving the hives were counted on several occasions. In winter the Queen Wadi bees are mainly active in the morning, foraging from about 6 to 10 h; activity is minimal at noon. Flowers are very scarce in the Dakhla oasis in November and December. The bees chiefly visit the *Eucalyptus* trees planted around most of the apiaries and along the roads, and from mid-December onwards, field beans (*Vicia faba*) provide nectar. The bees also collect pollen from *Casuarina equisetifolia*.

P. triangulum in the Dakhla oasis

P. triangulum has probably existed in the Dakhla oasis for a considerable time; in 1946 it was collected there by Mr. Mohammed Mahmod Abrahim. Possibly it had little chance to increase its numbers as long as its only prey was the 'aggressive' Egyptian bee. If so, it may have been able to build up large populations only after the Egyptian bees were replaced by the Queen Wadi bees in 1960. After a gradual increase for a number of years, an explosive growth must have occurred in 1972, with the results recounted above.

We have observed in southern France that, under favourable conditions, *P. triangulum* can build up an enormous population in a few years, and we assume that this was also the case in the Dakhla oasis. The above assumptions seem to be confirmed, since the only other area in Egypt where the wasp is a pest is Sidi Abel el Rahman (140 km west of Alexandria), where Queen Wadi bees are also kept. Although it is not completely established that *P. triangulum* predation was the only cause of the sharp decline in honey production, it seems likely to have been the main one.

P. triangulum hunts exclusively for honeybees[2,3]. Tills' statement that 0·5% of the prey consists of solitary bees[22] can hardly be true; over the years we have collected thousands of the wasps returning to their burrows with prey, invariably honeybees. In the Dakhla oasis, several experiments were made in which a *P. triangulum* wasp was put in a cage with a number of the most common wild bees of the oasis, of the genera *Andrena* (*Melanapsis*) and *Andrena* (*Plastandrena*). The wasps never showed any interest in wild bees, although when a honeybee was introduced into the cage it was immediately caught.

Under European conditions *P. triangulum* burrows are usually more or less clustered, near the burrow from which the wasps emerged. Moreover, suitable nesting areas—patches of barren, sunny, dry sandy soil—tend to occur only in restricted areas. We presume that in Egypt the presence of the open desert as a nesting site induces a wide scatter of the burrows. This scatter has several effects: availability of nesting sites is not a limiting factor in population control, and the scatter may well eliminate the pressure of brood parasitoids, that in more usual conditions may severely reduce wasp populations. During our stay only one specimen of a reputed *P. triangulum* parasitoid was found. Finally, the usual technique of mass-collecting the wasps at nesting sites is impossible when they are widely scattered.

Aberrant hunting behaviour

Normally the wasp catches honeybees foraging for nectar on flowers, but in the Dakhla oasis, during October, November and December, it attacks them close to the

hive, and sometimes even on the alighting board in front of a defended hive entrance. This hunting behaviour may be considered aberrant, and may be explained by the relative lack of flowers, which forces the wasp to hunt for honeybees in the only other place where they can be found. As soon as more plants come into flower the hunting area changes; in the last week of December field beans attract many bees, and more and more wasps are diverted from the apiaries. It would require a full year of observation to ascertain whether the wasp follows the bees from one plant species in flower to the next.

Populations dynamics

The total *P. triangulum* population in the Dakhla oasis is unknown; the only data at our disposal are the numbers that were captured, conceivably only a small percentage of the total population.

The government beekeeper, with 15 assistants, had captured *P. triangulum* near hives during the winter months from 1972 onwards. Numbers recorded were:

1975/76	14 000	in 5 months
1976/77	24 000	in 6 months, a premium of one Egyptian pound being paid for 100 wasps
1977/78	17 000	in 6 months, premium doubled, but mean temperature 2°C lower than in 1976/77, and often not reaching 18°, the temperature at which *P. triangulum* becomes active.

Seasonal variation was the same in all three winters, captures starting in September, reaching a maximum in December and falling almost to zero in February or March. The number captured does not reflect the size of the population, but the ease with which the wasps can be collected near hives, which is itself governed by lack of plants in flower.

The beekeepers believe that *P. triangulum* disappears in March and is dormant during the hot summer months. However, in our opinion dormancy is unlikely when honeybee populations are highest; more probably the wasps are so scattered in summer that the beekeepers do not notice them.

It seems likely that new generations appear about the end of the year in the Dakhla oasis. In the field and in the laboratory, male wasps emerge about 4 days before the females[16]. When we started collecting *P. triangulum* in mid-November in the Dakhla oasis, males were rare, and only 4 of the 7000 wasps collected before the last week of December were males; thereafter a higher proportion were males, sometimes 50%. This indicates that a new generation of males emerges in December, presumably followed by a new generation of females in the beginning of January. The number of generations emerging between February and November is unknown; during this period some *P. triangulum* can always be observed in the fields. In the Nile Valley *P. triangulum* is found all the year round[5].

In the Dakhla oasis it takes a year before *P. triangulum* becomes a pest, and about a year to get rid of the wasp once it has become established. This conclusion was drawn from data collected in Balat 7 and Ezeb-el-Kassr. In Balat 7 (Fig. 3, no. 8) no honeybees were kept until the summer of 1975, when the bees did well. *P. triangulum* did not become a nuisance until November 1976; it is not known whether the wasp was present before the bees, but even if so, it did not become a pest for well over a year. In Ezeb-el-Kassr (Fig. 3, no. 1) beekeeping had to be stopped in the summer of 1975 because of *P. triangulum*, yet in 1976 not a single wasp could be found, even during an exhaustive search. The wasp may not have disappeared, but it had become at least very rare.

Alternative hypotheses

In local agricultural circles, it is believed that the heaviest damage is caused more by panic evoked in the colonies by *P. triangulum* attacks than by the actual catching of bees: the bees become afraid to fly out to collect nectar, and cluster outside the entrance for the rest of the day. However, this theory is not supported by the facts, since our observations show the following. (*a*) When *P. triangulum* hunts near a hive and there are no guard bees on the flight board, it has a good chance of catching a home-coming bee, but this induces no reaction among the bees entering or leaving the hive. (*b*) When a few guard bees are present, there is a fight from which the wasp may escape alive, but never with prey. (*c*) With a large cluster of guard bees, the wasp is invariably killed in the ensuing fight.

During our extensive observations we never observed that the bees became 'panicky'. Even during a fight between the wasp and guard bees, foraging bees entered and left the hive in a normal way. Clusters of bees were present at the entrance of certain hives, but early in the morning, before any of the wasps were around. The formation of a cluster seems to be associated with conditions in the individual colony, such as overcrowding or swarm preparations.

Another theory we encountered was that home-coming bees warn those in the hive when there are wasps near the flowers, and all foraging bees then stay at home for the remainder of the day, either out of fear or as a precaution. This assumption seems highly improbable: as far as is known honeybees do not warn each other when they are attacked by a wasp while collecting nectar on flowers. Only when the hive is threatened by a large animal or by man do the bees alert each other with a pheromone, and they do not then remain in the hive, but fly out to attack the aggressor.

Control measures

Various methods to control *P. triangulum* pests have been tried. Adult wasps have been collected and killed[21]; the breeding sites have been covered with gravel or broken stones[20], or dusted with insecticide powder[9] which would kill the adults, leaving the offspring to survive until next year. Although some measures gave fairly good results, most were too laborious and therefore too expensive. Sometimes the pest disappeared after a few seasons without any apparent reason.

In the Dakhla oasis *P. triangulum* has apparently become a pest since a non-aggressive race of bees was introduced, which also retained its behaviour of clustering in winter. These bees are vulnerable to *P. triangulum*, which:

(*a*) preys only on honeybees;
(*b*) remains active in winter;
(*c*) if necessary flies close to the hive to catch its prey;
(*d*) has no significant local enemies.

Available control methods that have been successful elsewhere are considered below in relation to these circumstances.

1. *Destruction of P. triangulum breeding areas*

Complete breeding areas can be destroyed only if high concentrations of burrows can be found. Large-scale methods such as irrigation, spraying, ploughing, or covering the soil with some substance, can then be used. However, suitable concentrations of burrows have not yet been found. These methods can control the wasp only in its adult stage and in its nesting area.

2. *Chemical control*

Insecticide spraying of the wasps in the hunting area is not practicable, because the bees would also be killed.

3. *Capture and destruction of adult wasps*

It is laborious to catch the wasps one by one with an insect net, since they fly very fast, have good vision, and are skilful in evading pursuers. Even so it can be very effective. In at least two instances large populations of *P. triangulum* have disappeared in the course of one or two seasons simply through intensive capture by a few well trained collectors.

This method has been recommended for the Nile Valley[5], and has so far been the only control measure applied in the Dakhla oasis. Unfortunately it is not effective there: *P. triangulum* has been collected near hives since 1972, but still remains a serious pest. The failure has not been due to a lack of diligence by the collectors, especially between 21 November 1976 and 19 January 1977, when a premium was paid for each wasp collected. In all, 24 000 females were collected, yet next winter another 17 000 were caught. This suggests that in the first winter hardly any harm was done to the wasp population. The authors expect that collecting near hives will have little or no effect as a method of control.

Collecting the wasps in the field not only proved a failure, it was also a source of trouble, as the wasps were partly collected on flowering plants, and farmers objected to people walking through their fields and hitting their crop with nets.

4. *Control by means of parasites*

Like every insect, *P. triangulum* has its enemies. Of the six species that are the most important parasites in Europe, four have other hosts besides *P. triangulum*. The introduction of such polyphagous parasites is both ineffective and risky. Of the two monophagous parasites (which specialize on *P. triangulum*), one is a mutallid wasp *Dasylabris maura* L. and the other a chrysidid *Hedychrum intermedium* Dahlbohm. *D. maura* already occurs in the Dakhla oasis, although very rarely. But even if it were common its use for controlling *P. triangulum* would be doubtful, since the female is wingless and could be effective only if the wasp burrows were concentrated together. *H. intermedium* is mentioned by R. du Buysson as found in Egypt[4] (probably in the Nile Valley), under the synonymous name *H. rutilans* Dahlbohm[11]. However, this parasite was not found by the authors in the Dakhla oasis, which means that *P. triangulum* has no natural parasite of any importance in the oasis, and this may well be one of the reasons why the wasp can become a pest.

Recommendation of artificial introduction of *H. intermedium* has been seriously considered because of its specific behaviour, which is as follows. The females are constantly on the move looking for burrows of *P. triangulum,* which they do while flying or walking. When a burrow is discovered, the female returns to it frequently, waiting for the appropriate moment to deposit her egg on one of the paralysed bees, i.e. just before the cell is closed. The egg of *H. intermedium* does not take long to hatch, and the first larval stage has strong jaws, with which it destroys the egg or kills the larva of *P. triangulum*. The jaws are absent in the next larval stages, when the larva needs only sucking mouthparts adapted to consume the contents of the paralysed wasps.

This parasite is a very serious enemy of *P. triangulum*. In France we often observed that a population dropped practically to zero the year after a dense population of

H. intermedium was present. Introduction of this species may thus merit close consideration, the more so since damage to other insect species of the local fauna would not be expected. However, when this was suggested to the authorities, the issue was blocked by the fact that the Egyptian Government bans all artificial introductions of live insects.

Measures to protect the honeybees

Accepting the fact that direct measures against *P. triangulum* are not feasible, the only possibility to save apiculture in the Dakhla oasis is by protecting the bees. The simplest solution would be to replace the Queen Wadi bees by a more aggressive race[1,15], but this is unlikely to meet with the approval of the beekeepers. We therefore advised the following to the Egyptian authorities, in January 1978.

1. *Colony condition*

For every honeybee pest, the general principle holds that strong colonies are least affected. So, for instance, small colonies should be united to form larger, stronger colonies. At present the bees winter on only 3-5 combs per hive, and we recommended that they should occupy at least 10. This should also improve both queen rearing and honey production.

2. *Moving the hives*

Since *P. triangulum* is totally dependent on honeybees, its populations collapse altogether if there are no colonies in the area. So it could be eradicated by removing all hives from the Dakhla oasis for about a year. This idea is not new: in 1936, when the wasp became a serious pest in Germany, beekeepers were advised to move their hives at least 6 km from existing apiaries, to 'starve' the wasp[7,21].

It is easy to understand beekeepers' objections to this measure. However, the same principle can be applied on a smaller scale, although this will be less effective. The hives must first be concentrated in a few sites, which would clear the rest of the oasis of *P. triangulum*. Then, wherever the wasp becomes a pest in a locality, the hives there should be moved to a different area. Moves would not be necessary more than once a year, preferably in September so that the bees go into winter (when they are most vulnerable) in surroundings free from *P. triangulum*.

We suggested that not more than three sites should be used for hives simultaneously. The oasis would be divided into three areas, and three sites, as far apart as possible, allocated in each area. Fig. 3 shows what we had in mind. All colonies, reduced in number and therefore larger, would be divided between the apiaries at Ezeb-el-Kassr, Mut and Balat (Fig. 3 no. 1, 5, 7), which during our study were mostly free from *P. triangulum*.

As soon as *P. triangulum* becomes too numerous at any one site, the hives would be moved to the next site in the same area (as indicated by arrows in Fig. 3), and so on. In practice this would mean that hives would be present at each site for one year, and then absent for at least one or two years.

This method of repeated removal will be most successful if *P. triangulum* can find no prey at all. Therefore any local feral colonies should be eradicated when apiaries are evacuated.

It is not known how far *P. triangulum* flies when hunting, so only experience will show whether the bees have been moved sufficiently far away. If many of the wasps are still present soon after removal, the distance is clearly not great enough. In that

case the oasis should be split in two instead of three areas, thereby increasing the distance between apiaries within one area.

Although the authors still believe that the original advice (to remove the bees completely for one year) offers the best solution, the above modification is worth trying. The Department of Agriculture of the Dakhla oasis raised several objections to it. The first, that there would be insufficient pollination and that the crops would suffer accordingly, is unfounded. Many other pollinating insects occur everywhere in the oasis, in particular solitary bees and many species of flies, whose populations are large enough to guarantee the necessary pollination.

The second objection, the cost and the work involved in transferring the hives, concerns only the Dakhla authorities and cannot be judged by outsiders, but in Europe hives are transported quite frequently to take advantage of successive honey flows. It may be a question of what one is used to, although there could also be problems in the oasis that do not arise in Europe. The method would certainly be much cheaper than the present one, which keeps 15 workers occupied and results in an inefficient collection of adult wasps.

Acknowledgements

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Summary and request for assistance

Presumably due to the replacement of the relatively aggressive Egyptian bees by the more gentle Queen Wadi strain, *Philanthus triangulum* reached such densities in the Dakhla Oasis in Egypt that honey production dropped to almost zero. Mass collection of the adult wasps, usually a satisfactory control measure, failed. The cause of this failure is discussed, and an alternative control measure proposed: reducing the number of apiaries, and shifting their location in a rotation scheme which would prevent the build-up of large pest populations.

P. triangulum is widely distributed in countries around and east of the Mediterranean, and there is a danger that it will become a pest in other areas where non-aggressive honeybee races are introduced. The authors would very much appreciate being informed if *P. triangulum* becomes a pest, or increases to a large population, in any area.

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