INSECT-PLANT COEVOLUTION IN THE MOUNTAINS OF SINAI

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Evolutionary Ecology as a subject can feel a certain smugness since it is possibly the only branch of biology to have a patron saint (if you exclude Darwin): she is Santa Rosalia from Palermo in Sicily, designated by G Evelyn Hutchinson in 1959 after his visit there generated the ideas that gave rise to modern community ecology. I shall describe our work in evolutionary ecology done in the shadow of a much better-known saint, Saint Katherine of Alexandria. She tried to convert the notorious persecutor of Christians, the Emperor Maximanus, and for her pains she was mutilated and martyred on a wheel (hence the Catharine wheels of firework displays). Her body was said to have been transported by angels to the top of the highest mountain in southern Sinai, which now bears her name.

A recent guidebook states that 'parts of the mountains of Sinai are as isolated and wild as anywhere on earth'. Since 1986, I have been visiting this area for my research, and can confirm the truth of this statement: Sinai has wonderfully beautiful habitats, well worth preserving. The peninsula of Sinai can be divided into three regions: the flat and generally low-lying north, the vast low plateau of El Tih in the middle, and the mountainous massif of the south, rising to 2665 m at the top of Mt St Katherine. Almost 5000 km² of the massif was declared the St Katherine National Park in 1994. It has by far the richest biodiversity of all Egypt: for example, it probably harbours half of the great variety of Egypt's plant species, including 33 endemics; two-thirds of Egypt's butterfly fauna have been recorded there, including two endemics, one of which (*Pseudophilotes sinaicus*, a Lycaenid) is possibly the smallest butterfly in the world. Unlike almost every other inhabited region of the world, there are no social bees of any kind. The area is seriously threatened by expanding tourism and by overgrazing.

The Monastery of St Katherine nestles at the foot of Mt Musa, traditionally identified as Mt Sinai where Moses obtained the 10 Commandments. The original chapel of the monastery church, dating from about 330 AD, was built over the roots of the Burning Bush, and expanded into the Monastery by the Emperor Justinian by 600 AD. It is almost unchanged today. The Monastery has been a pilgrim destination since the 4th century. However, while thousands went to Jerusalem, few added Mt Sinai to their itinerary, and only the Russian Count von Tischendorff went more than once (for quite a different reason – to steal the Codex Sinaiticus!). The reason for the relative paucity of visitors was that the journey was long, difficult, dangerous, and very expensive. In the words of Arnold von Harff in 1497:

> *'In these three days there died ... two brothers, ... whom we had to leave half-alive lying in the sand, which was most pitiful to see. ... If anyone is ill, or from weakness is unable to go on and prefers to die, then the company has to*

> *leave him lying alone, and press on on account of the water, which lasts only one day, otherwise all would die. ... We came across more than 50 persons ... lying exposed in the sand, all suffocated by the heat of the sun ... "*

Having struggled up the wadis (dry valleys) to reach the Monastery at 1600 m above sea level, the final stage of the pilgrim's journey was to climb the 3750 stone steps to the summit of Mt Sinai. Most visitors today climb in the early hours of the morning so as to be at the top to watch the unforgettable sight of sunrise over the entire peninsula; 400 m higher than Mt Sinai is Mt St Katherine, which today also has a chapel at its summit. In 1483, filled with religious fervour, Felix Fabri climbed Mt Sinai and Mt St Katherine in a single day!

What do *we* do in this awesome landscape? Our work in Egypt has been supported by ODA, the British Council, the Royal Society, and other smaller grants, and is a joint project with St Andrews (Drs Pat Willmer, Richard Abbott, Simon Potts, Jaboury Ghazoul & Kirsten Wolff), Oxford (Drs Graham Stone & Alex Rowe), Ain Shams (Dr Somia El Akkad) and Suez Canal (Drs Samy Zalat & Fayez Semida) Universities, with developing collaboration from Dr Tomas Wolf (Cambridge University), Dr Sue Hartley (ITE Banchory), and my colleagues from Nottingham (Prof Barnard, Drs Behnke & Hurst). Its research aims are twofold:

i) to map the biodiversity of plants and insects in the wadi systems of the new National Park. This is a necessary part of developing a rational management plan for the Park. For this work, we mount camel expeditions along wadi systems, recording, collecting and mapping the organisms. There are many beautiful and unusual species there, several of which are new to science.

ii) to study insect-plant coevolution. 'Coevolution' is one of the buzz-words of evolutionary ecology, under many different guises in the literature: reciprocal adaptation, arms races, or the 'Red Queen' hypothesis. The strongly subdivided habitat of the Sinai mountains is an ideal place in which to study micro-coevolution, coevolutionary differences between populations of the same coevolved species. We are interested in the possibility that each wadi constitutes a semi-isolated environment in which the coevolutionary process has operated more or less independently.

Our studies on coevolution have been done in and around the town of St Katherine (see Figure 1), in the wadis of Tofaha, Arbaein, Dir, and the 'Plain' (the wide wadi containing the town itself). Most work has been carried out in the middle section of Wadi Arbaein, within 100 m of Moses Rock, traditionally the rock that Moses struck for water.

The coevolved system

We chose to look at a pollination system to take advantage of the ease of quantifying at least some of the costs and benefits to the interacting partners. Nectar is relatively easily measured, and is costly to produce, but is necessary to attract pollinators: the amounts of available nectar can be measured easily, and represent a cost in terms of photosynthate, lost seeds, or water (which might be more important in a desert plant). In an outcrossing plant, the payoff to the plant of producing this costly nectar, and the result of attracting pollinators, is the flow of plant genes via pollen import to set seeds (the female function of the plant) or pollen export to fertilize seeds of other plants (the male function of the plant). One way of ensuring that only true pollinators receive the rewards is to modify the structure of the flower so as to exclude non-pollinating visitors. This generates selection pressure on visitors to match floral morphology.

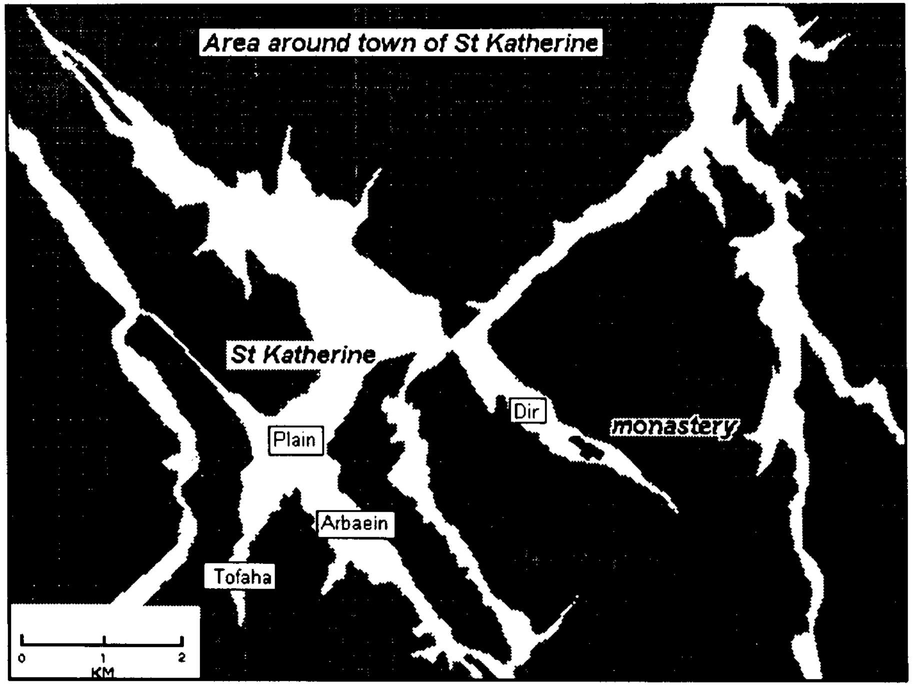

Fig 1. A map of the study site, showing the wadis and their connections. The Monastery of St Katherine is in Wadi Dir

The result, we assume, is coadaptation. This process may take different paths in different sites. Our reasons for thinking this are: i) selection pressures on floral characters can be inconsistent even over short distances (eg, 100 m); ii) theoretically, two genetically identical populations even under the same selection pressures can diverge because of differences in mutations arising randomly in either population, or because of the order in which similar mutations occur. Whether one actually gets genetic differentiation between populations of the plant or the pollinator will depend on the degree of genetic mixing, the distances the genes move. If this is restricted, then the genetic composition of both plant and pollinator should differ among sites. In the pollinator, genes move because of dispersal of males or females away from the natal site. In the plant, genes can move either as pollen carried by the pollinator, or as seeds carried by whatever seed dispersal mechanisms operate.

Which system should we choose for this work? Most Sinai plants are definitely to be avoided. Most are heavily defended against passing entomologists: the vicious boot-penetrating spines of *Acacia*; the dangerous poisons of henbane (*Hyoscyamus muticus*); the debilitating eye-irritants of the endemic species of Jerusalem sage (*Phlomis aurea*). As the best of a bad lot, we settled on the Yellow Gromwell (*Alkanna orientalis*). This perennial plant has an eastern Mediterranean distribution, occurring on mountain tops in Greece, Turkey, Israel and in Sinai, with an isolated outpost in Algeria. In Sinai it occurs almost exclusively above 1500 m, forming cushion plants that eventually can grow to be quite large, a metre across, with several hundred yellow flowers. Like the other plants, it is also horrible to work with, being covered with sticky glandular hairs exuding a nasty defensive chemical, probably a phenol. This deters most herbivores, including goats and camels unless very hungry, such that the plant comes to dominate overgrazed habitats.

The plant fulfils our requirements, however, since it needs insect visitors to set any seed; our experiments have shown that a single visit from an appropriate visitor on average fertilizes one of the four seeds. It is visited almost exclusively by a single insect species throughout most of its flowering season, and like many Boraginaceae it produces truly vast quantities of fairly dilute nectar (up to 6 µl per flower at 25-40% sugar concentration).

The yellow flowers are male first, as they produce pollen before they are pollinated, and are odd in that the anthers have already opened to reveal their pollen by the time the flower bud opens. After a day or two of life fully open, the flower usually turns pale or white, possibly as a result of pollination, and eventually drops off. We divide the life of the flower into four stages: the closed bud, the newly-opened bud, the fully-open flower, and the old pale flower.

The overwhelmingly dominant pollinator is a solitary bee, *Anthophora pauperata*. Males appear in mid-March, apparently well before the females; they also seem to disappear before the females, in late April. Males appear to have a number of mating strategies, and each male seems to adopt one of them: some are territorial apparently throughout life; others have a home range covering a number of the territories of other males; yet others appear to be 'floater males', flying widely and at a considerable speed over the 100 x 100 m study area of the wadi bottom. We do not know much about this last group since they are very difficult to catch even once, let alone twice to read a mark. In contrast, territorial males are easy to catch and observe.

Male bee behaviour

We mark both males and females with bee tags, the numbered discs used for queen bees. Having watched different marked individuals over several years, we have a reasonable idea about how they live out their lives. The environment is unusual in that we can watch males all day long on their territories without ever losing sight of them.

Territorial males spend most of their time flying around their territory. In one year, we mapped all the plants and the territories in three regions of Wadi Arbaein, and found that the whole wadi was saturated with territories. Males can retain their territories for a very long time: one individual kept exactly the same territory for 18 days. The length of time they defend a territory may depend on how they defend them: some males have a 'sit-and-wait' strategy, but most adopt constant aerial patrolling. This appears to be very exhausting, since we have seen several territorial males suddenly stop feeding (control of the long proboscis seems to fail) and die within 30 minutes.

Behaviour in both sexes is driven by the daily march of the sun, enhanced by the shadow cast by the steep sides of the wadi. The sunlight arrives at the bottom of the wadi between 7 am and 9 am depending on the orientation of the wadi, and leaves again between 2 pm and 4 pm. These events strongly affect the air and ground temperatures, and hence the thermal window within which bees can be active. Temperatures in early spring at an elevation of 1600 m are low; it always comes as a surprise when I tell people just how cold it is at our study sites in Egypt! Air temperatures are between 1 °C and 10 °C before the sunlight arrives, and rise to 15 °C to 25 °C at midday, only to plunge again when the shadow returns.

The male arrives at his territory as the shadow leaves. At first he spends much of his time basking and feeding from one of the patches of *Alkanna*, but increasingly he begins to spend more time in flight, patrolling between the patches. As the temperature rises, he spends more and more time in the air, feeds less, and expands his territory to incorporate more patches. He also speeds up his flight. This leads to more and more contact with neighbouring territory holders, and when they meet, terrific fights ensue; however, the only time we have seen territories change hands has been when the incumbent dies, and the adjacent territory holder expands his to take up the space. By 1 pm, each male is whizzing around his territory at high speed, never stopping flying: one male flew 12 km in four hours during a single day! As the shadow returns, the male suddenly stops defending the territory, and within minutes has disappeared under a stone or into a burrow.

In this situation where we can watch males all day long, we can work out their energy budgets fairly accurately. We can measure the nectar standing crop easily, and from observing when males feed, we can estimate the energy they get from their visits to flowers. We know the times they spend in flight, and since flight costs are constant whatever the speed of flight (known from measurements of bumble bees and the similar-sized honey bees), we can calculate their energy costs straightforwardly. Males feed early on in their diel cycle of activity, going into energy surplus; then they go into energy deficit during their territorial defence. One male bee had an overall deficit of 750 J on two days of intensive watching, the equivalent of the contents of 230-300 flowers at the end of the day and an amount easily restored by visiting flowers.

We can do the same thing for water budgets, but the result is less satisfactory. There are two inputs and one output. Making reasonable assumptions, it is easy to calculate the inputs in the form of metabolic water from burning sugar, and water ingested along with nectar sugar. Working out respiratory water losses relies on equations developed from experiments on male bumble bees; some of these bumble bees were about the same weight as *Anthophora pauperata*. The results seem to suggest that there is a large water surplus; water losses from evaporation are about the same as the water gains from metabolizing the sugar needed for territory defence, but the water input from the dilute nectar is three times greater, and the bees should therefore be flooded out with water. This situation seems very unlikely in a desert bee; attempts to extract water from our males to check our calculations failed because the males were more or less dry. It seems much more likely that males are water-stressed in this very arid environment, and that there are significant errors in the calculations for respiratory water loss.

Female bee behaviour

Females are larger at about 125 mg, as opposed to the 85 mg of the males. They nest solitarily, directly in the ground, digging several nests one after another during their lifetime. Each nest has 3-5 cells, each of which has a single egg provisioned with pollen and a relatively large amount of nectar. The eggs appear to hatch straight away, and at least some larvae are mature within a month.

The activity pattern of females is exactly the opposite of males. Although there are always a few females foraging further into the day, the vast majority have a bimodal pattern of foraging activity, avoiding the middle part of the day when territorial males are active. Females start foraging in the early morning, before the sunlight strikes the flowers and when the air temperature is only about 8-10 °C. After about 10 am, they largely disappear for the rest of the day, reappearing in the afternoon just before the shadow returns onto the flowers, and continuing to forage while the air temperature is above 8-10 °C. The actual timing of female activity varies in different wadis because of variation in the timing of the shadow. In order to be active at these low temperatures, females generate heat so that their flight muscles achieve a more efficient working temperature. Females are also excellent thermoregulators, maintaining virtually constant thoracic temperatures regardless of air temperature; in fact they are the best thermoregulators known amongst the smaller solitary bees, and are substantially better than males.

In the morning, females feed mainly on fully-open flowers; these flowers have lost all their pollen, and only offer nectar as a reward. At least in some years, nectar seems to be superabundant, since females do not visit the most rewarding flowers in terms of nectar sugar, and they ignore the old flowers even though these still contain large quantities of nectar. Eventually these old flowers drop off the plant; in the year during which the data were obtained, the dropped flowers still contained 40-50% of the nectar sugar produced by the plant – presumably nectar production was not a limiting factor.

In the afternoon foraging bout, females are visiting mainly freshly-opened flowers that have a lot of pollen. We can tell that they are collecting mainly pollen because they 'buzz' the flowers; like many Boraginaceae, *Alkanna* is probably buzz-pollinated. In order for pollen release to occur, the flower must be vibrated at the correct frequency. However, most buzz-pollinated flowers are pendulous, but *Alkanna* flowers are not; this probably makes it difficult for the bees to get pollen out of the flower. In contrast to nectar, all the pollen is rapidly collected by females; we can tell this because when the flower is freshly opened and full of pollen, females buzz them several times, but the number of times they buzz flowers rapidly drops to once.

Why are males territorial?

There is little evidence of mating, although we have seen some. It is difficult to say exactly what is a mating and what is a rejection by the female, since they might look very similar. In the British species *Anthophora plumipes*, rejections are very quick, a few seconds, but true matings last up to 40 minutes with a complicated courtship by the male, involving lengthy stroking of the female's antennae and face by the plumed middle tarsi of the male. Nothing like this has been seen in our Egyptian *Anthophora* (males of which do not have modified legs). Interactions between males and females do occur commonly, but often it is the females that chase the males away, or males chase females but never contact them; equally often males inspect females, but then leave. Males sometimes strike females, and fall with them onto the ground, but the maximum length of time we have seen them remain on the ground is about 15 seconds; is this a mating ?

There are two scenarios that we can think of that might explain male territoriality. However, at the moment we don't know the key piece of information – the number of times females mate – but we are using molecular techniques to provide it. We intend to use PCR-based DNA methods to look at the diversity of sperm in a female's spermathecae, and the diversity of fathers of the larvae from a single nest. In the UK, *Anthophora plumipes* females probably mate only a few times in their lives, possibly each associated with starting a new nest; interestingly,

females searching for a new nest site have a unimodal activity pattern, quite different from that of foraging females.

If females mate only once, or only when starting a new nest, then the territories might be 'for' catching newly emerged females, or nest-searching females. This fits in with the early emergence and disappearance of males; if there were matings to be had, one would not expect males to disappear well before the females. In addition, when we mark up females, the few 'matings' that we do see tend to be with unmarked females, which are presumably the newly emerged ones (certainly their wings are in pristine condition). Males frequently include some non-flowering plants or rocks as points of inspection in their territorial circuit; could these be emergence sites? During the short period of overlap of male and normal female activity, males frequently inspect foraging females, only to fly away without touching them. Presumably some females are unavailable for mating. The few females active during the middle of the day, when males are territorial, might be those starting new nests, and hence possibly available for mating either for a first or subsequent time.

If females mate repeatedly (and we have seen a female apparently mated by two different males within 30 minutes), then the male might be guarding resources as a form of paternal investment. We think the female's daily activity starts by finishing one cell, provisioning it with a lot of rather dilute nectar (presumably providing the larva with both energy and water). Then she lays the egg, seals the cell, and spends the middle part of the day digging a new cell and lining it with the special secretion that prevents microbial growth. Energetically demanding, this digging might be constrained to happen in the middle part of the day because only high soil temperatures make it energetically feasible, hence generating the bimodality of female foraging. When complete, she then forages at the end of the day, provisioning the cell mainly with pollen until the cold finally prevents further activity. Under the multiple-mating hypothesis, therefore, the territorial male should mate the female just before she lays her egg, ie, in the morning before territoriality starts. His territory might then be 'for' guarding floral resources – pollen in particular since it is the limiting resource – for investment in the egg which he will fertilize.

There are some obvious difficulties with the latter interpretation. It suggests that mating should be very common – exactly the opposite of what we think we see (unless it is extremely brief). In addition, the male must be sure of paternity: it seems, in contrast to the former explanation, a pre-eminently cheatable system. Why should a male waste his energies in being territorial, when all he has to do is to mate the female at the right time, in the early morning? Many of the apparent matings we have seen have been by non-territory-holding males.

Furthermore, females should be associated with a male's territory – he should have a 'harem'; harem females should effectively hold a group territory that corresponds to the territory of the male, and their nests might even be contained within it. The male's inspection points noted earlier might possibly be nests, although we have looked and not found any at these positions. In reality, individual females forage in an area much larger than the territory of a single male, overlapping with several territories. We have plenty of evidence that females commonly fight and drive off some females, but forage perfectly happily next to others. It is possible that there are 'bands' of females, perhaps genetically related to each other, that associate together during nesting and foraging. Experimentally, if we increase the pollen availability by protecting it from visitors, the result is a higher level of this female-female antagonism; hence aggression between females looks like direct competition for the key limiting resource.

In *Anthophora plumipes* in the UK, male harassment is a significant cost to female foraging, causing them to alter their foraging behaviour in order to avoid contact with males. It is possible that females are also doing this in Sinai, and are using their better thermoregulatory abilities to forage before and after male activity, thereby avoiding harassment. This is an alternative, but not mutually exclusive, explanation for the bimodality of female diel activity.

Is there evidence of genetic differentiation between sites?

In the plants

If male and female bees forage within localized well-defined territories, this will inevitably restrict gene flow via pollen movement, a prerequisite for localized genetic divergence. Thus we looked for evidence of genetic differences among wadis.

We used a quick, but very effective, molecular method to study population genetic structuring – Randomly Amplified Polymorphic DNA, or RAPDs. This involves cutting up the DNA using random primers, and looking for polymorphisms in the resulting bands. The resulting pattern of relationships among the wadis we studied is based on the degree of sharing of RAPD bands.

The pattern shows that wadis are genetically distinct, especially Wadi Dir: about 1/3 of the genetic variation in *Alkanna* is among wadis, with 2/3 among individuals within wadis. There is some mixing of genes between Wadi Tofaha and the Plain, and between Wadi Arbaein and the Plain, but Wadi Dir has unique bands shared with no other wadi.

If you refer back to Figure 1, you will see that this pattern is consistent with the major agent of gene flow being seed movement by the rare event of flash flooding moving genes down the wadis, occurring perhaps once every 10-20 years. Since the Plain area is the collecting area for water from Wadis Tofaha and Arbaein, but not Dir, this explains the pattern of gene mixing. Gene flow by pollen movement must indeed be very localized. We plan to develop single-locus genetic markers so that we can look at patterns of paternity among seeds, thereby looking in detail at successful pollen flow mediated by pollinators from plant to plant.

In the bees

At the moment we know nothing about the bee genes, but this is the next stage of the work. We have collected samples of territorial males, males intruding into their territories, females foraging within the same territories, and larvae from nests of these females. We are developing microsatellite markers in order to ask whether the territorial males have fertilized the eggs of the females foraging in their territories. As an extra benefit of developing these markers, we will be able to estimate the extent of bee genetic differentiation among sites.

Have genetically distinct populations coevolved to be recognisably different?

Since we have found genetic differences in the plants among wadis, the key point is whether these are the result of coevolution with their pollinators. For this to be true, there are various ways of demonstrating it. Without a selection experiment, these methods must necessarily be indirect. The clearest such way is if the selection pressures involved have led to morphological differentiation consistent with an interpretation based upon the relationship between plant and pollinator behaviour.

The plants

To answer this question, we measured hundreds of flowers in each of the sites.

Alkanna flowers have a very interesting structure, with five anthers at two different levels: three upper and two lower. The upper anthers dehisce slightly earlier than the lower ones. The length of the female parts of the flower, the styles, are at least trimorphic and possibly quadrimorphic (which may well be unique, if true). The stigma is held at the level of the lower anthers, or half-way between the upper and lower anthers, or at the level of the upper anthers; there are some flowers where the style pokes right out of the flower. Each flower can set a maximum of four seeds, which develop separately and are thus easily scored. We measured the corolla width, corolla length, style length, anther positions, and seed set on five flowers from a large number of plants.

There certainly are substantial individual differences in floral morphology: the shortest corolla we measured was less than half the length of the longest! To test for site differences in all our morphological variables simultaneously, we used a multivariate technique called Multiple Discriminant Function Analysis. Virtually all (94%) of the highly significant discrimination lay in the first axis, which was more or less equivalent to a flower display-size effect (ie, mainly corolla width), and the main difference was between the Plain and the other sites (Dir, Tofaha, Arbaein). Flowers from plants on the Plain are bigger and, in addition, there are more flowers per plant, and more of the old white flowers because these are retained for longer before dropping.

Are these differences caused by pollination-induced natural selection? We measured the rate of visitation by bees in the four sites, and found them to be very different, with very few visits made to flowers in the Plain. Furthermore, there was a direct relationship between the visitation rate and proportion of seeds set; pollinators appear to limit seed set, with a low proportion of seeds being produced in the Plain. We interpret these patterns as indicating that there is selection on plants in the Plain for increased allocation to attractive structures – the 'showiness' of the plant – designed to attract visitors to the flowers. As a major reward for bees, this should also include rate of nectar production; while Plain plants have twice as much nectar standing crop in their flowers, interpreting this is difficult because it is confounded with the low rate of visitation.

If we are correct in our interpretation, we should be able to measure the selection gradient in favour of large flowers in the Plain (ie, larger-flowered plants should on average set more seed), but not in the other sites. We measured the seed set and floral morphology of many plants in all the sites, and looked for a relationship between flower size and seed set. Despite a lot of variation, there was indeed a significant relationship only in the Plain plants – those with large flowers tend to set a greater proportion of their seeds; in no other site was this relationship significant.

The bees

We do know that there may well be morphological differences among the bees at different sites. Females don't seem to be different, but the males may differ in size and the length of the proboscis. However, our sample sizes are still too small, and we would not wish to claim too much about our present data set.

Conclusion

I think we have discovered that apparently straightforward relationships are not at all simple, requiring several years of effort to establish even fairly 'obvious' features of the system. The St Katherine National Park is currently being established and a management plan being developed and implemented. It is important to Egypt and to the world that the Park authorities succeed, preserving the environment of the mountains of southern Sinai for future generations to enjoy. I hope I have shown that southern Sinai is an environment worth preserving, with systems worthy of study for their ability to shed light on the operation of natural selection.

Acknowledgements

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