OF BEES AND BIRDS, AND OF THE FLOWERS THEY POLLINATE

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For the last few years before coming to Wiko, my main research area was the evolution of biological signalling systems. In particular, I focused on the interactions between parents and offspring at lunchtime. Offspring cry and parents use the intensity of their tantrum to estimate how much food they need. Why? How? All sorts of unanswered questions, plenty of work remains to be done. And yet, I had long wanted to shift gears and move from behavioural to ecological questions. Being a permanent post-doc, living on short-term contracts, it was not easy. Every two-year project had to be sufficiently successful to provide funding for the following project. And suddenly, the pressure lifted. Not by being at the Wissenschaftskolleg: a ten-month contract is not much stability, that's not what Wiko is

about. The pressure lifted because, upon arrival in Berlin, I already had the next contract: a five-year appointment back home. All together, six years. No need to publish anything straight away, I could just read and look around.

This does not mean that I had no idea at all of what I wanted to do. It means that I was not strongly attached to it. The original project was simple. I was to develop a series of theoretical models to study the evolution of seed size in variable environments, and the results of these models were to lay the foundation of further empirical and theoretical research. There was some beauty in the near-austerity of the project which, incidentally, fit well within the framework of the Risk focus group, with which I have been associated this year. But it was not to be. I started working on the project. I developed some models, ran some computer simulations, and even wrote things down. Then, just by accident, I came upon a new problem. Species invasions and extinctions. It is not a new problem for sciences, to be sure. It has long been the subject of research. The traditional approach was to consider invasions and extinctions the result of a competitive process. If the competitive ability of the newcomer is higher than that of the resident species occupying its ecological niche, it will invade and drive the resident species to extinction. This approach has been useful, but many problems remain. So it was recently suggested that it might be necessary to take mutualistic relationships into account if we are to understand the dynamics of species invasions and extinctions. An interesting proposition. Would it be of any use? I set myself the task of finding out how much of the data we could explain on the basis of mutualistic relationships alone. A typical example of mutualism, and a strong candidate to affect the probability that a plant species becomes established in a community, is animal pollination. Years ago I had prepared an application for a project on pollination. It was a long shot, an ambitious project that was never funded. So I went back to my birds and their begging and forgot all about the flowers and their bees. It all came back when reading about mutualisms and invasions.

Each of these ideas has been germinating and growing throughout the year, expanding its roots and shoots within my head (or was it the stomach?) in an odd contest not to monopolise incoming light and available water, but rather time, attention, and library resources. The result: seven manuscripts at different stages, three of them almost ready for submission, and a number of half-worked-out ideas, the list being so long that, I am sure, some of them will have to wait not till my retirement, but till my death, before I can finally set myself to work on them. So many cultures have demanded that their dead be buried with food, clothes, and other instruments to help them through their last trip, that nobody

should be surprised if I ask for some pens, plenty of paper, and a handful of candles to illuminate the interior of my coffin. And, since I cannot read while lying on my back, they better bury me on my belly, should there be not enough room in my coffin for me to turn around. – Incidentally, although I am not really worried about my coffin sinking deeper into the ground, an unlikely event given the physical properties of most graveyard soils, I am still working on a device that will keep the water away in case of rain or irrigation. To keep my papers dry, that is.

Looking back on the ten months at Wiko, I see that most of the projects I have worked on have been little more than distractions. The work on pollination seems to have won the competition for attention and time devoted to it. And by a wide margin, at that. But how can one study animal pollination from a dark, partly underground office? Let me try to explain it with an example. The Malagasy Star Orchids, *Angraecum sesquipedale*, have extremely deep corolla tubes: over 40 cm long. The nectar they produce is stored at the bottom of those long corolla tubes, and it is consumed by hawkmoths, *Xanthopan morgani praedicta*, that have almost as long a tongue: 35 cm. The moths pollinate the flowers while probing for nectar. It is a beautifully odd system. How did it ever come to be? The traditional explanation, first suggested by Darwin, goes as follows: if the corolla tube is longer than the moth's tongue, the moth must insert all its tongue in the corolla in order to reach the nectar. The head and body of the moth will contact the anthers and stigma of the flower and pollination will take place. If, on the other hand, the moth's tongue is longer than the corolla tube, the moth's head and body will be far away from the flower while it probes for nectar, and pollination will not take place. As a result, flowers with deeper corollas have higher reproductive success and corolla depth will tend to increase. As for the hawkmoths, the longer their tongue the more nectar they can extract from flowers. So there is some sort of evolutionary arms race between flowers and moths. The flowers are better off if their corollas are longer than the tongues of the moths, the moths are better off if their tongues are longer than the corolla tubes of the flowers, and they both get longer and longer as time goes on. In a further thousand million years, if there is still any coastal rain forest in Madagascar, corolla tubes and moth tongues may have reached a meter. Of course not. The above discussion ignores any cost of corolla and tongue elongation, and such costs certainly exist.

The story sort of makes sense. The nicest bit in it is that, at the time when Darwin proposed his hypothesis, no moth was known with a sufficiently long tongue to reach the orchid's nectar. Hence its name. There are, all the same, some problems with it. Among

them: longer corolla tubes are not always associated with higher pollination success in moth-pollinated flowers. Or another one: moth pollination and hummingbird pollination are in many ways similar. Some hummingbird-pollinated flowers, like the Andean *Passiflora mixta*, have very deep corollas indeed (although nothing compared to the Star Orchid: only 15 cm). But it is not clear that hummingbird-pollinated flowers with deep corollas are more successfully pollinated. The anthers and stigma of hummingbird-pollinated flowers tend to protrude beyond the flower, so that they contact the foraging hummingbirds even if they do not need to get very close to the flower in order to collect its nectar. If moth-pollinated flowers are not being pollinated because the moths stay too far away, why don't they just elongate their styles and filaments? And, above all, why is it that so few moth-pollinated flowers have very deep corollas?

The answer that I have come to favour revolves around behavioural niche partition. Animals tend to forage whatever resources they can exploit efficiently. If there is variability in animal traits and in the resources available, some animals will often concentrate on some resources, others on the remaining resources. Potentially, this can lead to flowers with very deep corollas. The explanation requires, once again, that short- and long-tongued moths differ in their ability to pollinate flowers. But, unlike Darwin's suggestion, for this mechanism to induce corolla elongation it must be the long-tongued moths that are better pollinators! Just an idea. Theoretically, it can work. The published evidence concerning foraging behaviour of nectarivorous animals and resource partitioning is consistent with the mechanism. But the real test has to be done with moths and flowers, not with paper and pencil, and it will have to wait till Wiko has faded in the distance. Which, unfortunately, will happen only too soon.

But why should I miss my dark office at the Wissenschaftskolleg when I find myself watching bees or moths visiting flowers in full sun? For a number of Fellows Wiko is mainly an excuse to get away from teaching and other faculty business. Not so for me: I have no teaching duties and little contact with the administration. For others, Wiko means research facilities. The library is certainly great (although that is the baseline assumption for a number of lucky Fellows), but there is an absolute and understandable lack of experimental facilities and no empiricist could stay here much longer than a year. (I considered for a time the possibility of refurbishing the garden in order to do some pollination experiments, but in the end I decided against it.) Finally, there are those who find Wiko special because of the odd mixture of characters, backgrounds, and disciplines that it represents. Much has been said about the advantages of multidisciplinary studies. It is possibly true

that, everything else being equal, an individual who makes the personal effort to become familiar with several disciplines and bring them together has a greater chance of making a significant contribution than an individual who does not make such an effort. But bringing together specialists from different disciplines is neither a necessary nor a sufficient condition for multidisciplinarity to arise. Personally, although I realise that it is far too early to judge the impact that this year will have on my future research, I believe that, in terms of work, the most important discussions I have had this year are those I have had with biologists. In fact, there have been a number of explicit attempts this year to come to terms with the arts-sciences border. None of these attempts have I found productive. On occasion, I have come out with the conviction of having thoroughly wasted my time. It is, of course, not true that arts and sciences have nothing to say to each other. But attempts by a member of a discipline to tell members of another discipline how to proceed will most likely fail. First of all, because he or she who pretends to teach will most often know of the other discipline little more than hearsay, and most importantly, because even when correct, the teaching is likely to be unnoticed or simply misunderstood. In view of our experience this year, it would seem that large, open-ended meetings are not much use either, and it is very possible that only those individuals who are genuinely interested in the problem can make any progress through personal discussions and hard work, as at least one of this year's Fellows has done. Wiko certainly provides the context where such discussions can take place, and the Tuesday colloquia bring up relevant questions, so the setting at least is adequate.

Life, however, has the graceful property of spreading well beyond the realm of work and research. Few of us, I believe, have the great luck to live in an environment where there is always somebody around with whom to discuss whatever idea crosses our mind, no matter how odd and out of place the idea happens to be. And all that within half an hour's bus ride from Berlin's city centre.