WIKO – A VERITABLE INCUBATOR FOR COMPETENT RADICALS

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This was my second year at Wiko. Having been able to spend only five months during the previous year as a Schering Fellow, I was kindly invited as a Guest of the Rector for another five months this year. This year was as exciting as the previous one – my excitement was not numbed by familiarity with Wiko, as many of the neurophysiologists in this year's class might have predicted. Being in a unique position of having spent two consecutive years at Wiko, it was tempting to make a comparison of the two classes. Indeed I could not

help attempting comparisons throughout my stay. But my prediction failed completely. In the ecological literature, we find many examples of taxonomically different but ecologically similar species replacing each other in different habitats. For example, the hornet *Vespa tropica* is the major predator of the social wasps I study in Bangalore and is responsible for keeping the wasp populations in control. In the New World tropics, similar wasps occur, but not the hornets. Here, ants do the job that hornets do in Bangalore, keeping the social wasps populations in check. Similarly, I had assumed that there would be Fellows this year, morphologically different but with behaviour and other attributes matching those seen last year. For example, I had assumed that in this year's class I would find a Sanjay Subrahmanyam, a Claude Gilliot, a Patricia Springborg … But I did not find this pattern at all. The class of 2001/02 was an equally interesting but quite a different assemblage of species. Perhaps the number of 40 Fellows is too small to get a full representation of human behavioural types and it may take many years before the patterns keep repeating themselves – long live Wiko!

A very happy moment in the year for me was to see the release of my book *The Social Biology of Ropalidia marginata – Toward Understanding the Evolution of Eusociality,* on which I had done the final bits of hard but thoroughly enjoyable work during my previous year at Wiko. In addition to writing several technical research papers, during this year I began work on a new book tentatively entitled *Reproductive Strategies*. This book is intended to be a sequel to my previous *Survival Strategies* and, like the previous book, will be aimed at a general audience and the beginning student. As I did in *Survival Strategies*, I will attempt to show that achieving a fine balance between cooperation and conflict is the secret not just of successful social behaviour, but also of successful sexual behaviour. The ethological literature is full of examples of cooperation and conflict among a mated pair of individuals, some of which are now being studied from an evolutionary perspective. The result is stunning – the range of sophisticated behavioural and physiological strategies that animals employ to be ahead of each other in the race for evolutionary fitness is truly amazing. But perhaps the most satisfying message that emerges from these studies is that cooperation, or at least a moderate balance between cooperation and conflict, is often the automatic end-result of each individual's selfish behaviour. Most of my time this year was spent in studying the vast relevant literature. In addition to many technical papers, I studied two memorable books – *The Ant and the Peacock* by Helena Cronin (Cambridge University Press, 1991), which contains some of the most elegant prose I have read in some time, and *The Handicap Principle* by Amotz and Avishag Zahavi (Oxford University Press, 1997),

which contains some of the boldest ideas I have come across in a long time. I will always associate the facts and ideas I read about with one or another of the objects or people that I encountered at Wiko during my stay. I left Wiko yearning to begin writing my own book.

Toward the end of the year, I was surprised but delighted to be told that I was being considered for appointment as a Non-Resident Permanent Fellow at Wiko. This set me thinking about the true function of an institution like Wiko. Here is my answer:

Creative intellectual activity is a complicated business. It is necessary to be both "correct" and "creative". The relevance and importance of being correct, i.e., of conforming to some accepted standard, diminishes as we move from the natural sciences to the social sciences, humanities, literature and finally the arts. Inevitably, one's ability to be original and creative falls rapidly as we move in the opposite direction from the arts to literature, humanities, social sciences and finally the natural sciences. In the natural sciences in particular, there are strong forces that prevent you from being original or creative and rightly so, because what is original and creative can often be wrong. The publication and acceptance of almost anything in the natural sciences is based on peer review and acceptance. This has the function of ensuring that too many falsehoods are not perpetuated in the name of science. But at the same time, this often curbs radical departures from widely accepted positions. There is no simple way to censor the vast majority of original and creative ideas that are wrong and accept only those that happen to also be correct. It is typical for a reviewer to reject anything out of the ordinary and typical for most of us to accept peer judgment and fall in line with the accepted position. But of course there are occasional exceptions. And it is these exceptional individuals that make the transition between what Thomas Kuhn has called "normal science" and "scientific revolution".

My favourite example is that of Amotz Zahavi of the Hebrew University in Jerusalem and his handicap principle. Biologists since Darwin have wondered why the peacock has such an elaborate tail that must surely be a handicap to him while running away from predators. The commonly accepted explanation (attributed to Ronald Fisher, one of the architects of the genetic theory of evolution), is that in the past there must have been a positive correlation between tail length and male quality and females must therefore have been shaped by natural selection to favour males with long tails. With simultaneous selection on males for having long tails and on females for preferring males with long tails, it has been suggested that through a process of runaway selection, male tails can get longer than is good for their own survival. This is because even when the positive correlation between

tail length and male fitness disappears, females who mate with long-tailed males will have sons with long tails who will in turn be preferred by females of the next generation. Indeed there are several mathematical models that show that such a runaway selection can produce tails that are longer than are good for the males' survival. Zahavi refused to accept this explanation because, to paraphrase his words in a lecture he gave at the Indian Institute of Science, "first we have to assume that females are so clever that they 'know' that long tailed males are fitter and then we have to assume that later females become so stupid that they do not realize that long-tailed males are no longer fit because their tails have grown too long!" In the 1970s, Zahavi wrote a series of now famous papers in which he made the radical suggestion that the peacock's long tail is selected precisely because it is a handicap, not in spite of being a handicap. By carrying around such a handicap of a tail and by not yet having succumbed to a predator, the peacock reliably demonstrates to females that he is indeed fit enough to survive despite the handicap. Zahavi derived from this idea a far-reaching general principle that animal signals in general must impose a cost, a handicap, on the signaler in order to be reliable and thus resistant to faking. Zahavi's ideas were rejected outright by the scientific community. Several distinguished theoretical evolutionary biologists wrote mathematically sophisticated papers arguing that the handicap principle cannot work. One paper was actually entitled "The handicap mechanism of sexual selection does not work" (*American Naturalist*, 127, 1986, 222–240).

Then everything changed in 1990 when Oxford evolutionary biologist Alan Grafen published two papers showing, with the aid of more economically inspired mathematical models, that Zahavi's handicap principle can indeed work, both in the evolution of honest signals in general and in the context of sexual selection. Today Zahavi's handicap idea and the more general, costly, honest signal idea are widely accepted and have considerably altered the way in which we model and study animal communication and behavioural evolution. The well-known evolutionary biologist John Maynard Smith has graciously admitted publicly that he was wrong in hastily concluding that Zahavi's idea was in error. But of course Maynard Smith says it in his inimitable style: "I was cynical about the idea when I first heard it, essentially because it was expressed in words rather than in a mathematical model. This may seem an odd reason, but I remain convinced that formal models are better than verbal ones, because they force the theorist to say precisely what he means. However, in this case my cynicism was unjustified. It has proved possible to formulate mathematical models showing that what Zahavi called the 'handicap principle' can lead to the evolution of honest signals." (*The Times Literary Supplement*, August 3, 2001). I must confess to a

certain degree of unhappiness in that many people today accept and use Zahavi's handicap principle but call it (disguise it?) as the "good genes model". More recently, Amotz Zahavi, along with his wife Avishag, has written a book-length essay on the wide-spread ramifications of the handicap principle. In a most remarkably bold style they explain more or less the whole world with their handicap principle – why does a gazelle jump up and down at the approach of a predator, wasting time and energy and making itself visible, why do skylarks sing while fleeing from predatory merlins, why do pelicans in the breeding season grow a bump between their eyes that interferes with their ability to fish, what is the function of the small horn of the rhino, why do animals groom each other, why do host birds not reject the eggs of brood parasites, why has homosexuality evolved, why do animal and human infants beg food so noisily that they attract predators, why was the use of lace by humans so popular among the wealthy in the past and why is it not so today, why do we shout while issuing a threat to someone standing nearby, why do men grow beards and wear bow ties, why do people attempt suicide … their list is endless!

This enterprise of attempting to explain everything with the handicap principle will surely fail at some point but we will never know exactly where it will fail unless someone pushes it past the precipice and, very likely, falls along with. I think we should be grateful to the Zahavis for altruistically doing this for us. But not everybody thinks so; the peer review system is harsh. The Zahavis' book has been roundly criticized – one reviewer has called it "a work of advocacy" rather than of science and another has almost dismissed it with the statement that "The lack of data does not seem to dampen the Zahavis' enthusiasm – Who needs data when metaphors abound?" (*Q. Rev. Biol.* 73, 1998, 477–479). I will come back to this, but first permit me to cite one more example, also very dear to my heart.

In the 1940s and 1950s, Karl von Frisch discovered that successful honey bee foragers return to their nest and perform dances, by means of which they are able to communicate to their sisters the distance and direction to the source of food they have discovered. What makes this unique among many examples of communication in animals is that bees appear to use a system of arbitrary conventions, hence a form of language, to communicate with each other. Von Frisch's dance language hypothesis has since been verified by hundreds of independent researchers and has now become an extraordinarily powerful experimental paradigm for studies of animal communication and sensory physiology. Karl von Frisch shared the 1973 Nobel Prize for his discovery with two other ethologists, a rare occasion on which the Swedish Academy has had the courage to correct Nobel's anomalous use of the phrase Physiology or Medicine rather than Biology for one of the prizes in his name.

But Adrian Wenner of the University of California at Santa Barbara refused to believe the dance language hypothesis. Since the mid-1960s, Wenner has been conducting experiments that in his view disprove von Frisch's dance language hypothesis and support his own alternative olfaction hypothesis, which states that honeybees use only odours to locate food. Many researchers starting with von Frisch have periodically attempted to answer Wenner's criticisms but the latter remains unconvinced. What I find most fascinating in the history of this controversy is that successive supporters of the dance language hypothesis praise Wenner and Wells for generating a controversy and forcing them to do better experiments, while in the end they conclude that the dance language hypothesis holds. But Wenner and Wells continue to remain unconvinced.

For example, after reviewing some of the cleverest experiments to address the issues involved, J. L. Gould concluded: "Throughout the dance-language controversy, Wenner has made perceptive and valuable contributions …Wenner is certainly correct in saying that an endless repetition of ambiguous experiments does not add anything to the evidence. He is also correct in asserting that all of the previous evidence for the existence of a dance language was circumstantial. Wenner is probably right in refusing to be persuaded by teleological arguments, even when the catchword 'evolution' is added. He has reminded us of the great importance of olfactory recruitment in honey bees, and by that, has affected the scope and course of future research. But in the end, the dance-language paradigm cannot be discarded … the misdirection experiments provide evidence that admits of no other explanation than that von Frisch is correct, and that honeybees do have an abstract system of dance communication. Perhaps the time has come for 'normal science' to face … the aftermath … of a scientific 'uprising' which has served the valuable purpose of forcing upholders of the dance-language paradigm to provide objective evidence in its defense."

But nothing can convince Wenner; he sticks to his position with conviction, and in 1990, along with Patrick Wells, he wrote a book-length argument entitled *The Anatomy of a Controversy* (Columbia University Press) saying that "After presenting the reasons for our disillusionment with the dance language hypothesis, we cover in the next three chapters various personal encounters as they relate to the sociology, psychology, and philosophy of science". More recently, Michael Polakoff reported his experiments in an article entitled "Dancing Bees and the Language Controversy" (*Integrative Biology* 1, 1998, 187–194) in which he claims to have "avoid[ed] many of the pitfalls of previous dance language experiments". Praising Wenner's odour search hypothesis as "a valid and more parsimonious alternative to the flashier and more seductive dance language hypothesis" which "did not

receive a warm welcome despite the compelling data", he goes on to conclude however that his new results "suggest that odor alone is unable to account for the behavior of the bees recruited by waggle dances" and therefore that "recruits are indeed learning the direction of a food source when they follow dances, as von Frisch asserted 50 years ago".

I cannot imagine Zahavi accepting the failure of his handicap principle or admitting that signals need not necessarily be costly to be reliable, any more than I can imagine Wenner accepting the honey bee dance language hypothesis of von Frisch. Is this unfortunate? Actually, I think not. In my view, scientists like Zahavi and Wenner, by sticking to their extreme positions, by refusing to compromise, are doing the scientific community a favour. There is no great harm if individual scientists have their pet biases and prejudices and therefore pursue their pet hypotheses to the extreme. It is only important for the community as a whole to be objective. One way for the scientific community to be objective and get at the truth is to train all practitioners of the scientific profession to be objective, a task I think is impossible. Indeed I think that it is neither necessary nor possible to train all scientists to be totally objective and to pursue truth totally objectively. Not necessary because, if there are enough radical scientists embracing diverse radical opinions and pursuing their pet hypotheses in different directions, the community can average over these extremes and remain objective. I tend to think of people like Zahavi and Wenner as altruists, who uncompromisingly embrace radical positions and are not even persuaded by data contradicting their positions, who put their own reputations at stake and thereby let the community discover how far each hypothesis can be stretched. Without people like Zahavi, we will never know how much of the world we can explain with the handicap principle, and without people like Wenner, we would not have seen the kind of clever and sophisticated experiments about the bee dance language that his criticisms have engendered. Of course Zahavi's handicap principle will fail at some point and Wenner may be proved wrong in the end. But we benefit from them and their uncompromising courage to pursue their points of view.

But aren't scientists supposed to be objective and have an open mind in testing hypotheses and accepting conclusions? Well, I don't think so and therefore I think that is not possible to train all scientists to be totally objective. The reason for this has never been expressed more clearly than by Richard Lewontin in his masterly *The Genetic Basis of Evolutionary Change* (Columbia University Press, 1974): "It is a common myth of science that scientists collect evidence about some issue and then by logic and 'intuition' form what seems to them the most reasonable interpretation of the facts. As more facts accumulate,

the logic and 'intuitive' value of different interpretations change and finally a consensus is reached about the truth of the matter. But this textbook myth has no congruence with reality. Long before there is any direct evidence, scientific workers have brought to the issue deep-seated prejudices; the more important the issue and the more ambiguous the evidence, the more important are the prejudices, and the greater the likelihood that two diametrically opposed and irreconcilable schools will appear."

So why not let different scientists pursue their prejudices and see how far they can go? I would like to see the scientific community be more tolerant of such radical scientists. But of course if everybody is allowed to be a radical, there will surely be chaos. What we need are impeccably competent radicals. We should set our thresholds very high and demand the highest possible level of competence before we become tolerant of radical scientists pursuing their radical positions. For the rest of us there is always the harsh peer review system! Such differential treatment of the more and less competent is not easy to institutionalize. It has to be done in a subtle and inoffensive manner. The influence of peers that serves to cull out unfashionable points of view operates not merely during publication. It operates inexorably and invisibly at all times, in formal seminars, in informal discussions, at the coffee table… This is where an institution like the Wissenschaftskolleg plays such an important role. The Kolleg identifies 40 of the most accomplished and creative scholars from around the world and puts them together in very agreeable living and working conditions. For completely different reasons, the Kolleg attempts to give fair representation in each year's class of 40 Fellows to as many different disciplines of scholarly activity as possible. The useful but unintended consequence of this is that it also ensures that each scholar has few or no peers to trim away shoots of thought sprouting outside the narrow radius of acceptability. In fact the opportunity to present one's work and ideas to scholars from completely different backgrounds and training often forces each scholar to go beyond the turf that she would normally restrict herself to during conversation with "insiders". I know of no better method of fostering unhindered creativity.