THE ENVIRONMENT MATTERS: FROM PARASITE RESISTANCE TO A WIKO STAY

BEN M. SADD

Born on the 28th of April 1981, Dr. Sadd studied Zoology at the University of Sheffield. During his Master's Degree, Dr. Sadd became interested in the intimate interactions between parasitic organisms and their hosts, particularly the evolution of immune defence and how this is shaped by the surrounding ecology. During his Ph.D. (2004–08) at the ETH Zurich, he further studied immune system phenomena in the context of Evolutionary Ecology, working predominantly on antibacterial defence in social insects. Taking a whole-organism approach, Dr. Sadd was able to demonstrate that insects are capable of long-lasting specific immune protection, with mothers even passing immunity to their offspring, a facet of insect immunity that was traditionally considered absent. Subsequently, during postdoctoral research at the ETH Zurich, he has expanded this work and further initiated projects investigating parasite evolution and how environmental heterogeneity influences the outcome of parasite infection. – Address: Institute of Integrative Biology, ETH Zurich, 8092 Zurich. E-mail: ben.sadd@env.ethz.ch

My first taste of the Wiko came with two brief trips to the Grunewald in 2007 when I was visiting Paul Schmid-Hempel, my doctoral supervisor at that time, and other members of an "Ecological Immunology" focus group. If all truth be told, I knew little of the Wiko at that time, being more excited to have a reason to visit the history-laden city of Berlin. Little did I know that only a few years later I would be participating at the Wiko myself as a short-term Fellow, enjoying the uniqueness of the environment offered by the institute. A large part of my scientific work considers how the heterogeneity of environments influences organisms, in particular their interactions with parasitic organisms, and ultimately their evolution. Here I will give a short summary of this work and additionally highlight how I believe I have been shaped by the environment that I experienced at the Wiko during my fellowship.

It is almost inevitable that at some point during an organism's life it will be faced with exposure to another organism that, in acquiring resources for its own benefit, will cause harm. These parasitic organisms are widespread and present a serious threat to the well-being of free-living organisms. Succumbing to infection by one of these parasites can have a broad spectrum of consequences on individual, ecological, evolutionary and, where associated with humans or domesticated animals, economic levels. Indeed, at the Wiko in 2010/11 Bruce Campbell proposed climatic change and parasitic organisms, both of which are frequently classified as "acts of God" in history circles, as major historical protagonists, citing the examples of the 14th-century Black Death in humans and the later Rinderpest epidemic in cattle. Further, persistent problems with parasitic disease that continue to present a major challenge and impede development were frequently highlighted by discussions with members of the focus group "Professional Dilemmas of Medical Practice in Africa" led by Steven Feierman and Julie Livingston.

By their very nature, parasites will place a selective pressure on the hosts that they infect. Individuals that succumb to infection by parasites will have reduced evolutionary fitness in terms of either the quality or quantity of offspring that they produce. This selective pressure coupled with variation in resistance among individuals will, over time, lead to the evolution of anti-parasite defences. These defences can reduce parasite exposure, reduce infection probability on encounter, or limit the impact of parasitism following infection. However, despite the apparently clear benefit of these anti-parasite defences, not all organisms possess them, and even within populations their expression varies among individuals. A major question in the field of host-parasite Evolutionary Ecology is: why should this be the case?

Essentially, the variation that we see in anti-parasite defences can be attributed to evolution and the diversity of parasites, the diversity of environments, and the costs associated both with having and with using parasite defences. Parasites are clearly not inert in the face of the evolution of host defences against them. Parasites will evolve counter-adaptations to these host defences, which will render the defences either less efficient or even useless. These dynamic evolutionary arms races will usually proceed at a local level that will produce a global diversity of parasite and host types. This diversity means that a particular defence against one parasite will not necessarily provide defence against another distinct parasite. This will be the case for defence against different parasite species and even variant types of the same parasite. Thus, the exact defences that are present in an organism will depend upon the parasite community that it has evolved with.

The risk of being parasitized will also vary across environments in both space and time. If we think of a parasite that is vectored between hosts by an insect that develops as a larva in pools of standing water, e.g. malaria and many viruses that are transmitted by mosquitoes, the risk of infection by this parasite will be linked to spatial proximity to such pools of water and also to temporal variation in rainfall. While this is a simplification, it demonstrates that parasitism risk will vary depending upon the environment within which the host lives. The variation in this risk will lead to a variation in parasite defences, in part because of the costs involved in evolving, maintaining, and utilising anti-parasite defences. Evidence for costs at each of these levels is well documented. For instance, organisms have only a limited resource budget and they must allocate this between different traits, be it the costly immune system, body size, ornaments for the attraction of mates, or production of offspring. The optimal allocation to these different traits will depend upon the environment in which the organism is living, including its risk of parasitism. Under high parasitism risk, investment in anti-parasite defences should be high, and vice versa, under low parasite risk investment in anti-parasite defences should be lower. In some cases, organisms have evolved a certain degree of flexibility in their investment in parasite defence, which can be adjusted depending upon environmentally provided cues related to the risk of parasitism. I work on bumblebees, which are social insects living in colonies in which a single mother queen produces worker offspring that stay at the nest and help raise their siblings. At the end of the year the colony produces new queens that leave the nest and found their own colonies. The relationship between the mother queen and her worker offspring is such that the environment encountered by the mother, including parasites, will likely be correlated with the environment that her workers experience later on. In this case it would make sense for allocation to costly anti-parasite defence in worker offspring to be in someway determined by their mother's experience. Indeed this is the case, with offspring of mothers who received a simulated parasite exposure showing higher investment in immunity than offspring of mothers that did not. This allows for investment in costly immunity when the payoff is high, when parasitism is likely, but not when the investment may be wasted because the probability of encountering a parasite is low.

So far, I have referred only to variation in the environment in terms of a varied biotic environment of host and parasite types, and the abiotic environment that can influence the risk of parasitism and hence investment in anti-parasite defence. However, the abiotic environment may also play a role in determining the outcome of an encounter between a particular parasite and a particular host. While resistance to parasites and infectiveness of parasites may appear fixed, changes in environmental variables such as food composition or temperature may have profound consequences. Hosts may be better able to defend themselves in certain environments or parasites may be better able to infect. Furthermore, complexity introduced by the abiotic environment may have differential effects on individual types within host and parasite populations. This is indeed the case in bumblebees, where the outcome of infection by a gut-infecting parasite is influenced by the quality of the available sugar water solution, a surrogate for nectar from flowers. However, the influence is not unidirectional, but rather dependent also on the combination of parasite and host type. Understanding the environmental dependence of the outcome of host-parasite interactions has important applied aspects, given continuing environmental change and accidental and intentional species introductions into new environments. Where introductions are intentional, for example where parasites are used for biological control of pests, variation in the environment is a factor that should certainly be taken into account in preliminary trials and tests.

Working in the areas briefly outlined above, I was very fortunate that my time at the Wiko coincided with that of the focus group "Limits to disease control – failures in disease" headed by Janis Antonovics. Joining this group allowed me to interact with a number of inspiring evolutionary biologists, ecologists, and parasitologists. Discussions were broad, but particularly focused on two main topics: (i) what role does evolution have in our failure to control disease, and what can be done about it? and (ii) how do relationships between a parasite and its host species progress from an initial "chance" infection to a specific co-evolving system. I will go no further into these topics, on the assumption that others from the focus group will address them in more depth. I would simply like to say that the focus group discussions, whether during set meetings, at the Wiener Café, or in restaurants, were enjoyable and productive. However, one point that struck me was that although we were all apparently from closely related fields and thinking about similar questions, our terminology was distinct. This often led to discussions that were essentially semantic in nature. I believe that while complete congruence may never be achieved, integrative workshops, seminars and forums like the Wiko allow interdisciplinary crosstalk and understanding that will ultimately lead to devoting more time to discussing the real issues at hand.

Of course the Wiko brings much more diversity together than was found in the "Limits of disease control" focus group. This diversity is interwoven at the Wiko in such a way that it would be hard for a Fellow to stick solely to discussions and thoughts in his or her own discipline, even if he or she wanted to. Seminars, receptions, meals and of course German classes consistently involved new topics and the extension of horizons. However, it was not just the topics that I took delight in, but also a common thread that was clearly apparent in all Fellows. Irrespective of the topic, even sometimes in spite of a lack of overall understanding on my part, listening to people talk about their chosen subjects was a fulfilling experience. Peoples' eyes and voices showed a childlike wonder, inquisitive nature and passion for their topic. This reminded me of why I work as a biologist, and in particular as an evolutionary biologist. In science we are constantly exposed to and encouraged to use new high-tech methods. However, these technological advances should not take precedence over concepts and ingenuity, nor eclipse the motivation for doing what we do. For me this motivation is based on a passion for the natural world, but not accepting it as a given, but looking to understand the patterns and interactions that make it as amazing and fascinating as it is.

I chose to take my short-term fellowship from October 2010 to January 2011, which was at the beginning of the Wiko year. I feel this choice was vindicated in terms of integration into the 2010/11 Wiko cohort. A combination of several welcoming social events and intensive German classes made this task relatively easy, and I believe a good deal simpler than it may have been had I arrived later in the year. Additionally, the spring and early-summer months are typically a very busy time for me in my work, as this is when I collect my main study organisms, bumblebees. Although this is a hectic period in the year for me, I was glad that I was able to make time for a final one-week visit to the Wiko at the start of May. I felt this week was instrumental in bringing the whole experience of the Wiko together, and this visit confirmed all of the positive aspects of the Wiko. Once again, the Wiko and its staff were welcoming, interactions were frequent, discussions were omnipresent yet relaxed, and to complete the experience my breakfasts were serenaded by the melodic tones of a nightingale in the Wiko garden.

In conclusion, I will remember my time at the Wiko with great fondness. Immersion in the diverse and high-calibre academic environment was a truly rewarding experience. Interactions, both professional and personal, have left their mark on me, and I believe that they will shape my thoughts and the directions that I take in the years to come. As described before, my own work on the evolutionary ecology of host-parasite interactions focuses on the importance of the environment within which the interactions take place. However, it is clear that the impact of the environment extends beyond this sphere and is a major player in numerous facets of the world we live in. With this in mind, the environment of the Wiko certainly had an impact and an overwhelmingly positive one at that.