



ECOLOGY OF MIMICRY: HOW INTERACTIONS  
SHAPE INTERACTIONS  
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Johanna Mappes's decades-long interest is to understand how species interactions (mutualistic and antagonistic) shape traits that help individuals to fight their enemies. She finds it fascinating to experimentally solve evolutionary mysteries like how rare, initially disadvantageous traits of prey can become advantageous via natural selection. She studied Ecology and Environmental Science in Jyväskylä and Stockholm (Ph.D. 1994), had the Academy of Finland Postdoctoral Fellowship followed by the Senior Research Fellowship, and had visiting affiliations in UC Santa Cruz, UC Santa Barbara, and Australian National University. She was appointed Professor of Evolutionary Ecology (2008) at Jyväskylä followed by the Academy Professorship (2009–2013, 2019–2023) and at Helsinki University as the Professor of Ecology (2020). She led the Centre of Excellence in Biological Interactions (the research consortium between Jyväskylä and Helsinki) from 2012 to 2018. Her scholarship has been recognized with elected memberships in the Finnish Academy of Science and Letters, the American Academy of Arts and Sciences, and the Royal Physiographic Society of Lund. – Address: Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, Viikki Biocenter 3 PO Box 65, 00014 Helsinki University, Finland. E-mail: johanna.mappes@helsinki.fi.

Predator-prey interactions are a strong driver of the diversification of life, promoting the evolution of a large variety of defenses in prey, including conspicuous coloration associated with unpalatability. Predators usually learn its association after several sampling events. This promotes convergence in warning signals between different chemically protected prey species from the same local community: sharing their appearance reduces individual

predation risk. Biologists call this convergence mimicry. Antipredatory mimicry is one of the most celebrated examples of Darwinian natural selection. Mimicries have been traditionally classified as Batesian when the mimicry is profitable but resembles the distasteful (or otherwise unprofitable) model's warning signals. When all mimics are distasteful, they are classified as Müllerian mimics. The crucial difference between these two types is that in Müllerian mimicry, all co-mimics are expected to educate predators mutualistically, whereas in Batesian mimicry the relationship is based on deception (parasitism). The mutualistic versus parasitic nature of the relationship between co-mimics has been debated ever since Müller's (1879) foundational paper, and the general conditions that favor mimicking remain unresolved. As an intellectual exercise for evolutionary biologists, mimicry does not lack applications. Mimicry theory has, for example, been recently used to better understand the deceptive strategies of SARS-CoV-2 and their key role in the COVID-19 pandemic!

During the Wiko fellowship, we planned to work with my colleagues Professor Marie (Mariella) Herberstein and Dr. David Kikuchi on the topic of how natural communities affect signal evolution and (rather ambitiously) to ponder how signaling between species can, in turn, affect the dynamics of their communities. Mimicry has been almost solely handled as an evolutionary paradigm, and both the theory and the empirical tests have largely lacked ecological realism. For example, whether mimetic species compete for resources, whether there are more than one predator type that attacks mimetic prey, and whether these predators move between patches of prey. It is well expected that all these ecological factors influence the outcome of the evolutionary dynamics between the model and the mimic. Professor Bob Holt from the University of Gainesville, Florida crucially influenced the project, too. Prof. Holt is one of the most influential theoretical community ecologists; his research tasks are linking ecology with evolutionary biology. So, we were a group of behavioral ecologists, evolutionary ecologists, and community ecologists who worked together. First, however, we needed to learn to work together and communicate.

Mariella, David, and I were neighbors in the Villa Walther; we shared an office and explored museums and nightclubs together. Discussions and workshops with other biology Fellows, in particular Sharon Strauss, Mark Schwartz, Kimberley Prior, and Hannes Becher, were fun and stimulating and opened new collaborations and research lines. I am a strong believer in the discussion method and a classic auditive learner, so it is not surprising that I loved Wiko and its atmosphere, seminars, colloquiums, and discussions. I also loved beautiful Grunewald and vivid, busy, crazy, fun Berlin. Although seminars,

colloquia, German lessons, and the overwhelming cultural offerings of Berlin ate a big chunk of time from work, I felt privileged to be involved in such a unique research environment. On the other hand, it was mentally hard to leave behind my lab (my moths, postdocs, and students) and it took weeks before I learned to relax and concentrate on Wiko's possibilities, like amazing librarians and their services! The extraordinary care, the friendships offered, the care delivered, and the home that was created for us Fellows will always stay with me. Thank you!

Our first achievement was to finish a paper we had started before arriving in Berlin with David. The topic of the paper is (surprise?) Müllerian mimicry in alpine *Oreina* beetles. What makes these beetles fascinating is that there are several species within the genus, they all are toxic, and they come in two colors, blue or green; but in any one location, only one color exists. A beautiful and rare example of European Mullerian convergence! Our paper analyzed the morph localities and color frequencies and analyzed an experiment that tested how birds learn to avoid differently colored beetles. We learned that birds bias their attacks on blue beetles and also generalize their learned avoidance from blues to greens, but not vice versa. We concluded that this biased predation pressure drives convergence, but also maintains diversity among beetles.

Our second goal was to get to the bottom of confusing terminology. "I thought natural scientists are less confusing," said Anja Brockmann of the library to me when I went to collect books and old articles from her office. What she said describes perfectly the confusion and obscurity around terms like "mimicry ring" or "mimicry complex."

Our main goal, however, was to produce both review and theory paper around our major topic "ecology of mimicry," which focuses on neglected factors like moving predators and the role of alternative prey on mimicry. Bob came to visit Wiko, and we spent an intensive week putting together our ideas. As usually when working with mathematical models, the biggest challenge is not to create a complicated or simple model, but a useful model!

We had so many plans for spring and my calendar was full of booked seminars to be given in Prague, Vienna, Basel, Hamburg... And so many plans for our Focus Group! First, David planned to visit Florida to clarify details of the model, and then Bob planned to visit in Berlin again in May, but then, in early March, COVID-19 hit Berlin and everything in the whole world changed. We suddenly just followed the news about the pandemic and all became frightened. When it became clear that my husband was not allowed to travel to Berlin anymore and everything was switched to online, several other Fellows

and I made a difficult decision and decided to travel home as long as there were flights available. We continued working remotely – even colloquia were online – and we managed to accomplish something, but, of course, it was not same as working at Wiko! I feel super-selfish thinking about the lost opportunities in Wiko while millions are infected, hundreds of thousands are fighting for their lives, and the economic damage is the greatest the world has experienced in decades. Still, I hope the Wiko board will consider the possibility of allowing those of us who lost a big chunk of our fellowship an opportunity to apply again for the fellowship.

#### Papers we produced in Wiko – the mission continues

- Kikuchi, D., S. Waldron, S. Dobler, J. Valkonen, and J. Mappes (2020). “Biased predation could promote convergence yet maintain diversity within Müllerian mimicry rings of *Oreina* leaf beetles.” *Journal of Evolutionary Biology* 33: 887–898.
- Herberstein, M. E., D. Kikuchi, and J. Mappes. “What’s in a mimicry ring – concepts and practical considerations” (in prep.).
- Kikuchi, D. W., M. E. Herberstein, M. Barfield, R. D. Holt, and J. Mappes: “Why aren’t warning signals everywhere? On the prevalence of aposematism and mimicry” (in prep. to be submitted to *Biological Reviews*).
- Mappes, J., and P. Niemelä. “Do leaves of paper mulberry (*Broussonetia papyrifera*) resemble herbivory damage? Experimental test on deceptive anti-herbivory mimicry in plants” (submitted).