biological information required for biosafety assessments, and to suggest a means of proceeding with such assessments. A major component is a set of decision-making trees designed to aid the user in identifying, assessing and managing specific risks for specific organisms and applications. The need for such a document derives from extreme variability in regulatory oversight and from a general dearth of information regarding the behavior of GEOs in the environment. The users of the document are expected to be scientists, managers, policy-makers and others with a need to evaluate the environmental and human health impacts of specific GEOs intended for release.

Discussions during the meeting helped to point out areas of concern and potential risk. Some of these risks are by now well recognized (e.g. the potential for introgression between engineered crops and wild relatives), but others remain less obvious. The diversity of target organisms and applications is large and increasing quickly, and this jeopardizes efforts to ensure safe release. Factors influencing safety (or, conversely, risk) include the scale of release and the size, taxonomic affinity, life history, and habitat of the GEO. Other important factors include the intended application or use, the means of containment or dispersal, and the use of drive mechanisms to achieve persistence of the construct in target populations. Characteristics of the accessible ecosystem (that is, the ecosystem receiving a GEO or engineered construct) must also be considered in evaluating the safety of release. For example, the presence of potential wild mates, predators, competitors, prey, suitable open niches, etc. can all accelerate or impede the spread of a GEO. Trophic cascades will move some GEOs (or their constructs, or novel products), through the accessible ecosystem once introduced. The expression of secondary or unintentional traits could significantly alter the behavior of GEOs in the field. Similarly, pleiotropy could produce unintended effects. The ultimate mutability of genetic constructs suggests that GEOs in the environment will change over time, thereby changing the relative risk.

An additional concern lies in the nexus between environmental effects and human health effects. For example, the human food chain cannot be wholly isolated from elements in the larger environment, and novel genes or gene products introduced for purposes other than human consumption could (and will) eventually find their way into the human food supply. The effects of novel proteins on human health and development are largely untested, but at least some novel proteins are likely to confer allergenicity or other negative impacts on human health.

The group recognized that the likelihood of safe, long-term releases of GEOs could diminish as the technology expands and as human need increases. Indeed, safe release will become a shifting target as technology changes to meet need. Risk assessments and management strategies must accommodate these changes if a margin of safety is to be maintained. The challenge to consumers, policy-makers and scientists alike is to find a balance between that which is clearly beneficial and that which is potentially detrimental to human health and the environment. This is a great challenge, and one that can only be met through commensurate amounts of attention and effort from all concerned.

Terrie Klinger

University of Washington,
Friday Harbor Laboratories,
620 University Road, Friday Harbor,
WA 98250, USA (tklinger@u.washington.edu)

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Ethology: at 50 and beyond

When a dictionary of ethology describes the field as having 'wide range, baffling diversity, and fuzzy outlines'[1], its practitioners are justifiably unnerved. And yet there is some truth in this image. The richness of ethological explanations has provided such ample seed for the generation of other disciplines that ethology itself might seem to be in danger of disappearing. When Tinbergen famously posed ethology's four central questions (cause, function, development and evolutionary history), he framed the research program for many years to come. But, disappointed at the loss of Lorenz's grand theory of instinct and enticed by the predictive power of gene thinking, interest among ethologists and behavioral ecologists has more recently focused on adaptive function and has largely overshadowed interest in proximate mechanisms or the evolution of behavior.

The 25th International Ethological Conference, held in Vienna, Austria, last August, provided an opportunity to take stock. This largest-ever gathering of ethologists (nearly 1000), celebrating nearly 50 years of comparative behavioral research, was organized by Michael Taborsky [Konrad Lorenz Institute for Comparative Ethology (KLIVV) Vienna, Austria] in the cradle of ethology. Browsing through the published abstracts[2] verifies that ethology remains one of the broadest-based areas of modern biology, embracing neurobiological mechanisms to population genetics. Coherence comes from a unique recognition of the proximate/ultimate crux and a focus on the organism as the inspiration for hypothesis testing; what does the animal do and how does it do it? Most researchers would agree that modern ethology requires an interactionist stance, and among the vast range of topics presented were several that should help to refocus ethological efforts.

Evolutionary lability

Ethology arose in the service of phylogenetic reconstruction[3] and intraspecific variation has often been viewed as a stumbling block to the use of behavior as a phylogenetic character. Emília Martins (University of Oregon, Eugene, USA) exemplifies how the 'naive intuition'[3] of the classical ethologists has more usefully matured into strategies for inferring the evolution of behavior. Her generalized linear model[4] provides a smorgasbord of realistic microevolutionary models, allowing us to identify where significant behavioral change has occurred, and pose questions concerning ancestral states, the degree of phylogenetic effect, the relationship between traits and environment, and the rate of phenotypic evolution. She illustrated the method with an analysis of the head-bob display of *Cyclura* iguanas, which showed the value of incorporating intraspecific variability and various spatial scales. Even the stereotyped displays of reproductive behavior, it seems, can undergo rapid, major change between populations.

If signals used in sexual selection vary between conspecific populations, what then holds a species together[5,6]? John Endler (James Cooke University, Townsville, Australia) outlined his studies on visual signaling in fish and birds to demonstrate how interactions between signal design, environmental conditions, behavior and sensory systems[7] allow us to generate explicit predictions for the form of signals and signaling systems. While some aspects of signals are predictable from first principles of biophysics and sensory ecology, selection on traits involving various aspects of a sensory system, or directly on preferences, may result in 'unexpected'

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results, which are not fully understandable unless the sensory mechanisms are known.

The questions of greatest interest in sexual selection theory are those concerning the conditions under which the stabilizing influences on the male–female communication system may be overcome and the mate recognition system altered[8]. Endler showed how chance differences in selection generate diverse responses among populations, disrupting the common sensory environment. In Kenneth Kaneshiro's (University of Hawaii, Honolulu, USA) view, population size is paramount, having a significant directional effect on mate-choice mechanisms. This intuitively appealing qualitative model awaits formal development, but is supported by observed changes in mating preferences in several Hawaiian Drosophilidae following bottlenecks. Density-dependent mechanisms of population biology were also prominently featured by William Sutherland (University of East Anglia, Norwich, UK). He demonstrated how understanding the behavioral basis of density-dependent competition is critical for the optimization of conservation management strategies and constitutes what is arguably the most important applied aspect of ethology today.

Behavioral flexibility

Learning is purported to alter the selective pressures an animal experiences and thus facilitates the use of new habitats[9]. Latest findings from Joanna Girvan and Victoria Braithwaite (Edinburgh University, UK) suggest that fish from contrasting environments may exhibit variable learning and memory strategies. Whereas three-spined sticklebacks from different populations all performed equally well in color discrimination tests and a simple maze learning task with visual landmarks, some populations learned significantly slower when landmarks were absent.

The division of labor in social insects, is in some sense, the essence of behavioral flexibility, occurring spontaneously even among individuals of solitary species when they are induced to cohabit[10]. Robert Page (University of California, Davis, USA) summarized his studies on honeybees, in which he has defined specific pathways from genes through sensory physiological mechanisms, through individual behavior, to a colony phenotype, to understand how selection results in changes in complex social organization. He demonstrated how colony-level selection for the amount of pollen stored in the comb rapidly resulted in allelic substitutions at three major, mapped quantitative trait loci (QTLs). At least two of these three major QTLs ap-

pear to be affecting the response thresholds of individual workers, which determine their roles as foragers (i.e. whether they collect pollen, water or nectar), and, in the latter case, the preferred sugar concentration of the nectar.

The machinery of behavior

For classical ethologists, species-typical behaviors evolved through natural selection and represented the outward manifestation of inherited hardware. Two contributions explored aspects of the neural mechanisms subserving social behaviors. Firstly, using a combination of pharmacological and intracellular stimulation experiments, Berthold Hedwig (University of Göttingen, Germany) elegantly unraveled the neuronal control of complex courtship displays in gomphocerine grasshoppers. These involve three patterns of hindleg movements and associated sound signals (i.e. three classical fixed action patterns, or FAPs). He showed that recording from three types of interneuron in the brain reliably elicits just one of the three behaviors. Courtship sequence is therefore controlled by successive activation of the three neuron types, each constituting a necessary part of the FAPs of stridulatory behavior. Even more surprising, it seems that in contrast to the distributed control seen in many other systems, this stridulatory behavior is hierarchically organized; the motor patterns for leg movement may emanate from the metathoracic ganglion but their production is controlled by the brain.

Neural mechanisms subserving more enduring social relationships are the province of Michael Raleigh (University of California, Los Angeles, USA). Experimental alteration of serotonergic function showed that this system underlies social effectiveness in vervet monkeys. Males with high serotonin levels show less frequent but more effective aggression, form and maintain more coalitions and social alliances, and are more likely to attain high social status in new groups following dispersal. Moreover, serotonergic system receptor density in the frontal cortex and amygdala correlates strongly with substantial and persistent individual differences in aggression and social rank. Those individuals possessing high receptor densities exhibit less destructive, aggressive behavior over their lifetime, and have an enhanced capacity for cooperative behavior.

The general superiority of the tit-for-tat strategy is well recognized and has become the prototypical cooperative strategy in theoretical and empirical studies of the evolution of cooperation[11]. Charlotte Hemelrijk (University of Zürich, Switzerland) questions that conventional wis-

dom by using an individual-oriented model to show how apparent cooperation may emerge from simple self-reinforcing interactions without invoking genes, games or sophisticated cognitive capacities. Several counterintuitive results will surely resonate among those studying motivational mechanisms. For instance, the more aggressive individuals were also more cooperative and larger cognitive capacities did not lead to more intricate patterns of social interactions. While the generality of this mechanism is not yet clear, Hemelrijk's study challenges ethologists to generate parsimonious hypotheses for animal behavior; studies aiming to explain social complexity must ask what part is explicitly encoded in qualities of individuals (genetic or cognitive) and what part determined by interactions between them.

There was a sense of rejuvenation at this meeting, of a reorientation in ethology stemming from the striking success of the interdisciplinary approaches. It was somewhat surprising, though, that with few exceptions, delegates tended to view behavior purely as a result rather than a potential cause of evolution. Mayr saw behavior as the pacemaker of evolution[12] (but provided no data), and Wright developed models[13] in which ecological opportunity (read 'behavioral adaptation') was the *sine qua non* of evolutionary change. Recent population genetic models incorporate behavior more explicitly[14], but without further empirical efforts from ethologists, the claim that behavior is an evolutionary pacemaker will not survive another 40 years[15]. If ethology is to fulfil its historical aspirations we must put behavior back at the center of evolution. It is gratifying to recognize that ethologists are providing the means to do just that.

Moira J. van Staaden

Institute for Zoology, University of Graz, Universitätsplatz 2, A-8010 Graz, Austria (m.van-staaden@kfunigraz.ac.at)

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Counting the cost of disease resistance

A well-known fictitious race of predatory alien would always admonish the species they intended to subjugate with the unforgettable phrase 'RESISTANCE IS USELESS'. A recent paper in Nature[1] shows that an animal's ability to mount a robust immunological response to incoming pathogens, while being far from useless, may indeed be less than useful in certain circumstances. Evolutionary biologists have suspected this for some time. The central observation fuelling these suspicions is that genetic variation exists among conspecifics in the capacity to repel or control infection successfully. If resistance is useful, in the sense that it contributes positively towards an individual's fitness, then why are some genotypes refractory to disease and others congenitally defenceless? Why does natural selection not fix genes conferring resistance throughout animal populations?

There are numerous explanations[2]: for example, large asymmetries between host and parasite generation times may leave hosts 'lagging' behind pathogens in coevolutionary arms races. Alternatively, substantial genetic variance, for instance due to the effects of dominance, can remain at the limits of artificial selection, and similar constraints might obtain in nature. Nonetheless, a major possibility is that resistance correlates negatively with other important fitness components (a so-called 'cost' of resistance). Consequently, so the idea goes, resistance genes are subject to antagonistic selective forces which conspire to impose an equilibrium frequency somewhere short of complete fixation.

So far, so good. The great problem with the cost of resistance model, however, has been a continuing lack of direct evidence identifying the all-important costs themselves. Recent years have seen a quickening of interest in this problem, and now in an elegant experiment with an insect host–parasitoid system, Kraaijeveld and Godfray[1] add convincingly to a small but expanding body of empirical data in support of the 'cost' hypothesis.

Using the parasitoid wasp Asobara tabida, a common biological enemy of several European Drosophila species, the authors selected replicate lines of D. melanogaster for increased resistance to parasitoid attack. Ovipositing females of A. tabida lay their eggs in the body cavity of larval flies. The young wasp then develops within its host, ultimately causing its death. Occasionally, however, a larval fly successfully contains the intruder within multiple layers of immune cells and deposits a dark pigment upon its surface. If this process, known as melanotic encapsulation, is successful, the invading parasitoid is destroyed and the larval fly can develop to adulthood. The dark melanotic capsule remains visible through the fly's abdominal wall so that as an adult, a larva that survives parasitization displays the little black spot like a badge of honour.

Kraaijeveld and Godfray used these spots as the phenotypic marker in their selection regime, choosing only those flies with a melanotic capsule to parent subsequent generations. The response to selection was rapid and substantial. In the original field isolate, c. 5% larval flies encapsulated wasp eggs, a figure typical of northern European D. melanogaster populations. After eight generations, encapsulation rates in the selected lines exceeded 50%. Aside from confirming the genetic basis of encapsulation ability, the magnitude of this response suggests that in wild populations there may be considerable constraints on the evolution of resistance.

The authors then turned their attention to locating possible costs associated with the resistant phenotype. Comparison of a battery of traits between selected and control lines revealed that at high population densities resistant larvae suffer a significant decline in ability to compete for a limited food supply when measured against a genetically marked 'tester' strain of D. melanogaster. According to Kraaijeveld and Godfray, the population densities imposed in these competition assays are frequently encountered by developing larvae in the field. By demonstrating a negative genetic correlation between larval encapsulation ability and competitive performance, these experiments provide hard evidence of a trade-off between resistance to parasitoids and other components of fitness.

Data pointing to a cost of resistance are now accruing in a diverse assemblage of host–pathogen systems. The conditional inferiority of resistant phenotypes has been demonstrated in the interactions of bacteria with bacteriophages[3] and moths with viruses[4] as well as mosquitoes with protozoan[5] and nematode parasites[6]. These latter two results have implications for the successful control of debilitating human diseases – specifically malaria and the tropical filariases, in which mosquitoes act as vector. Eradication programmes based on the release of pathogen-resistant vectors to the field could ultimately prove futile if resistant mosquitoes pay too high a fitness cost in the absence of parasitism[5].

In plant[7] and vertebrate[8] biology, the genetics of resistance mechanisms have been intensively studied. Our understanding of the genetics underlying host resistance mechanisms in invertebrates is less impressive, but progress is being made. In the case of mosquito refractoriness to Plasmodium spp., both susceptibility and resistance respond to selection in the laboratory[9] and, more recently, QTL mapping suggests a complex basis to the mode of inheritance of resistance[10]. For some parasitoid systems at least, the genetic basis of resistance may be much simpler. For example, melanotic encapsulation ability of D. melanogaster larvae