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2012 Animal Behavior Workshop Report

Report of a Workshop held at Airlie Center, Warrenton VA
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Report of a Workshop
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Introduction

This document is the result of an NSF-funded workshop on animal behavior research, held at the Airlie Center, Warrenton VA, 27 April to 1 May 2012. Here we describe what research into behavior entails, why it is important, and what some of the most exciting future directions are.

The Opportunity

Animal behavior is the study of what animals do, why they do it, how they do it, and with whom they do it. It is a fundamentally integrative field that depends on ties to genetics, development, and physiology on one side and to ecology and evolution on the other. The last decade has seen a veritable explosion in tools and methods for analysis of complex systems, opening non-model organisms to sophisticated analyses.

We are at a time of unique opportunity in the field of animal behavior. Integration of functional and ecological/evolutionary approaches is now truly possible in diverse biological systems. The resulting increased understanding of behavior is essential for progress on the five grand challenges the National

Research Council put to biology. It is therefore crucial that integrative approaches in behavior be nurtured and advanced in order to exploit this opportunity.

Below we highlight some of the most important frontiers for behavior, focusing in particular on those that take advantage of ties to other disciplines. In the ten sections we do the following. 1.We show how understanding behavior is essential for dissecting relationships between genotype and phenotype. 2. We cover behavioral flexibility, which is important for adaptation. 3. We discuss the major transitions, demonstrating that our understanding of how organisms came to be is based on behavioral theories. 4. We explain the importance of behavior in social interactions, including those among relatives and those among unrelated individuals. 5. Theory derived from behavior has motivated a new physics ("smart particles"), important for understanding group movement of everything from birds to tumor cells. 6. Microbes have important roles in our environment and health. They can be used to test behavioral theories using experimental evolution and full genome sequencing, for example. 7. Microbes and parasites can also impact animal actions directly. 8. Synthetic life can be simulated with computers and interactions studied using animal behavior principles. 9. We include a section on important practical applications of behavior. 10. We conclude with a section on exactly why behavior is important for the grand challenges.

The history of animal behavior research

The field of animal behavior has ancient roots, but the modern practice might be considered to originate with the birth of ethology, the study of behavior in its natural context. In 1973 Niko Tinbergen, Karl von Frisch, and Konrad Lorenz were awarded the Nobel Prize in Physiology or Medicine for founding ethology. In an attempt to organize this new endeavor, Tinbergen codified the study of behavior in a 1963 paper, "On aims and methods of ethology," by identifying the four main questions of behavior: causation, ontogeny, survival value, and evolution. The first two address proximate (mechanistic) causes and the latter two ultimate (evolutionary) causes. However Tinbergen himself never lost sight of the importance of integration across these approaches. He ended his four questions with a single question, "Why do animals behave the way they do?"

Tinbergen was renowned for both his field experiments on the adaptive significance of behavior as well as his analyses of sign-stimuli to understand behavior within the subject's perceptual universe. Lorenz's studies of imprinting addressed questions of how animals acquire behavior, while his arguments for the use of behavioral characters to reconstruct phylogenetic relationships emphasized the importance of evolution. Finally, von Frisch discovered the function and purpose of the honeybee dance language.

In the 1960s and 1970s a huge advance to our understanding of how cooperative behavior evolved came with William Hamilton's theory of inclusive fitness, or kin selection. Led by Robert Trivers and Richard Alexander and popularized by Richard Dawkins, the theory was rapidly appreciated as applying to both cooperation and conflict. Some of the most interesting early applications were to parent-offspring conflict. This discovery also revolutionized animal behavior as an explicitly genetic model.

It is beyond the scope of this white paper to cover the many discoveries of behavioral research in the last few decades. But it would be incomplete if we did not mention some of the highlights.

Phylogenies are very important to animal behavior because they can tell us how a trait evolved, or the order in which the pieces of a complex trait arose. How behavior develops in young organisms can tell us much about its genetic and environmental background and about the role of learning in behavior. The neuro-endocrine basis of behaviors as complex as exploration, mate choice, and fidelity is a field that is advancing rapidly. The ecological side of behavior has explored feeding with optimal foraging theory, for example. Interactions are important in nearly every kind of behavior, from mate choice to territoriality to parent-offspring interactions to altruism. Animal behaviorists have made most of the theoretical contributions to these areas including game theories like hawk-dove, inclusive fitness, multilevel selection, and optimality theory. These and other theories are increasingly found to be important in the study of life at all levels. Animal behaviorists have thought very clearly about how communication evolves. They have developed models used at many levels from cell adhesion and quorum sensing to alarm calls and begging. Humans are animals, of course. Scientists trained in the animal behavior tradition have made major advances in explaining why humans behave as they do. The vibrancy of within-discipline studies is ever increasing and important. However, here we focus on extensions and bridges of the field, not on the core material found in animal behavior textbooks.

1. Behavior's key role in understanding phenotypes from genes

Behavior is the ultimate endpoint of the whole process of converting genetic information into action. Gene expression is the first step, followed by all the mechanisms of cell biology, interactions among cells, nerves, and the brain. Behavior is the ultimate phenotype. Phenotypes can emerge from single individuals or from interactions among individuals.

Until recently the tools needed for rigorous genetic studies were difficult to obtain in many organisms; the tools are very expensive and time consuming to develop and maintain, and therefore were available in only a very limited set of model systems (e.g. *Drosphila, Mus, Caenorhabditus*). But now the revolution in genomics, transcriptomics, and proteomics provide essential tools to advance functional studies of behavior in virtually any system. Therefore, there are unprecedented opportunities to integrative functional and ecological/evolutionary research in systems already developed by behaviorists as strong models for different aspects of behavior (e.g. sociality, parental care, sexual selection, aggression, communication, migration).

An example of the kind of integration we can achieve comes from comparisons of closely related rodent species that differ in male parental care. Careful studies revealed the behavioral effects of changes in the distribution of vasopressin receptors in the brain. Another example is comparisons of natural genetic variants in foraging behavior in fruitflies revealed the genetic pathway involved, which is also involved with foraging behavior in honeybees.

Understanding why a particular behavior works in a particular context is enhanced when the mechanism is understood. For example, in humans one component of attraction is based on allelic variants at the MHC locus. In mice the attractiveness of a mate is partly based on odor, but variation cues depends on immune profiles and on the microbial consortia that impact scent. Some gene deletions in both mice and yeast have no apparent phenotypic impact until the organisms are put in natural environments where the cost becomes clear. Such integrative studies will likely explode in the coming decade, leading to a much richer understanding of behavior across biological levels.

Important questions for genotype to behavioral phenotype studies

1. What is the genetic basis of behavioral traits, including complex traits such as parental care, mate preference, territoriality, and migration?
2. How variable are these traits within individuals and species, and what are the genetic and epigenetic bases of this variation? How do gene regulatory mechanisms contribute to gene-by-environment interactions?
3. How do epigenetic changes in gene expression in the neuro-endocrine system bring about changes in behavior, and how do behavioral feedbacks alter gene expression?
4. How do genetic architecture and interactions among organisms shape behavioral responses in relation to social and other environmental contexts?

2. The behavioral phenotype adapts most rapidly to changing environments

Individuals can respond flexibly and nearly instantaneously to changes in their social or physical environment by changing their behavior. This is not true for many other phenotypic attributes. For example, when it gets hot an animal might respond physiologically by sweating or panting and by dilating capillaries close to the skin. But the first response is likely to be behavioral. The individual can stop moving. It can shelter under a cool rock. Observing behavior is often the quickest way of understanding how the individual is responding to its environment.

There are multiple levels of behavioral flexibility. An individual may display different behaviors at different stages in its development, at different times (circadian and seasonal plasticity), and after different experiences. The type of behavior an individual displays might also be influenced by its genotype and internal state (motivational or arousal state, physiological state, microbial community) or external context (social or abiotic environment). An individual may display flexibility by rapidly switching among behaviors, or by taking advantage of multiple resources and environments (generalists vs. specialists).

Rapidity of behavioral responses. Quick action is often called for in response to other living organisms, whether they are social competitors, potential mates, predators, prey, or parasites. Behavior is the fastest response. A male holding a territory might aggressively attack a larger invader while hiding from a smaller one.

When flexibility is required. Some kinds of situations require more flexible responses than others. Flexibility can take many forms. It may change with age and development. Learning may hone responses. The more nuanced an approach to a situation is needed, the more likely that learning, intelligence, and experience will be involved. Clearly, the brain and its capabilities can only be fully understood by examining the actions it orchestrates.

Flexibility is itself evolved. The plasticity of behavioral responses is itself an evolved trait, dependent on the likelihood of encountering changing and unpredictable circumstances. Any thorough study of behavior will include an examination of the variation in responses across situations, age, experience, in a phylogenetic context.

Importance of flexibility beyond animal behavior. Flexibility is a key concept in many areas of science and society. Besides being crucial for understanding animal behavior, flexibility can impact state changes of many kinds. Flexibility in computational systems refers to the ability to move rapidly between multiple tasks. Flexibility can be considered along three axes: speed of task switching (time to switch/time in task), number of tasks, and difficulty of tasks. There could be trade-offs between these as well as with respect to speed and accuracy of the response.

Important questions for flexibility and learning studies

1. What kinds of circumstances are most likely to require a flexible phenotype? What constrains or enhances flexibility?
2. What are the mechanistic roots of flexible responses at the genetic and neuroendocrine levels?
3. What are the triggers to flexible responses and how do they differ for different kinds of tasks?
4. How do evolutionary forces shape the type of flexibility exhibited by a species or taxon, and are there common underlying mechanisms that drive these different strategies to achieve flexibility?
5. Flexibility of responses of differing kinds may be crucial to surviving climate change. For example, how does degree and type of flexibility in bird migration mesh with flexibility in plant and insect phenology?

3. Cooperation, conflict, and major transitions

Much of animal behavior has to do with interactions with other individuals. Choosing mates, competing for resources or territories, communicating, cooperating for mutual benefit, and cheating on cooperators are important aspects of fitness molded by selection. Animal behaviorists have made great advances in understanding social interactions. They have developed major theories of ultimate mechanisms like kin selection, sexual selection, game theory, and reciprocity and a number of important possible proximate mechanisms regulating social interactions (hormonal, neural, genetic, cognitive, emotional, empathetic).

The impact of social evolution. The study of cooperation and conflict in animal behavior has had a huge impact in how we understand the organization of life. Reaching below the level of the animal, it is clear that many of the major transitions in evolution involved the evolution of such extreme cooperation and conflict suppression among individuals that a new type of individual was produced. Examples include the evolution of the first cells, eukaryotic cells and their organelles, multicellular individuals, and some eusocial societies. Each of these transitions is governed by the same principles, discovered in animal behavior research, of evolution of cooperation and conflict suppression among individuals. Reaching up to level of human social behavior, these ideas have penetrated anthropology, economics, political science, psychology, and even the humanities. Researchers in those fields are now asking how biological evolution has influenced culture, political institutions, economic utility, and morality.

The balance of cooperation and conflict. Cooperation is the interaction among individuals for their mutual benefit; this also includes symbiotic interactions among species. We have learned some of the surprising ways that cooperation can evolve in a seemingly competitive Darwinian world, but cooperation can be hindered by conflict. Non-cooperators can cheat or free-ride. Understanding the balance between cooperative and selfish forces continues to be a major area of research. For example, the sexual process is a fundamentally cooperative one where a male and a female unite their genes in the common project of offspring, but the process is riddled with conflicts, including who should mate with whom, and who should invest in the young. Studies of social insects have been instrumental in showing how conflicts can be reduced or even eliminated.

These kinds of studies can reveal the fundamental selective forces that shape the balance between cooperation and conflict under different kinds of group living situations. They can also inform as to how the environment affects these fundamental behaviors in predictable ways in very different organisms. For example, kin selection theory has made useful and similar predictions for social behavior in ants and in social amoebae. Studies in this area can provide a broad-based approach for considering the major transitions in evolution, address the flexibility that is inherent in behavior, and provide understanding that will influence all the biological and social sciences.

Important questions on cooperation and conflict.

1. What are the costs and benefits of cooperating in different systems?
2. What explains cooperation among relatives and among non-relatives?
3. How do proximate constraints on individual selfish behavior aid cooperation?
4. Does the size of groups influence the ways in which cooperation is maintained?
5. What can we learn about the forces shaping human social behavior by comparative studies in animals?
6. How does social evolution affect microbial cooperation, and how does microbial cooperation impact the success of pathogens?
7. How often do conflicts lead to evolutionary arms races, with the genetic signatures we expect for arms races?
8. What mechanisms restrain conflict and how do they arise?
9. How do ecological circumstances shape conflict and cooperation?

4. Collective behavior and individual intelligence

Animal groups can display compl**e**x collective behavior. Often the sophistication of their group-level problem solving strategies is not directly related to the intelligence of the individuals that comprise the group: for example, ant and bee colonies are renowned for their abilities to make complex group decisions that surpass the sensory and cognitive limitations of the individual insects. Animal groups are an excellent example of complex systems, comprised of many interacting but semi-autonomous units. Therefore, animal behavior research in this area has made huge contributions to the study and engineering of complex systems, such as telecommunications networks, production workflows, and collective robotics. In addition, animal groups allow us to study phenomena such as social information transmission, collective action, and social selection that are vital in shaping human societies.

There are many open questions regarding the transmission and processing of information in collectives. Understanding social influence and collective intelligence is essential, not only to inform the evolution of social life in many animals, but also to understand the dynamics of information exchange in human societies. Information in collectives can be transmitted socially. In humans this is what the huge field of culture is. But some animals also have cultural transmission, causing behavioral traits to vary among populations. These are deserving of intense study as the only other window on this all-important human phenomenon. Learning, collective action, and culture are part of the phenotype and need to be understood if we are to link genotypes to phenotypes successfully. How the social parts sum to the whole is variable and can be very counter-intuitive.

Distributed cognitive functions. Animal groups are an effective test model to study the emergence of distributed cognitive functions since individuals make effective decisions across a range of contexts and in the face of incomplete or changing information. Central to this question is the relationship between individual-level and collective or cultural cognition. How these systems evolve, and what kinds of information are distributed and what is not is another challenge.

Group decision-making. Information can emerge from collectives that would not be predicted from summing individual information. Sometimes the collective information is more accurate as group size increases simply because it is the average for independent estimates. In the earliest study, in 1906, Sir Francis Galton made a near-perfect estimate of the weight of an ox by calculating the mean of nearly 800 guesses made by others.

But other circumstances can result in positive feedback loops that increase the weight of erroneous estimates. The problem arises when the estimates are not independent, which is a common situation in collectives. For example, social influence can result in positive feedback loops, such as when musical preference is biased by the perception of the opinions of others or when social influence diminishes the diversity of group opinions without improving accuracy. Understanding why some group estimates are reliable and others are not challenges us to identify the circumstances favoring reliance on social, as opposed to personal, assessments.

There are many examples of animal group decision-making. Honeybees find new nest sites together. Ants, swallows, and fish schools find sources of food from collective processes more rapidly than they could alone. Social information may be better than individual information when more of the environment is sampled, or when the abilities of highly informed individuals are combined with others that are not. The trick is to understand exactly how these collective decision-making processes work and when they lead to better outcomes and when they lead to worse outcomes. It is emerging that previously hidden social influences based on group structure and individual perceptual abilities can help spread information quickly and widely in groups. Consequently, these processes play important roles in shaping the complex social interactions that govern collective action of groups. Coordinated action is rapid and requires a type of information transfer that differs from direct message passing from individual to individual.

Learning in groups. Group membership can profoundly affect the processes by which social organisms learn. Each individual could serve as a separate information-gathering entity, and by pooling learned information together, individuals in the group may obtain a more accurate representation of true environmental contingencies. But what if the individuals do not sample the environment independently? Animals in a group are likely to detect the same cues as their close neighbors. As a result, there is inherently some redundancy of information within the group. In general, the more correlated an information source is, the less potential there is for collective intelligence. For groups, then, the value of an information source depends not only on its reliability but also its degree of correlation. Both the reliability of cue detection and the degree of correlation will vary for different sensory modalities in different environments. Even biological processes as seemingly well understood as classic associative learning become much more complex in a group context.

Culture and behavior. Animals learn from their own experiences, or from others. What they learn from others may have been discovered by others. Broadly speaking, this is what culture is, information shared past direct experience. It is the overwhelmingly largest part of human knowledge. Its maintenance and transmission is central to our very existence, more important to how we live than our individual intelligence. Culture exists in animals of various sorts. It is often identified when behavioral traits vary among groups. Culture can determine actions that are beneficial or harmful. Because cultural traits can spread much more rapidly than genetic ones, they can be the first to change in changing environments. This is an understudied and important area of animal behavior.

Important questions for collective action, learning, and culture studies

1. What kinds of problems are best solved by group decisions?
2. What are the universal elements of effective collective action and learning?
3. What makes swarm intelligence different from summing up individual intelligences?
4. Where is there culture? What kinds of traits are most likely to be transmitted culturally?
5. How can we optimize learning in groups?
6. How does collective action change responses to environmental change?
7. Does collective action provide increased buffering to changing environments or faster responses to such changes?

5. Collective behavior reveals a new kind of physics

In the physical sciences great progress has been made in understanding the collective action of systems in thermodynamic equilibrium, notably through statistical mechanics. One of the most important breakthroughs in this area has been the realization that systems which differ greatly in terms of the dynamic details (such as inter-molecular forces) can display common, or universal, collective behavior. Thus system-level behavior can be formally independent of the degree of complexity of the individual agents that make up the system.

Biological collectives are not in equilibrium. Some of the most meaningful and important collective behaviors, such as migrating cells in a developing organ or tumor or the vast swarms of devastating locusts or migratory schools of fish, do not exist in thermodynamic equilibrium. Unlike in physics, where theories regarding collective behavior can be developed around quantities that are optimized by their dynamics (such as free-energy or entropy), biological systems are far from equilibrium and are driven by self-propulsion, as opposed to thermal or other physical sources of energy. This fundamental difference dramatically changes both how collective biological systems function and also how interactions among organisms in collectives are best studied.

Biological 'particles' do not follow standard rules of physics. In mobile groups of cells or animals, diffusive processes impact behavior. These include the transmission of both errors and valuable information. Why are flocks and schools so robust to perturbations driven by environmental noise like turbulence and yet simultaneously highly responsive to perturbations driven by localized attack by predators? Error diffuses extremely rapidly through mobile animal groups because of their self-stirring nature. Since error caused by things like sensory noise or movement error is largely uncorrelated among individuals, errors leak from the system faster than they accumulate. This stabilizes the structural integrity of groups and minimizes the demands on sensory apparatus required to coordinate motion.

Importance of correlated perceptions. Correlated information, on the other hand, such as when a small subset of individuals respond to a localized threat by moving away, spreads in an entirely different fashion. It can propagate rapidly across the entire structure, requiring no adjustment from the sensory system (although adjustments could, in principle, also affect such percolation). Again we cannot understand the sensory requirements, or make predictions regarding the information pertinent to individuals in groups, without considering the nature of collective information transfer. Unlike the traditional view of message passing (such as when on individual influences a neighbor who influences a neighbor, and so on), here the group is capable of responding effectively as a singular unit, with information near-instantaneously spanning the entire group, regardless of it size.
This line of inquiry would not only influence our understanding of perception, action and the evolution of coordinated behavior, but also would inform new directions in the study of non-equilibrium systems, one of the main challenges in contemporary science.

Important questions for behavioral physics studies

1. How do we understand the physics of interacting entities that could be considered as particles when they are not at equilibrium, and respond to stimuli like gradients both independently and collectively?
2. What kinds of information are likely to be correlated and how does this change the physics of interaction?
3. What are the universal principles guiding interacting 'smart' biological particles?
4. How do sensory systems constrain the flow of information in groups, leading to variations in collective behavior patterns?

6. Microbial behavior, experimental evolution and genomics

The small genome sizes, ease of genetic manipulation, simplified behavioral action sets, more direct connections of genotypes to phenotypes, and absence of brains make many kinds of behavior easy to study in microbes. Microbes are also amenable to experimental evolution, which allows us to directly alter the environment, physical or biotic, and to study predicted responses. In microbes, we can examine responses to environmental gradients in microfluidic landscapes. We can study community level interactions with replicates. We can look at the genetic basis of behavior in ways unparalleled in animals. For example, we can classify genes as social or non-social and examine their patterns of evolutionary change. We might predict rapid change in social genes since they involve arms races with others. This is easily tested in microbes. The same might be true for genes conferring pathogen resistance.

The power of behavioral studies in microbial systems is something that has been recognized in the past decade or so. The field is booming. There are many fascinating studies of behaviors once thought to be restricted to animals like altruism and social feeding. There are others that are uniquely microbial but have conceptual analogues among animals, like quorum sensing behaviors and bacteriocins, where some die to benefit relatives by killing others.

Microbial genotype to phenotype. In microbial systems we can combine proteomics and transcriptomics to identify genes upregulated under conditions of interest. We can tie these changes to specific kinds of actions and interactions. We can sequence strains within natural microbial populations that differ in the performance under various environments, physical and biotic. Once we identify genes of interest we can knock out genes that we predict are important in social interactions and look at the consequence. We can also replace genes with variants in an isogenic background. For example we can compare genes involved in secreted products and those on the cell surface to genes involved internally, predicting the former more likely to experience rapid evolution than the latter. Such systems are ripe for performing experiments that will identify the connections between mechanism and function that have been the foci of most behavioral studies on vertebrates.

From Microbe to Multicellular Organism. The features identified for social genes in microbes would provide novel insights into microbial interactions and could be targets for applied microbiologists to disrupt social interactions that are critical for some pathogens (*e.g.,* biofilm formation of *Vibrio cholerae* and *Pseudomonas aeruginosa*) or possibly promote social interactions in applied systems where microbial interactions facilitate useful processes (*e.g.,* bioremediation by *Pseudomonas putida*). The bigger goal, however, is to move beyond microbes to determine whether the features of social genes identified through this microbial approach could be used to identify genes underlying social behaviors in eukaryotic organisms. We could determine whether already identified social genes of eukaryotes exhibit some of the features of social genes in microbes. We could use the features of social genes in microbes to predict social genes in a multicellular eukaryote that could be genetically manipulated, then alter the function of these genes to determine if they alter behavior. We could predict social genes in a eukaryote and couple this with genome wide association studies to determine if both methods point to social genes in the same genomic regions. The examples here have focused on social traits, but other traits are also amenable to study in microbial systems, from resource tracking, to crowd sourcing of information, to coordinated evolution under climate change.

Important questions for microbial behavior studies

1. What is the impact of resource structure on behavior?
2. Are there common patterns of selection for social genes?
3. Are social genes in particular regions of genomes clustered into cassettes where coordinated selection is facilitated?
4. Is there an identifiable difference between the structure of gene networks in which social genes (vs. non-social genes) are involved? We predict that social genes have cascading effects and are thus typically part of complex networks.
5. Are social genes more or less likely to be transferred laterally between bacteria? If social genes only function in a complex network, then we would expect lateral gene transfer of single social genes to have little benefit to the new host genome and thus they would not be maintained.

7. Microbial and Parasitic motivators of behavior

We commonly expect behavioral reactions of individuals to visible challenges. A gazelle stots as it moves away from a predatory lion. A male bird preens and puffs in front of a female. Visible motivators of behavior are important. But there are others, the unseen bacteria, viruses and parasites that can manipulate an individual's behavior to their own end. These parasitic manipulators can make mice approach cats, ants lock onto the ends of grass stems, or rabid raccoons bite. These tiny manipulators are underappreciated causes of behavioral variability. In addition to specific parasites, no animal exists without a complex microbiome. There is mounting evidence that the animal microbiome is engaged in complex feedbacks with host behavior. These impacts can be positive and mutualistic, or negative and pathogenic, depending on the interaction or interests of hosts and their parasites and microbes. Many host behaviors, from diet to social interactions, can affect microbiomes and the microbiomes themselves can influence behavior in dramatic ways. Understanding how and why microbes interact with animal behavior remain major open questions in biology.

The study of the animal-associated microbiomes is undergoing an unprecedented expansion. Recent breakthroughs in DNA sequencing technology unleashed a metagenomic revolution by allowing affordable study of complex microbial communities without the need for microbial isolation and culturing. Furthermore, in addition to the advancements in DNA sequencing, there is a repertoire of microbial genetics tools that can be readily applied to study animal-microbe interactions. Especially important is the use of mutagenesis in the identification of microbial genes involved in interactions with hosts. The field is advancing rapidly, and encouraging results suggest a range of applications to human health. However, while a central goal of the study of microbiomes has been to elucidate consequences for immunity, infection and disease, we still lack a fundamental understanding of how microbiomes affect a critical component of the animal phenotype: behavior.

Identifying the microbes that alter behavior. Animal microbiomes can be made up of thousands of species of bacteria, many of which cannot be cultivated outside of the host due to their adaptation to the host environment. Rapid advancements in high-throughput DNA sequencing and metagenomics are allowing characterization of microbiomes beyond the few microbes that we are capable of isolating and culturing in the lab. Determining which microbes alter behaviors, however, will require manipulation of the composition of the community. Model organisms are paving the way in this regard with recent developments in experimental techniques such as germ-free mice and colonization with select microbial consortia. Antibiotics can also be used to remove microbes in controlled experiments. Equally promising is the application of microbial genetic techniques such as random mutagenesis to identify microbial genes influencing behavior. A challenge for the application of microbial genetics is that it requires isolating and developing specific culturing conditions for the microbes of interest from among the thousands of microbes that constitute the microbiome.

Identifying the mechanisms and patterns of microbiome establishment. Microbiomes can range from extreme specificity to extreme generalization, and their acquisition can depend on specific behaviors or be a function of general environmental exposure. Mechanisms of establishment are poorly understood, particularly with regard to their specificity and their dependency on animal behavior.

Elucidating the mechanistic links between host and microbiota. Recent studies on anxiety and brain development in mice suggest that the gut microbiota can interact with host nervous systems. What are the mechanisms for the interaction that lead to neural stimulation? There may be many physiological mechanisms linking the nervous system and the host microbiome.

Understanding the feedback between microbes and host social behavior. Recent studies linking microbes with the behavior of mice have focused exclusively on single individuals. Yet an important component of animal behavior is its social dimension, i.e. how animals interact with others both cooperatively and competitively. How symbiotic, commensal and pathogenic microbes influence or are influenced by social interactions among animals of the same or different species is an important question at the frontier of animal behavior research.

Untangling the dynamics of complex, host-associated multi-species microbial communities. While some behaviors will be modulated by a single microbial species, many will involve multispecies microbial communities. Environmental microbiologists have made important progress toward understanding multispecies communities. A future challenge is to understand these community dynamics in association with hosts and their behaviors.

Exploring consequences of microbial-influenced animal behavior at a global scale. Many animal behaviors, such as migratory patterns of disease-carrying birds and plagues of insects that decimate crops, have profound consequences at the global scale. Are these behaviors shaping changes in host-associated microbes that impact global processes? Human behaviors inducing climate change, for example, can cause increases in sea temperature that stimulate corals to expel their photosynthetic symbionts, a phenomenon known as coral bleaching. Such cascading events dramatically shift microbiomes and could have enduring consequences for ecosystems. Unveiling the hidden dimensions of animal behavior may further our understanding of how and when animal behaviors are likely to have a global impact.

Important questions for microbe-host behavioral studies

1. How prevalent are microbial manipulations of host behaviors? What elements do they have in common?
2. How can one disentangle when the microbiome is impacting behavior and when behavior is impacting the microbiome? Is a bi-directional feedback between the two the norm?
3. How variable are host reactions to parasite manipulations? Are there certain parasites that cause similar reactions in a wide variety of hosts?
4. To what extent do variations in the microbiota or in the genes present within the microbiota impact host behaviors?

8. Behavior, synthetic systems, and computer science

Behavioral synthetic systems take experimentation to a new level. The power of an experiment over a correlation is that we have a clear idea of cause and effect, and can reliably distinguish a response variable from a correlated reaction to a perhaps unknown third variable or set of variables. But even this kind of careful study is rooted in life as it has evolved. We cannot know all the steps or correlates that are important. What if we were able to study behavior of organisms that were completely transparent because they were bits of computer code, *in silico?* Any system that looks at ecology and evolution using synthetic systems like Avida has a behavioral component. It is also an important platform for understanding response to change. The potential of artificial life systems for understanding animal behavior is huge.

Behavioral robots reveal what is important. Another kind of artificial life is that which interacts with living organisms. Researchers use artificial animals to study responses to potential sexual partners, as in lekking sage grouse, and predator-prey interactions as in rattlesnakes with robotic ground squirrels. Researchers also use artificial competitors to understand exactly what features of a male's display are important, as in some lizards and frogs. Similarly, the ability to use remotely controlled predators to feign attacks can provide insights into how collective information percolates through and organizes groups or how mothers adjust their behavior to alter the behavior of predators for the benefit of their young. The power of robots is that the researcher can manipulate the phenotype, both physical and behavioral, changing it element by element and from context to context for a comprehensive understanding of what is important.

Synthetic systems go beyond computer simulations and help us understand group actions of real organisms. Information sharing in groups can change the behavior of members. Comparing estimates with others is central to a class of 'particle swarm optimization' (PSO) algorithms inspired by the collective behavior seen in flocks of birds, schools of fish or herding ungulates. In PSO, a 'swarm' of software agents (particles) move through search-space. Unlike real animal groups, these swarming particles compare their best estimates and pass this information, as well as where the estimate was made, directly with those made by others and modify their motion accordingly. This helps the swarm to converge on optimal solutions, although not necessarily guaranteeing that it does so. PSO algorithms have proved very successful in testing different hypotheses about group decision making.

Behavioral data challenge computational paradigms. Behavioral data are often voluminous, heterogeneous, and noisy. Such data benefit enormously from computer science approaches that allow high throughput data collection and processing, sophisticated analysis paradigms and insight on how to synthesize information. On the other hand, behavioral studies can enhance and challenge computational processing. Datasets for behavior generated by automatic video capture can be huge, messy and complex. It could even be said that some of the heterogeneous data challenges the physical constraints of computation, particularly with respect to highly factorial databases, requiring sublinear solutions and intelligent sampling. Furthermore, computational models of interactions and social networks in humans can be tested in animal systems. Behavior can also inform about synthetic or artificial systems with avatars, robots, and coordinated sensing. In addition, real time analyses can help adjust sampling protocols and fine tune real time perturbation experiments. Clearly these two fields have a great deal to learn from each other.

Important questions for computational behavior studies

1. What can synthetic systems like Avida, an evolving form of *in silico* artificial life, tell us about how behavioral interactions evolve?
2. How can we use Avida and synthetic systems like it to understand the interplay between behavioral specialization and generalization in the face of rapid climate change?
3. How does altruism evolve in a synthetic system? What are the key necessary features for this to happen?
4. What can robots tell us about behavioral responses to others?
5. How can we automate and make sense of huge, interactive, messy datasets such as those captured by video systems?
6. How can we overcome the computational challenges of going from huge genomic datasets to behavioral ones in a comprehensive genome to phenome study?

9. Practical applications of behavioral studies

There is no problem more serious and yet potentially manageable than a behavioral problem. These problems can come from genetic deviants that cause risky behaviors, like canine rage syndrome. They can come from parasites that manipulate the behavior of their hosts, like rabies in mammals. They can emerge when individuals find themselves in new environments where normal constraints on behavior are removed, as is so often the case when species invade new locales. Perhaps most importantly, behavioral problems can reduce the beneficial impacts of animals on our ecosystems and increase harmful impacts. Only by understanding behavioral interactions do we have any hope of enhancing beneficial species and controlling harmful ones. If we know what animals need, we can provide it to beneficial species and take it away from harmful ones. We learn what they need by observing them to see what they use in the environment and how they interact with others.

Problem behaviors. Animals and humans carrying certain genetic variants tend to engage in more risky behaviors. A full understanding of these important issues and under what conditions these behaviors appear can only come from behavioral studies.

Crop pollination. Pollination by honeybees is a behavior that adds at least $15 billion a year to US agriculture, according to the USDA. Nearly every fruit, nut, and vegetable that comes from a plant with showy flowers is insect pollinated. (Others, like corn, wheat, and other grains are wind pollinated.) How do bees choose the flowers they visit? How can we raise crops in a ways that favor healthy honeybees and other pollinators? How do we adjust bee husbandry techniques to manage the more aggressive African bees that are prevalent in much of the US today? How do we address colony collapse disorder in honeybees so we can continue to use them as pollinators? What can we do to enhance native pollinators so we are not so dependent on honeybees? These are fundamentally behavioral questions that require research on behavioral actions from genes to neuroendocrine systems under natural circumstances.

Animal foods, domestic and wild. We cultivate and eat meat, mostly from cows, pigs, sheep, goats, chickens, turkeys, and fish. Many of these animals are farmed. The better we understand their behavior, the more efficiently we can raise them while still meeting ethical animal care standards. What those standards should be is best understood by careful observation and understanding of animal behavior. Typically, species lose plasticity when reared in captivity. What are the consequences of behavioral canalization on efficient husbandry and if this reduction in behavioral diversity is detrimental to animal production or welfare, can an understanding of behavioral repertoires, syndromes and 'personality' be harnessed to minimize or overcome these problems? Fisheries managers need to understand the behavior of species they are managing in order to be successful. For example, the dispersal, mating, migration, and predatory behavior under different levels of abundance are crucial for the wise harvest of wild fish. Species in which only the largest individuals are harvested show major life-history changes that push breeding to younger and smaller individuals. Alternative strategies emerge and become prevalent. Knowledge of how behavior and life-histories co-evolve are necessary for maintaining robust populations and developing sustainable fishing strategies.

Human recreation. Understanding behavior is also important for human recreation. Understanding human-wildlife interactions can mitigate the negative effects humans can have on behavior of animals. Understanding this is important for conservation biology. Hunters and fishers study their prey, enhance the environment for their prey, then lure them in for capture in the flesh or on film. Many magazines, books, and videos promote learning about the behavior of fish and game species. Non-predatory observation of wild life is an increasingly important hobby. Enthusiasts are especially likely to watch birds and butterflies. Nature shows of behavior of wild organisms on television and other media captivate children and adults alike. Building upon the natural inclination of children, their parents and the general public to understand how the world around them works will create a cadre of committed citizen scientists. Animal behavior, because it is visible and compelling, can become the hook for transforming human behavior. Fascination with animals and their behavior can engage and empower people, making them aware of how changing their own behavior could enhance ecosystem function and create a more sustainable planet.

Endangered species. The human impact on the planet is huge and growing. This means that organisms whose land use overlaps too extensively with humans, or whose needs are too specific are in danger of extinction. Somewhat ironically, even enthusiasts sometimes have negative impacts on species. Large assemblages of bird watchers, for example, force resting migratory shore birds off their preferred feeding sites. Without adequate refueling, prospects for arriving on breeding grounds is diminished. How to save these animals requires a detailed understanding of their needs, including dispersal, territoriality, mating behavior, migration, fear of humans and disturbance. Only with this information will it be possible to create successful management programs. Those needs are revealed by behavior. For example, endangered golden-lion tamarins use the beach habitat of the Atlantic rainforest in Brazil, a habitat also prized by humans. Initial efforts at bolstering populations of golden lion tamarins in the wild relied on use of surplus monkeys produced in zoos. However, these individuals, with no experience in living in trees, were not successfully integrated. By allowing monkeys at the National Zoo to be free-ranging in the trees during the summer, they learned the skills they needed for survival once released in the wild.

Another example is the use of recordings of bird calls (and decoys) to attract colonial seabirds to establish new colonies on safe islands. Again, experiences in captivity can endow endangered species with some of the survival skills they need once released in the wild. And where species' repertoires are limited and unaccustomed to coping with novel predators and competitors, or where individual behavioral flexibility is low, massive poisoning or fencing efforts can become an effective last resort for conserving endangered species. Only by knowing what comprises a species' behavioral repertoire and defines its flexibility were governmental and non-governmental organizations in New Zealand able to bring a number of endemics back from the edge of extinction.

Ecosystem management. An ecosystem may look like a static assemblage of plants, animals, fungi, and microbes all responding to the physical factors of geology, temperature, sunlight, and water. There is no doubt that these conditions are important, but perhaps even more so are the dynamic interactions among the living members of the ecosystem. These members eat others, parasitize others, and change behaviors in profound ways. One example is the way that wolves have rescued the riparian vegetation so crucial to migratory birds in Yellowstone National Park. In the absence of wolves, the fearless elk roamed freely throughout the park, browsing upon aspen, cottonwoods, and willows so heavily that there was essentially no survivorship of the youngest trees, resulting in a decrease of beavers and migratory birds. Reintroducing the wolves reintroduced the elk to fear, and kept them out of deep thickets and off snowpack, allowing regeneration and its cascading effects. Fear is also a key component of the effectiveness of phorid fly control of fire ants. The flies parasitize very few ants, but fear of the flies keeps the ants from foraging as effectively, which helps control their numbers.

Clearly, behavior is always an important element for understanding ecosystems. Well-known behavioral components of ecosystems include pollinators that may be generalists or specialists. How far they fly can impact plant population structure. If pollinators lose other resources, or find themselves out of synchrony with their plants because of differential responses to climate change, ecosystems will suffer. Ants, birds, mammals, and other organisms disperse seeds to sites away from the mother plant, further impacting plant communities.

The behavior of many organisms materially changes the environment. Earthworms, ants, and nematodes churn the soil, making nutrients available. The behavior of interacting species can also work in concert to improve the environment and enhance the success of each other. The behavior of wildlife and livestock show that differences in body size and fermentation system of equids and bovids generate differences in feeding and ranging behavior. Recent studies show that when sharing a landscape, these behavioral differences can convert competitive interactions into mutualistic ones under certain environmental conditions. Equids subsisting on stems and other low quality plant parts alter the structure and composition of the savanna facilitating the feeding and growth rates of cattle. In return, movement and feeding behavior of cattle reduced equid parasite burdens, enhancing their growth. In addition the combined feeding behaviors of the two species improved the overall quality of the rangeland and the diversity of its vegetation. Clearly, a direct focus and understanding of behavior is crucial if we are to understand and maintain ecosystem health and conserve of wildlife in areas where human husbandry is important.

Infestation by bird, insect and nematode pests diminish our crops, costing billions of dollars a year. Understanding how these pests communicate and behave is integral to their control. For example, pheromones used to attract males to females can be very effective in baiting traps for lethal tree pests like wooly adelgids or gypsy moths. Grasshoppers eat nearly every crop they encounter. In plague years their physiology and behavior change, making their infestation at biblical plague levels. As numbers increase, behavior flips for from one state to another. Hunger leads to cannibalism, which in turn leads to forced marching as the hunted escape to hunt others. Collective action emerges and plagues result. Any hope of preventing this behavioral transformation and curtailing impending crises will require understanding the drivers of this behavioral transformation. Other important issues include evolved pesticide resistance, and the power of Integrated Pest Management, which includes understanding behavior to cleverly combine chemical and biological control.

Forest destruction. Trees die by the millions when infested by certain insects. Knowledge of the olfactory and social behavior of many insect pests, such as bark beetles, allows us to regulate them by disrupting their social behavior, thus saving the nation untold acres of woodland while sparing the environment from the assault of pesticides.

Invasive and overabundant species. Control of invasive species, care for of endangered species, enhancement of game species and economically important species depend on behavioral studies. Biological control programs have had notable failures because of an insufficient understanding of the feeding or dispersal behavior of the herbivores, parasites, or parasitoids. For example, in many cases species introduced to control invasive plants or pest insects have become problems themselves when they began to feed instead on native plants or non-target hosts, or failed to disperse in order to locate new hosts. Similarly, changes in wide-spread pest control practices, such as the reduction of DDT use, has lead to population increases insectivorous birds, which around airports have created significant aviation problems. Comparative studies that identify fundamental underlying rules accounting for transformations in behavior are necessary to prevent future unintended consequences of management interventions.

Diminishing impact of climate change. Climate change has resulted in warming in many parts of the planet. In many areas this means that local flowering patterns have changed in response. If the behavior of pollinators is unable to adapt quickly enough, co-evolved synchronies will be disrupted to the detriment of plants and pollinators. In addition, insect outbreaks are likely to come earlier as temperature increases. But if migratory birds that depend on eating these insects to rear their young have not yet arrived, insect infestations will be more severe. Also, when the birds do come, there will not be sufficient food for their young. Again, disruption of behaviorally co-adapted systems can harm all interacting species. Rearrangements of ecosystems are likely and the consequences for species themselves and humans depending on them are likely to be negative. Understanding exactly what these relationships are will help us identify ecological systems at high risk and devise mitigation programs. These kinds of relationships are inherently behavioral.

Important questions for practical behavior studies

1. What behavioral traits make species susceptible or resilient to rapid environmental changes and changes in climate?
2. What role does individual behavioral flexibility or behavioral diversity within species play in allowing species to adapt to changing environments?
3. How do internal and external factors interact to shape individual, group and species level responses to environmental stressors?
4. How do animals perceive stimuli developed by humans to attract or repel species? What types of stimuli are best suited to managing target species without detrimental consequences for associated species?
5. How can an understanding of the behavior impacts on survival and recruitment of threatened species be used to change human behavior so that these vital rates are enhanced?
6. What type of human environmental interventions or modifications of species behaviors are possible and how likely are they to enhance rather then harm species survival and sustain ecosystem function?
7. What strategies are likely to be most successful in using behavior to engage and empower people to change their own behavior in ways that sustains rather than harms species and their environments?

10. Behavior and the grand challenges for biology

Animal behavior research is central to each of the grand challenges for biology, from the National Research Council. In fact, there may be no other discipline that encompasses the challenges as comprehensively. The first challenge, **synthesizing life-like systems** is impacted by animal behavior theory in at least three ways. First, any synthetic living system will have independent parts that replicate and compete. How the elements do so is dependent on the behavioral theories of predator-prey interactions, mutualisms, cooperation, disease, competition as well as mating and reproduction. Second, animal behavior research is developing a new physics of collective action because living entities as 'smart particles' do not behave in ways understood by traditional physics, like gas laws, because of novel attraction and repulsion characteristics and novel ways of information processing. Third, one of the hallmarks of life is its ability to transition from simple to complex forms, as cooperation surmounts conflict at lower levels. The theory of major transitions comes from animal behavior.

The second grand challenge, **understanding the brain**, is deeply involved with animal behavior. The brain's most important function is integrating information from its abiotic and social environment, deciding how to respond to this information in a manner that enhances individual fitness, then integrating and marshaling the motor systems that generate these responses. Each of these functions is grounded in the animal's genetic heritage, but is molded by the effects of experience and learning. However, learning may be different in groups where collective decision-making occurs. We can test changes in the learned brain by observing behaviors under different circumstances. Numerous pathologies cause changes in behavior. Behavior can occur without a brain, but brains do not matter much without behavior.

We are a long way from **predicting an individual's characteristics from their genomes,** the third grand challenge**.** Perhaps the most important characteristics we wish to predict involve individual behavior. Who is best suited for what job? What makes one individual aggressive and another cooperative? Do individuals exhibit consistent behavioral syndromes or personalities or do they exhibit plasticity in their response to environmental releasers? Can they do both depending upon context? Are genomic variants up to the challenge imposed by human-induced environmental change? How genetically based is aggressiveness, gregariousness, adventurousness or monogamy? And if so, to what extent do developmental or environmental contingencies modulate them? In both animals and humans, we are making progress with understanding the genetic differences of different behavioral choices, as is made clear by the young Gordon Conference entitled Genes and Behavior, begun in 2004.

The fourth grand challenge is to understand **interactions of the earth, climate, and biosphere.** The physical features of the earth are in large part created by organisms, from soil to the very oxygen content of the atmosphere. Many of the impacts of organisms on the planet result from behaviors from the churning of the soil to dispersing plant seeds. Climate changes first impacting organisms include changes in temperature and in rainfall. The first responses of organisms to unfavorable conditions are behavioral. They can behave in ways that allow them to better tolerate change, or move to locations that have become more favorable. Climate change is likely to favor organisms that are already more flexible over those that are more specialized and less flexible in their behaviors. Advantages of generalists over specialists could have huge impacts on our living communities. Behavioral studies following these changes and their impacts are urgently needed.

Climate influences how organisms interact. Interactions are coordinated in space and time, a linkage that may be threatened when partners that depend on each other respond differently to climate change. For example, pollinators and flowers need to be in the same place and time, but may not be if the former arrive later than the latter blooms. Similarly, disease vectors may find themselves out of synchrony with their hosts. The responses to these kinds of dependencies depends on the partner's behavioral or evolutionary plasticity. There is no particular reason to suppose that dependent partners have similar potentials, so they could be differently impacted by climate change. Any disjunct in relationships caused by differential responses to environmental changes can have huge impacts on the biosphere. Therefore it is a topic we urgently need to study.

Finally, the behavior must be taken into account for **understanding biodiversity**, the fifth grand challenge. Organisms live in biomes and habitats where their needs can be met. This is an interplay of actions of many different species, from those we can see, like predators and prey, to those we can't like the parasites that influence behavior and abundance. The presence of humans and their associates can change how animals use their environment, with consequences throughout the biome. We are in the midst of a great extinction. Never before since humans have dominated the planet have we had so many invasive species throwing communities into crisis, and endangered species threatening to slip away entirely. Biodiversity is in crisis as we till more and more of our planet for food, or pave it for cities. Behavioral studies are crucial for answering basic conservation questions like the size of reserves, or how to mitigate the harm of barriers like roads by understanding behavioral propensities and plasticities of species.

Understanding behavior is the grandest challenge of them all, for it is the synthetic expression of the organism's interests in the context of what is possible.

Conclusions

Behavior is central to life. It is the phenomenon that interfaces all that is inside the organism to all that is outside of it. The first response to change by an organism is an action. Because behavior is visible and measurable, it reveals the outcome of complex inputs more clearly than nearly any other response variable. The inputs that determine behavioral choices are usually complex. They include the neurophysiology, ontogeny, and experience of the individual and its physical and living environment, including relatives, potential mates, other conspecifics, predators, prey, parasites, and microbes. Behavior is the phenomenon that explains how organisms have formed in the first place; interactions among primordial cells led to a potent mutualism and the formation of multicellular organisms. Behavior ultimately ties genotype to phenotype. Behavior impacts ecology and ecosystems. The first responses to climate change will be behavioral ones.

If nothing makes sense except in the light of evolution, as Dobzhansky famously said, that light shines brightest on studies that use behavior to understand what is important.

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