

## WORK IN PROGRESS: AN IN-DEPTH EXPLORATION OF AN ONGOING

The diversity of culture results not only from the ease with which societies elaborate or reject possible aspects of existence. It is due even more to a complex interweaving of cultural traits. The final form of any traditional institution, as we have just said, goes far beyond the original human impulse. In great measure this final form depends upon the way in which the trait has merged with other traits from different fields of experience. ...The possibilities are endless and the adjustments are often bizarre. The nature of the trait will be quite different in the different areas according to the elements with which it has combined.

—Ruth Benedict,  
*Patterns of Culture*,  
1934



FRANS DE WAAL

Powerful adult male macaques, such as this, and females ones as well, impartially break up conflicts among group members, often by simply approaching conflicts or using mild threats.

The development of [animal] form depends on the turning on and off of genes at different times and places in the course of development. Differences in form arise from evolutionary changes in where and when genes are used, especially those genes that affect the number, shape, or size of a structure. We will see that there are many ways to change how genes are used and that this has created tremendous variety in body designs and the patterning of individual structures.

—Sean Carroll, *Endless Forms Most Beautiful*,  
2005

# Complex Form Evolving

BY JESSICA FLACK

**Seventy-one years** and a huge disciplinary chasm separate Ruth Benedict—an anthropologist famous for her work on the culture and society of American Indians—and Sean Carroll—a biologist who studies the genetic mechanisms underlying the development of the adult fruit fly. Yet these brief excerpts reflect concern with a question so fundamental it is not only relevant to understanding the diversity of cultures and the evolution of fly development, but also the origin of life and the evolution of signaling systems. *Patterns of Culture* and *Endless Forms Most Beautiful* both take as their subject the question of how forms—organizations in the former case, organisms in the latter—are built, and how the rules of building influence complexity and diversity of structures we observe in the world. Beyond this fundamental question, Benedict and Carroll are united by an interesting hypothesis: complexity and diversity at any particular level are not so much the result of the enormous diversity in the underlying materials out of which a form is built, but in the way existing materials can be recombined.

Most contemporary research on the role of recombination in generating complex form concerns the evolution of animal development—that is, the study of the process by which an adult form “unfolds” or

develops from an embryo. There is almost no comparative research on rules governing the building of forms, to include, for example, viruses, fly body plans, animal societies, and corporations. And almost nothing is known about the role of recombination generally in this process, despite the common character of Carroll’s and Benedict’s remarks. That Benedict and Carroll both have favored a “recombination” hypothesis, hints, however, at the possibility of general construction principles agnostic to substrate that reoccur again and again because problems arising at higher levels recapitulate those at lower levels. In this essay, I will explore one such problem—conflict, and its role in generating complex forms. In doing so, I will consider the utility of recombination for solving problems posed by conflict.

A common misperception is that conflict is only a problem in systems composed of unrelated individuals or individuals with widely varying objectives, or in systems in which there is a division of labor and some jobs are more desirable than others. One of the biggest challenges to structural or functional integrity of nearly all complex adaptive systems, no matter how well integrated they appear, is conflict. One reason for the near ubiquity of conflict is the lack of perfect informational overlap between components, providing incentive for components to

replicate or persist even at the expense of the larger system from which they might be deriving benefits. This can cause what biologist Leigh Van Valen called the “red queen effect”—an evolutionary arms race in which components try to outdo one another. The outcome of an arms race is often (but not always) the evolution of concerted mechanisms for competing or for controlling the negative consequences of competition. The evolution of regulatory mechanisms translates into increased structural complexity—suggesting that selection for robustness (the ability of a system or its features to persist despite disruptions of critical components) can drive the evolution of increasingly elaborate forms. Finally, robustness is only one important feature of biological and social systems. The ability of cells, organisms, and societies to adapt to environmental change by invention and innovation is another, and the raw material for innovation is often provided by conflict. A challenge for biological

and social systems is to find the level of conflict that fosters invention, but does not jeopardize robustness. The following examples of conflict and its consequences in two very different systems—the genome and animal societies—illustrate these ideas.

## Conflict Across Systems

### *Intragenomic Conflict*

Transposons, also called “jumping genes,” are sequences of DNA that can switch positions in the genome by, for example, encoding a protein, called a transposase, that cuts the transposon out of the host or “donor” DNA and reinserts it elsewhere (pioneering research on transposons has been conducted by External Professor Nina Fedoroff and was the subject of her recent Ulam Lectures). Often, reinsertion will occur during the process of meiosis. After DNA replication, the chromatid (one of two identical strands making up a chromosome) containing the transposon is



Alpha male chimpanzee, Jimoh, impartially intervenes into a dispute among females, breaking up the fight without taking sides.



duplicated, resulting in two transposons: the original and a copy on the duplicate chromatid. The transposon on the original chromatid switches its position on that chromatid, leaving a gap. The host repairs this broken chromatid using the duplicated chromatid as a blueprint. This process results in the number of transposons increasing from one to three (the original that moved positions, the copy on the second chromatid, and a replacement for the gap created when the original moved positions).

By switching positions, transposons cause mutations. Transposons move around the genome and copy themselves without regard for the host, and are consequently considered “selfish genetic elements.” This can cause conflict not only with other genetic elements and other transposons, but also with host organisms. Hosts, in turn, have evolved conflict management strategies for dealing with transposons. For example, hosts suppress prevalent transposons, either by causing transposons to mutate, or by “silencing” them. The story, however, is more complicated than a simple arms race between transposons and host organisms. Although most inserts are harmful and selected against, transposons, by duplicating, deleting, or rearranging genes, are potentially a rich source of genetic variability. The transposon-as-genomic-alchemist is hypothesized to be important during times of stress and when the environment is changing rapidly because, by facilitating genomic rearrangement, the space of potential solutions can be more completely sampled. Finally, functions of transposons, such as their ability to cleave and rearrange DNA, have turned out to be very useful to hosts in some contexts.

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This DNA transposon is forming a characteristic stem-and-loop structure. Transposons are discrete segments of DNA that move around chromosomes joining together DNA segments that have no structural or ancestral relationship to each other. Their ability to recombine with dissimilar DNA segments gives rise to mutations, which, in turn, increases the diversity of genetic material available. They represent a mechanism for evolutionary change among biological systems.

For example, the evolution of the adaptive immune system found in vertebrates appears to have depended on the host co-opting the ability of transposons to recombine DNA. The adaptive immune system uses this generic recombination mechanism to build a multitude of slightly different components that play a critical role in recognizing antigens (substances that provoke an immune response). The production of many components with minor differences allows for the recognition of a much larger set of antigens and, consequently, makes the immune system more robust and adaptable to pathogens than it would be otherwise.

### *Behavioral Conflict*

In animal societies, conflicts over status and access to resources are common and can be resolved by combatants or through third-party intervention. In gregarious species, conflicts among pairs can spread to involve multiple individuals. In the case of large conflicts, containment and termination of aggression by third parties is important. In some societies, successful intervention relies on consensus among combatants about the intervener's capacity to use force. Consensus reflects a general perception that an individual is



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In 1979, the Egyptian-Israeli Peace Treaty was signed on the White House North Lawn. Egyptian President Anwar Al Sadat shakes hands with Prime Minister Menachem Begin. United States President Jimmy Carter helped negotiate the treaty by bringing the two leaders together at Camp David, Maryland.

powerful. In many macaque societies, the degree to which one individual perceives another as capable of using force is communicated using a special subordination signal. Group consensus about an individual's capacity to use force arises from the network of these signaling interactions, and this produces a power structure. The degree of variance in the resulting power distribution can modulate the cost to third parties of intervening into conflict. Third-party policing, a form of physically impartial intervention in which none of the combatants is treated preferentially by the intervener, appears to require a fat-tailed, or high variance, power distribution. This is because policing is intrinsically costly as the simple act of approaching a conflict increases the probability of being attacked. Individuals who are perceived by the group as very powerful (and are in the tail of the power distribution) run little risk of receiving aggression in response to their interventions and, consequently, can afford to break up fights.

Policing is critical to organizational

robustness because it controls (rather than completely suppresses) the frequency and intensity of conflict. Conflict management through policing enables individuals to build more integrated, larger, and diverse social networks providing critical social resources. Thus third party policing is an important social invention that promotes robustness and social complexity and yet allows for innovation by managing rather than eliminating conflict or pathologically eliminating components that only occasionally create problems. This invention of policing was itself made possible by two others: the invention of special signals communicating subordination and the coding of a fat-tailed power structure into the network of these signaling interactions. It was the combination of these three inventions that enabled pigtailed macaques to build oligarchical societies ruled by small groups of benign despots (the policers). In contrast, other macaque species



have uniformly hierarchical societies. These arise from the combination of subordination signals, a uniform power distribution (in which there are power differences but no individual is disproportionately powerful), and partial (rather than policing) interventions favoring one combatant over the other, used by third-parties to prevent group members from moving up the dominance hierarchy. Facultatively egalitarian societies arise when unstable power structures (due to the absence of subordination signals) are combined with fluid, short-lived leveling coalitions between group members.

### Provisional Principles

The previous examples illustrate two provisional principles concerning the role of conflict in the evolution of form. The first principle is *conflict is a complexity ratchet*. Behavioral conflicts among monkeys drove the evolution of an elaborate mechanism—third-party policing—for controlling the severity, frequency, and spread of fights, and in doing so promoted more elaborate and robust forms of socially valuable interactions among group members outside the conflict context. Intra-genomic conflict arising when transposons copy themselves throughout the genome led to the evolution of mechanisms in the host for transposon control and suppression, and also provided a generic recombination mechanism critical to the invention of the adaptive immune system of vertebrates.

A second provisional principle is *conflict drives invention and recombination of inventions produces innovation*. The diversity of organizational structures characteristic of the macaque genus appears to be due partly to variation in the properties of three critical social inventions, each resulting from the need to manage conflict: status signals, power structure, and third-party intervention. The ability of transposons to recombine and

reorganize DNA allows them to compete more effectively against one another, the host, and other selfish genetic elements. Transposon mechanisms for duplication, deletion, or rearrangement of genes, although costly to the host in the context of host-transposon conflict, proved useful to vertebrate hosts in the context of host-pathogen conflict by facilitating evolution of an immune system capable of responding to a larger number of pathogens. Thus we may have a generic recombination mechanism arising out of conflict that was co-opted by the competitor for use against yet other competitors in other contexts.

The issues discussed in this essay reflect one component of a larger SFI research collaboration led by Research Professors Doug Erwin, David Krakauer, and myself. Critical objectives of this collaboration include (a) accounting for the diversity and complexity of forms in the evolution of living systems, and (b) developing a theory of form transitions. Of interest is how the invention of new information-processing mechanisms and new control, robustness, and variation production mechanisms interact with the environment in the generation of organizational complexity and diversity. Also of interest is how robustness requirements, the availability of neutral space, niche construction, and conflict drive or impede these inventions. The project draws data and insights from a number of fields, including macroevolution; evolution of development; behavioral and cultural evolution; ecology; population genetics; game theory; computer science; and information theory; and builds on the work of other SFI researchers including Walter Fontana, Jim Crutchfield, Eric Smith, Geoffrey West, Erica Jen, Brian Arthur, Marc Feldman, Jennifer Dunne, Nihat Ay, and Jon Wilkins. ◀

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