

mate source of voluntary attentional control, but this is little more than speculation. Recent findings from monkey neurophysiology and functional brain imaging in humans are providing insights that will move us closer to answering these questions.

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PERSPECTIVES: ECOLOGY

Social Slime Molds Meet Their Match

Bernard Crespi and Stevan Springer

Alleles of genes that code for altruistic behavior face an identity crisis. Such behaviors are costly, and alleles that cause them can spread only if the benefits of altruism are preferentially directed to individuals that also carry the helpful allele. In most cases, altruistic individuals rise to this challenge probabilistically: They help relatives because their close genetic relationship makes them the best bet for carrying an identical allele. But even relatives are not a sure thing, and the cost of errant helping behavior could be avoided if alleles for altruistic behavior could directly recognize themselves in other individuals. Hamilton (1), in one of his legendary thought experiments, described three conditions that would allow a single gene to direct altruistic benefits toward a copy of itself in another individual. The three conditions are: (i) bearing a phenotype that advertises the allele's presence (such as a green beard), (ii) recognition of that phenotype in others, and (iii) an altruistic response (that is, preferential treatment) of those recognized. It was Dawkins (2) who coined the colorful metaphor "green beard" to denote such altruistic genes. Biologists had presumed that green-beard genes required too complex an integrated set of effects to have evolved. Their view changed, however, with the discovery of the fire ant *gp9* locus (3) and the poison-antidote system of bacteriocin-producing bacteria (4). But these green-beard genes appear to comprise multiple tightly linked loci, so a single gene that could code for character, recognition,

and response remained a theoretical curiosity. Enter Queller *et al.* (5) on page 105 of this issue with their description of single-gene green-beard effects in the slime mold *Dictyostelium*. Their work provides spectacular confirmation of Hamilton's musings and demonstrates that social behaviors thought too genetically complex even for altruistic metazoans like ourselves are present in the humblest eukaryotes ever to locomote over damp dirt.

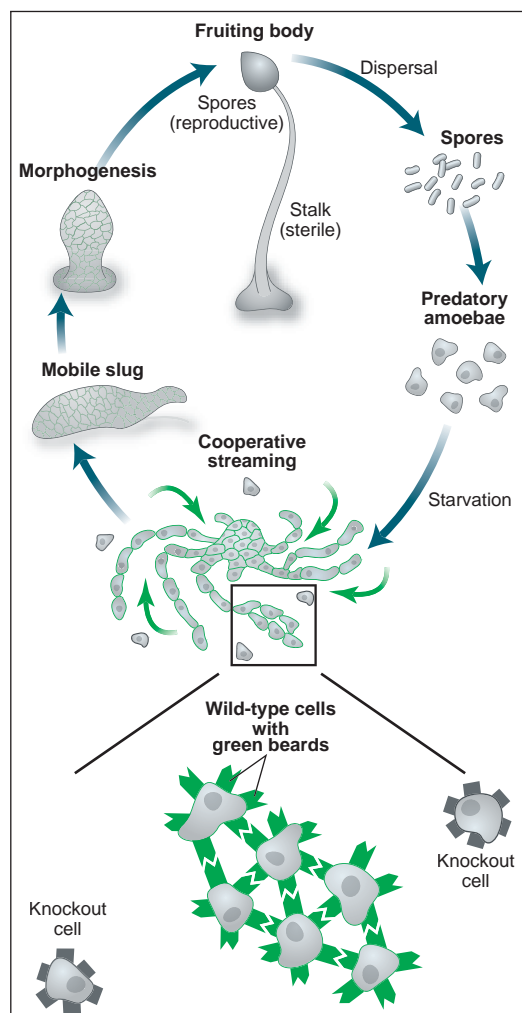
Queller *et al.*'s finding that social behavior in *Dictyostelium* is facilitated by green-beard effects has been a long time coming but, as it turns out, is not entirely unexpected. In a feat of inductive logic as remarkable as Hamilton's initial proposal, Haig (6) described the potential for green-beard genes in maternal-fetal interactions. He even predicted the functional class of protein—a homophilic adhesion protein that binds to itself—that would ultimately yield the first single-gene green beard. Homophilic cell adhesion proteins have exactly the properties required to operate as single-gene green beards. These proteins display themselves conspicuously on the cell surface and function as simple self-recognition systems, that is, they bind to copies of themselves expressed by other cells. Altruistic benefits to other cells can result directly via benefits from aggregation or movement, or indirectly through intimate connections between cell adhesion proteins and intracellular signaling processes (7).

How does simple "find and bind" activity generate multifaceted social effects in slime molds? *Dictyostelium* exhibits altruistic behavior in its simplest and most extreme form. Starving single cells coalesce into a mass, which transforms into a fruiting body composed of two parts:

reproductive spores and nonreproductive stalk cells that altruistically lift the spores high to aid their dispersal to a more food-rich environment (see the figure). Queller *et al.* recreated in the laboratory an evolutionary struggle for sporulation. They did this by pitting wild-type cells with a functional *csA* (contact site A) gene, encoding homophilic cell adhesion protein gp80, against knockout cells deficient in *csA* that showed defective adhesion. Their experiments revealed that wild-type, green-beard cells recognized and pulled one another into and along cooperative streams to the forming aggregate (mobile slug) via binding interactions among the homophilic cell adhesion proteins; but "clean-shaven" knockout cells were left far behind (see the figure). And with good reason—if knockout cells reached the aggregate, their reduced adhesion would displace them toward the trailing edge of the slug, an area that preferentially develops into spores. This would cause the good, green-beard cells to finish last. Such cheating is apparently disfavored, and green-beard alleles resist displacement by less adhesive mutants, just as green beards must have originally spread to supplant them. But might mutations also occur in beard genes encoding other colors, leading to clone-specific and thus nepotistic (rather than promiscuous) cooperation?

The discovery of molecular green beards has implications well beyond the niceties of slime mold social behavior. Single-gene green-beard effects could plausibly alter any biological process involving a close interaction between cells. Homophilic cell adhesion proteins were first studied because of their role in tissue differentiation. Tissue dedifferentiation leading to cancer is associated with expression of an altered suite of cell adhesion proteins, and metastasis correlates with reduced expression of this suite (8). Adhesion proteins whose expression is altered during tumor formation are all ideal green-beard candidates in a naturally selected although pathological context. Interactions between gametes can also be modified by green-beard effects. Cooperative sperm behavior, such as that of paired marsupial sperm (9) or wood mouse

The authors are in the Behavioural Ecology Research Group, Department of Biosciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada. E-mail: crespi@sfu.ca



sperm aggregations (10), may result from expression of a green-beard adhesion molecule. A single-gene green beard expressed on the surface of both sperm and egg could increase the rate of homotypic fertilization; divergence at this locus could result in the formation of species isolated by gamete incompatibility alone.

The effects of molecular green beards are not confined to cells: Evidence that interactions between biological units at multiple levels of organization are influenced by green-beard effects is accumulating. Such

Dancing cheek to cheek. The life cycle of the social slime mold *Dictyostelium discoideum*, showing the cooperative streaming of single amoeboid cells during times of starvation. The streaming cells form a mobile aggregate or slug, which metamorphoses into a fruiting body whose spores become dispersed and then develop into single amoebae. During cooperative streaming, the homophilic green-beard adhesion protein gp80 binds to gp80 molecules expressed by other cells. (Green-beard genes are those that are able to recognize and aid copies of themselves.) In this way, green-beard cells, but not knockout cells deficient in gp80, are disproportionately represented in the mobile slug and fruiting body.

interactions shape social interactions and colony organization in fire ants (3) and could result in maternal favoritism toward green-beard fetuses in placental mammals (6).

Dictyostelium began its scientific career as a model of development and has since become a celebrated example of a simple society; the discovery of single-gene green-beard effects is an important notch in the belt of this versatile organism. Direct cell-cell interactions, so important to aggregating slime molds, are fundamental to many biological processes. The rich diversity of molecules expressed on the cell surface hints at the wealth of information passed between interacting cells; parsing this information is one of the great challenges of modern biology. Understanding the mechanisms cells use to communicate will yield insights across all biological disciplines from development to disease, mate choice, speciation, and sociality.

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PERSPECTIVES: GLACIOLOGY

An Ice Sheet Remembers

Robert P. Ackert Jr.

The fate of humankind is linked to that of the remote West Antarctic Ice Sheet (WAIS) (see the first figure) through global sea levels. As ice sheets melt, sea levels rise. Even small changes in ice volume—a reduction in ice volume of 1% would raise sea level by 5 cm—could have significant impacts on the large percentage of the human population that lives near sea level.

The mass balance (that is, ice accumulation minus ice loss) of the WAIS therefore has important implications. But until recently, even the sign of the mass balance was unknown. Our knowledge is rapidly improving with the application of satellite radar altimetry, which can detect changes in surface elevation as small as 10 cm. It now

appears that in large and critical areas, the ice sheet surface is lowering and ice volume is decreasing (1).

Are we witnessing the early stages of rapid ice sheet collapse, with potential near-term impacts on the world's coastlines? To answer this question, we must view the new short-term measurements in the context of recent ice sheet history and ask whether the observed changes are unusual compared with those of the last 10,000 years. On page 99 of this issue, Stone *et al.* (2) provide a partial answer by reconstructing the recent history of a previously largely unexamined sector of the WAIS.

Ice sheets leave characteristic deposits and erosional features on the surfaces over which they flow. The distribution and age of these features, combined with ice sheet models, can be used to reconstruct the last deglaciation. Marine geophysical imaging of the seafloor and underlying sediments around Antarctica reveals abundant evidence

of the passage of ice. As a result, we know that the ice sheet grounding line (beyond which the ice floats on the ocean) advanced over the continental shelf during the last glacial maximum (LGM) (see the second figure). Radiocarbon ages from marine sediments overlying the glacial deposits suggest that retreat was under way by 14,000 years ago in the Ross Embayment (3–5).

Using radiocarbon-dated deposits from the ice margin at two coastal locations along the Transantarctic Mountains, combined with radar stratigraphy and ice flow modeling, Conway *et al.* (6) have calculated mean rates of grounding line retreat in the Ross Embayment between McMurdo Sound and the present grounding line along the Siple Coast (see the first figure). They found that over the last 7500 years, retreat has averaged 120 m/year—similar to that occurring at present.

The recently observed surface elevation changes may thus be part of a long-term trend that has continued despite the stabilization of sea level and climate following the final melting of the Northern Hemisphere ice sheets about 8000 years ago. Recent ice sheet dynamics appear to be

The author is in the Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA. E-mail: rackert@whoi.edu

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