arrive multiple times. All of the "smarts" of the net are at its periphery and embedded in "end-to-end" protocols (4) that are defined by applications.

Dave Parnas, one of the early software engineers, made a provocative and, we think, deeply important observation that helps to explain the success of the TCP/IP protocols. He pointed out that, when doing a design, the hardest decision to change is the one you make first, because all the subsequent ones to some extent depend on it (5). The decision for the TCP/IP protocols to do so little never had to be reconsidered, because it precluded so little.

Is there an analogy to the Internet message delivery design for security? Is there some minimal mechanism that would allow the construction of arbitrary end-to-end security protocols and allow an arbitrary number of these security protocols to coexist simultaneously? Is there a mechanism so simple that, while adequate to support the construction of security policies, does not preempt any decisions on the definition of security or how it is achieved? We think the answer is yes.

But why build multiple "end-to-end security protocols" rather than one really good one? We offer three reasons. First, different applications have different security needs: The requirements of law enforcement emphasize the integrity of the trail of evidence, the intelligence community is most concerned with disclosure of sources and methods, legitimate access to electronic medical records may change dramatically in emergencies, and so on. The point is that desirable security policy is a natural extension of the application; there is no single security policy that serves all needs equally well.

Second, multiple security protocols ensure that if one is broken, the others are not, or at least not in the same way. The current Internet clients form a predominantly Wintel/Cisco monoculture, so a single flaw can make almost the entire net vulnerable to the same attack. Incorporating multiple security policies and multiple implementations of the same policy can dramatically reduce this monoculture-induced vulnerability.

Third, the requirements of future applications cannot be predicted. In the same way as user-defined, end-to-end communications protocols allowed new applications that were not anticipated (such as the Web, search engines, and e-commerce), application-defined security protocols could accommodate unanticipated security requirements.

The lack of cybersecurity has been a consistent concern for 40 years. From time to time that concern flares up, and society resolves to "try harder," but the number of intrusions and their cost have only increased exponentially. It is time to reexamine the basic assumptions, like perimeter defense. Systems based on those assumptions have consistently failed. At least one alternative is an Internet-like minimal mechanism that enables application-defined security definitions.

Is such a minimal mechanism feasible? We think so. In particular, at the network level, an application can use any computable function to decide whether or not to provide its service to a client if it can be absolutely certain who is requesting it. There is a class of algorithms known as "cryptographic protocols" for doing this that require knowing the public key of an object—so we conjecture that by providing just a way of accessing the public key of an object, one could build an arbitrary end-to-end security policy.

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DEVELOPMENTAL BIOLOGY

Strategies to Get Arrested

Two gene families in the worm control survival strategies in response to stressful environmental conditions.

Akira Ogawa and Ralf J. Sommer

From bacteria to vertebrates, organisms can respond to changing environmental conditions by arresting their development. Animals in particular have invented a repertoire of diapause programs. As the environment can change at any step of an organism's life cycle, many independent strategies have evolved even within one species. Studies in the nematode *Caenorhabditis elegans* are beginning to show not only the diversity of these strategies, but also the genetic and genomic mechanisms mediating the response. On pages 994 and 954 of this issue, Kim *et al.* (1) and Angelo and Van Gilst (2) reveal how members of two multigene families—nuclear hormone receptors and G protein–coupled receptors—perceive and translate environmental cues to regulate diapause stages in the larval and adult reproductive stages, respectively.

C. elegans became a model organism in part because of the ease with which it can be cultured in the laboratory. On petri dishes with *Escherichia coli* as food source, this animal can complete its life cycle in as little as 3 days (see the figure). However, this is only observed when food is unlimited, a scenario that is unrealistic in the natural world. Not surprisingly, therefore, recent studies suggest that in nature, *C. elegans* follows a different path. Animals are most often found in the so-called dauer stage, a developmentally arrested stage (3). Lab-based studies revealed that the dauer stage occurs when larvae have little food or are exposed to high temperature or a high concentration of dauer pheromone, which is secreted constitutively by the members of a population (4). Although the existence of a pheromone was shown more than three decades ago, only recently have studies characterized it as a complex mixture of chemicals. Ascarosides, a class of glycosides with a dideoxysugar moiety and variable side chains, regulate entry of larvae into the dauer phase and also social behaviors in adults (5–8). Genetic studies have identified signaling systems involved in dauer regulation, including insulin and transforming growth factor–β signaling (9). However, how the dauer pheromone is sensed and how it is coupled to signal transduction have not been clear.

Kim *et al.* report that two chemoreceptors that are G protein–coupled receptors—*srbc-64* and *srbc-66*—mediate the effects of the dauer pheromone. When these two receptors, which are expressed in a pair of sensory neurons, were mutated, responses to ascarosides were impaired. However, a nematode strain carrying a mutation in both genes still retained some responsiveness to ascarosides, indicating that dauer pheromone perception involves multiple receptors. The results also reveal unexpected complexity in both pheromone production and sensing.

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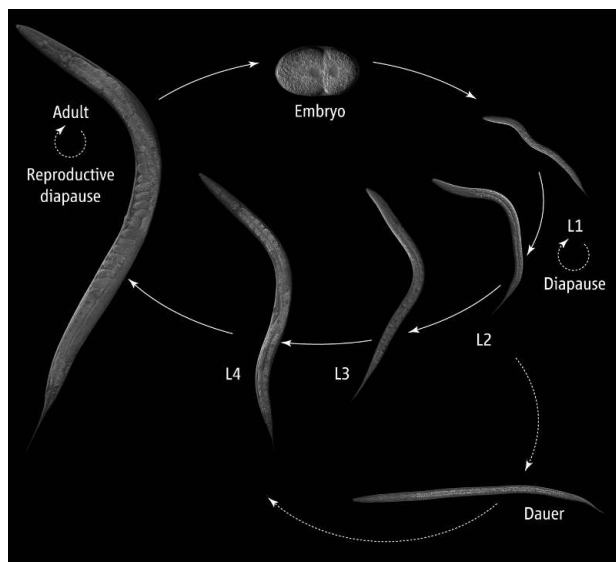
A worm's life. Self-fertilizing *C. elegans* lay eggs that complete embryogenesis in 14 hours (25°C). Four larval stages (L1 to L4) follow before a worm becomes an adult. Under stress conditions, young larvae enter the dauer stage, an arrested long-living dispersal stage. Young larvae can also arrest at the L1 stage, and adults can enter reproductive diapause.

The dauer stage of *C. elegans* is not only a survival strategy; it also helps dispersal of the organism by facilitating association with invertebrates. This phenomenon is thought to represent an evolutionary trend toward parasitism (*10*). Indeed, experimental support for a conserved endocrine mechanism that controls the formation of dauer and infective larvae in nematodes (*11*, *12*) indicates that a more detailed understanding of *C. elegans* dauer regulation might result in long-term practical applications.

Despite the long-standing interest in dauer development, *C. elegans* researchers have focused little on other survival strate-gies. This is surprising, as the dauer stage is an option to escape unfavorable conditions only for young larvae. Animals in other stages must find different means to cope with the environment. Angelo and Van Gilst describe an additional survival strategy of adult *C. elegans*. Starvation induces adult reproductive diapause, a delay of reproduction that results in increased longevity and protection of germ stem cells. By contrast, most other germ cells undergo programmed cell death (apoptosis), possibly providing nutrition (through resorption) required for survival. The gene *nhr-49*, which encodes a nuclear hormone receptor, controls adult reproductive diapause entry and exit, whereas the gene *daf-12* encodes another nuclear hormone receptor that controls dauer formation (*13*). These similarities strongly illustrate the importance of endocrine signaling in nematode survival strategies.

These two studies further establish nematodes as a unique model for studying animal survival strategies and the environmental regulation of life histories. One inter-esting aspect is that the genes involved in dauer pheromone sensing and adult reproductive diapause both belong to gene families that have undergone recent gene duplication (*14*, *15*). Such duplicated genes are believed to supply building blocks for new features without affecting preexisting biological systems. However, the function of duplicated genes is often hidden by redundancy, leaving open the possibility that the full complexity of environmental regulation escapes genetic analysis.

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OCEAN SCIENCE

Photosynthesis in the Open Ocean

A little-understood electron flow pathway helps cyanobacteria to adapt to high-light, low-nutrient ocean environments.

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Global primary productivity (the fixation of carbon dioxide, CO_2, into organic matter) fuels food production on land and in the sea. About half of this CO_2 fixation occurs in the sea, mainly by a type of phytoplankton called cyanobacteria (*1*). Recent reports (*2–4*) have shown that a key characteristic of oxygenic photosynthesis—the electron flux through photosynthetic reaction centers coupled to oxygen (O_2) evolution—is variable, thus uncoupling oxygen cycling from CO_2 fixation. This insight has implications for how phytoplankton have adapted to the marine environment and for how we measure the productivity of the oceans.

During oxygenic photosynthesis, energy is captured by linear electron transfer through two multiprotein reaction centers, or photosystems, coupled with reduction of CO_2 to sugars in the Calvin cycle. In a perfect world, the coordinated linear electron flow reactions (see the figure, panel A) would stoichiometrically couple O_2 production with CO_2 fixation, without a need for alternate pathways, and measurements of O_2 production or CO_2 fixation would estimate primary productivity, whereas fluctuations in fluorescence intensities would directly represent electron transport rates between photosystems (*5*). However, although linear electron flow from water to carbon is the most important pathway, because it results in CO_2 fixation, other pathways become important under suboptimal growth conditions, allowing photosynthetic organisms to balance input of light energy with production of adenosine triphosphate (ATP) and reductant.

Well-known examples of such pathways include the Mehler reaction, in which electrons are cycled around the photosystem I (PSI) complex, and the use of cytochrome oxidase to reduce O_2, forming water and ATP. Previously reported light-stimulated oxidation of photosynthetic electron carriers, or chlororespiration (*6*), was found to at least partially involve a third pathway using plastoquinol oxidase (PTOX). Recent papers (*2*, *3*) suggest that this pathway (see the figure, panel B) may be more widespread in open

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