one-pilin structures they examined were different. Sauer *et al.* (*2*) describe a complex between the PapD chaperone of *E. coli* and the PapK subunit of the P pilus assembly. PapK is an adaptor pilin subunit that connects the PapA subunits of the rod with the fibrillum composed of PapF, G, and H subunits. In contrast, Choudhury and colleagues (*1*) studied the structure of the FimC chaperone complexed with the FimH pilin component of type 1 pili. FimH has both a pilin domain to bind to its fellow pilins in the fibrillum and an adhesion domain that enables it to bind to the mannose sugars of host tissue surface glycoproteins.

Both reports offer atomic models of how the pilus rod is assembled. In these models, the pilin subunit is no longer complemented by the G1 strand of the chaperone; rather, each pilin subunit is complemented by the amino-terminal strand from another pilin subunit. By repeating this complementation, the authors are able to build a model with three subunits per turn, with an outer diameter of about 70 Å and an open central pore of about 20 Å. The implication for biogenesis of the pilus rod is that the amino-terminal strand of each pilin molecule, containing several hydrophobic side chains, replaces the hydrophobic side chains temporarily donated by the G1 strand of the chaperone. Thus, in the final pilus structure, every pilin subunit completes the immunoglobulin-like fold of the neighboring subunit (see bottom figure, previous page). During assembly of the pilus, the chaperone of a chaperoned pilin must be displaced by another pilin.

A complication that the authors encountered in building their pilus models is that in order to create the rod-like structure, the amino-terminal strand of each pilin subunit has to be oriented into the next molecule antiparallel to the neighboring F β strand, whereas the chaperone's β strand is parallel to the F strand in both crystal structures. Thus, if their compelling model for pilus assembly is correct, the complementation of the pilus subunit occurs by two different β strands (its own and the chaperone's), lying in opposite directions. This is a problem of intermolecular forces that is worthy of further study by computational chemists. The dilemma is akin to the difficulty in understanding the action of chaperones such as GroE that are nonspecific for their protein substrates. How can such chaperones perform a specific function with a range of substrate proteins?

The study by Choudhury *et al.* (*1*) raises another point. In the FimC–FimH chaperone-pilin complex, the FimH subunit actually contains two domains: the immunoglobulin-like domain that is complemented by the chaperone and a second sugar-binding domain. This sugar-binding domain—also built from antiparallel β-strands—contains a pocket into which a sugar analog can fit snugly. This presumably marks the sugar-binding site that enables the pilus to latch on to its host cell.

Thus, these two crystal structures illuminate much about how chaperones protect virgin proteins and how the pili of bacteria are assembled.

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PERSPECTIVES: ECOLOGY

A Tale of Big Game and Small Bugs

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For much of this century ecologists have puzzled over the fluctuations in numbers of animal and plant populations in the wild (*1*). Although usually irregular, these changes in population density can be remarkably cyclical, occurring repeatedly between well-defined upper and lower boundaries. Early theoretical ecologists proposed that populations could be regulated by a density-dependent feedback mechanism in which birth and death rates changed in response to an increase or decrease in population density (*2*, *3*). Birth rates would increase to exceed death rates in times of low population density, but would decrease to below death rates when population numbers were high. A central element of this feedback mechanism is the ability of the birth and death rates to operate with different lag times, potentially resulting in a cyclical rise and fall in population density.

By analyzing data on changing population densities in various organisms over many years, ecologists can address the causes and consequences of population dynamics. Thanks to the excellent bookkeeping skills of Canada's Hudson Bay Company, which kept detailed records of the fur trade between 1821 and 1939 (see the figure), ecologists have been endowed with long-term population data for many animals throughout Canada (*1*, *4*). Stenseth *et al.*, reporting on page 1071 of this issue (*5*), take advantage of the unique Hudson Bay Company time-series data set (and a second time series, from 1921 to the present, compiled by Statistics Canada, a government agency that keeps detailed statistics on forestry, agriculture, trade, etc.) to analyze population fluctuations in the Canadian lynx (*Lynx canadensis*). They found that the dynamics of lynx populations could be grouped according to three geographical regions of Canada that differed in climate and proposed that external factors such as weather had an influence on lynx population density. In a companion paper on page 1068, Turchin *et al.* (*6*) analyzed fluctuations in the population density of the southern pine beetle (*Dendroctonus frontalis*)—a pest responsible for destroying large tracts of forest in the southern United States (see the figure). In contrast to the lynx data, their time-series analysis—supported by field experiments—showed that predation was a crucial factor in determining the rise and fall of the beetle population. In both of these studies, the time-series analyses were critical to understanding the dynamics of the mammalian and insect populations.

Since the 1950s, ecologists have proposed that populations are limited either by extrinsic factors—such as weather, especially extremes of cold, drought, or rainfall—or by intrinsic factors—such as birth and death rates, or interactions with other species (prey, predators, or parasites) (*1*, *3*, *7*, *8*). The intrinsic factor hypothesis postulates that current and past population densities reflect the variations in renewal of the population, a view supported by the Stenseth and Turchin findings.

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Recent theoretical and empirical studies have started to combine the extrinsic and intrinsic hypotheses (*9*). Moran, an Australian statistician, attempted to correlate dependence on population density with external disturbances. His hypothesis (the Moran theorem) explained how two (or more) populations that showed density-dependent regulation could fluctuate synchronously. He suggested that stochastic (random) density-independent, but regionally connected, processes (such as weather) could cause synchronous variations in population size. This feature is clearly visible in the 10-year synchronous fluctuations in lynx populations from three different regions of Canada (Pacific-maritime, Continental, and Atlantic-maritime) (*5*). Synchrony in regional dynamics is less prominent in the southern pine beetle (*10*), although it is observed in large-scale fluctuations in many other forest pests.

The hunt for the causes of cyclical population dynamics, particularly in the Canadian lynx, has garnered a plethora of possible explanations—from solar activity (sunspot maxima) and external forcing (for example, adverse weather) to predator-prey interactions. Stenseth *et al.* have followed the Moran tradition, explaining the lynx population fluctuations in terms of both stochastic external factors (climate) and intrinsic density-dependent processes that affect birth and death rates. By analyzing the historic and modern Canadian lynx time series, the investigators were able to ask whether differences in structure between two Canadian ecosystems (the northern, open boreal forest and the southern, closed boreal forest) could explain the rise and fall in lynx population density. They also question whether regional climate variations could account for the observed patterns of synchronous population fluctuations. They conclude that density-dependent processes together with regional-specific variations in climate (related to the North Atlantic Oscillation) best explain the synchronous population fluctuations of the lynx.

A particularly important theoretical aspect of the population synchrony problem, exemplified here by the Canadian lynx, is provided by a recent contribution in *Nature* from Blasius *et al.* (*11*). They used a simple food chain model to explain the synchronized fluctuations in the snowshoe hare and lynx populations of North America. The well-established, continent-wide population synchrony was relatively easy to model yet was shown by the authors to be extremely complex.

The beauty of the Stenseth analysis is that it allows the exogenous and endogenous influences on the lynx time series to be disentangled. Turchin *et al.* have gone one step further and have designed a field experiment to prove the conclusions of their time-series analysis of the southern pine beetle. Prominent population oscillations are frequently observed in pest insects that attack trees and crops. The Turchin analysis reveals that predation is the driving force behind these oscillations, a finding that is clearly of great interest to population ecologists, forest economists, and foresters. The interactions between prey and their (specialist) predators or parasites is an important, although not the only, ecological factor underpinning these population variations. Theoretically, there should be a delay in the impact of predation on prey population oscillations (delayed density dependence). In such cases the mortality of prey due to predation will change depending on the density of the predator population.

In their field experiments, Turchin and colleagues investigated whether predation de facto could drive oscillations in forest insect populations. The 5-year study covered the rise, peak, and fall of one population cycle. They used cages to exclude predators in trees with known beetle densities and compared numbers of beetles in these trees with those in trees where predators were unhindered. They found that predators did indeed affect the southern pine beetle population but with a delay, suggesting that predation may be one of the causes of population oscillations in this insect. The authors predicted just such an outcome with mathematical modeling before they started their experiments (*12*). Their work also underscores the power of a combination of approaches—mathematical theory, time-series analysis of long-term observational data, and controlled experiments—to ecological problems.

Dynamic populations. A Canadian fur trapper in the 1700s (**A**). Fur pelts on display, the Hudson's Bay Company, Manitoba, Canada (1930) (**B**). The Canadian lynx (*Lynx canadensis*) (**C**). The southern pine beetle (*Dendroctonus frontalis*) (**D**).

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