condensates are proving to be an excellent test-bed for theories of quantum assemblies at finite temperatures. This is a subject of importance in a wide range of systems, including nuclear collisions and phase transitions in the early universe. The other crucial feature of the ultracold atomic condensates is their sensitivity to control by very modest strength fields, including laser fields. This makes it possible to manipulate and control their shape with surgical precision as has been shown in several recent experiments. External fields can be used to change the strength of the interactions between atoms, as was first shown by Wolfgang Ketterle's group at MIT (6). Atoms also have internal states into which the condensates can be transferred and retrieved at will.

The macroscopic coherence of the wave function was beautifully displayed in the earlier MIT experiments. Anderson and Kasevich (4) have been able to observe directly one of the most interesting and important effects: macroscopic quantum oscillations in a waveform. These Josephson effects have been observed and routinely used in superconducting junctions and more recently in superfluid liquid helium (6). They rely on the fact that a macroscopic wave can extend over an object such as a small wall. In the case of the Yale experiments (4) the wave extends over many wells of a potential formed by the standing wave of a laser field: an optical lattice. This is the advantage of ultracold atoms: The force due to a laser light field is enough to form a lattice in which the atoms' motion is confined and an extraordinary range of behavior investigated. This is done by first producing a Bose condensate of rubidium atoms with the methods that are now "standard". The atoms are then captured in the laser field that holds the wave function, spread across many potential wells. When atoms fall out of this arrangement, because of gravity, they do so in a way that has to be thought of as them moving coherently from all of the wells at the same time. This coherent escape produces beautiful interference effects in the form of pulses in the waveform that moves away from the lattice (see figure). The shape of the interference pattern reflects the nature of the coherence across the lattice and, hence, the macroscopic quantum coherence that is established. Small differences in the potential energy from one well to the next, due to the presence of gravity, give rise to a varying phase of the wave across the lattice and profoundly affect the shape of the output. This response to small changes means the system is exquisitely sensitive to weak forces and may thus be the basis for new types of measurements.

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PERSPECTIVES: POPULATION GENETICS

No Need to Isolate Genetics

Michael E. Soulé and L. Scott Mills

By the age of 16 every kid knows about the cultural taboos of incest—and that it is genetically contraindicated to marry your cousin, let alone a sibling. Avoidance of inbreeding is not limited to human beings, however. Many plants (1) and animals (2) evaluate relatedness (3) and avoid matings with close relatives. In a small isolated population, inbreeding occurs because of a limited number of mates to choose from, not from preferential mating among kin. This can lead to increased homozygosity, and, therefore, to homogeneity of the genes affecting the immune response (4) and to increased expression of recessive deleterious genes that reduce survival, fertility, and physiological vigor (5).

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Conservation geneticists have argued that in small populations the extinction probability should increase over time because these genetic effects magnify the extrinsic sources of jeopardy, including disease, inclement environmental conditions, and random demographic events. On page 1695 of this issue Westemeier *et al.* (6) provide one of the first extensively documented examples of these complex interactions pushing a formerly large population toward extinction.

Spring booming. Prairie chickens still thrive in a few areas of native grasslands, where courting males stomp their feet while making hollow moaning sounds.

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Westemeier *et al.* (6) monitored greater prairie chickens in Illinois for 35 years, noting a steep population decline as habitat was lost, as the population became isolated during the 1970s, and as the Illinois population reached a demographic low of less than 50 birds by the early 1990s. At the same time, adjacent populations in Kansas, Minnesota, Missouri, and Nebraska have remained comparatively large and widespread. Concurrent with the population decline, egg fertility and hatch success in Illinois prairie chickens also declined and was lower than in the neighboring large populations. The decline in egg hatching success in fully incubated clutches was correlated with a decrease in genetic variation, both for the Illinois birds when compared with the larger, nearby populations (7), and for the present population compared with historical samples collected before the demographic contraction (8).

Loss of genetic variation in small isolated populations is inevitable, as is an increase in the inbreeding coefficient of surviving individuals. Nevertheless, critics have pointed out that the theoretical inexorability of inbreeding in small isolated populations does not necessarily translate into inbreeding depression or an increase in the likelihood of extinction (9). For instance, such a small population is likely to be in dire straits already because of exposure to chance environmental events (droughts, storms, disease), or simply because of demographic accidents, including those that might skew the sex ratio. Although modeling results have demonstrat-

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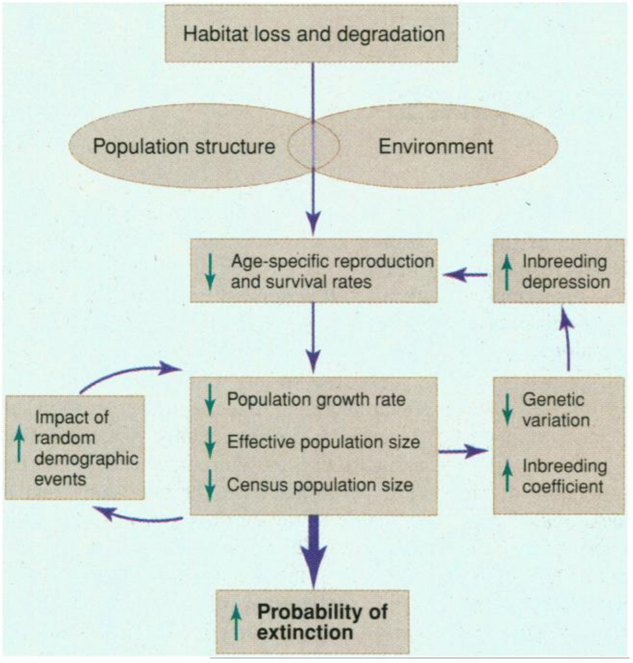

A simplified positive feedback extinction vortex. Habitat loss and degradation may also include invasion of exotics, overharvesting, or other factors. Population structure includes the age structure, sex ratio, behavioral interactions, distribution, density-dependent responses, physiological conditions, and intrinsic birth and death rates. Environment includes habitat as well as extrinsic factors that vary, such as weather, competition, predators, and food abundance. Each turn of the feedback cycle increases the extinction probability. The extinction vortex model predicts that some small populations are more likely to become smaller, and go extinct, each passing generation from the interaction of genetic and nongenetic factors.

ed how genetic and nongenetic random fluctuations are mutually reinforcing (*10*)—emphasizing how genetics interact with extrinsic factors—a polarization of opinion favoring one or the other of these two factors has persisted for more than a decade.

In part the controversy has raged because of the difficulty in untangling a complex web of causation. Some of the inherent complexity arises from the interaction of several loops of positive feedback (see the figure above). For example, as a population becomes isolated as a result of habitat fragmentation, it becomes increasingly inbred, which can lead to inbreeding depression—manifest as decreased reproduction and survival—resulting in fewer reproductive adults in the next generation (smaller effective population size), thereby amplifying the consequences of a population "bouncing downward" due to bad weather or the randomness associated with year-to-year fluctuations in breeding success. Such mutual reinforcement can lead to a higher rate of genetic fixation and inbreeding in each succeeding generation, and to iterative declines in reproductive output and survival. The expected decline to oblivion for small populations has been called the "extinction vortex" (*11*).

The Westemeier *et al.* study (*6*) is one of the first examples that brings together several of these components, including the likely role of inbreeding depression. Although any large-scale field study must wrestle with the difficulty of excluding other hypotheses that could cause demographic fitness changes, several lines of evidence support the inference that in this case genetic effects exacerbated the decline of the Illinois prairie chickens, as opposed to being merely correlated with it. First, the decline in demographic rates and population size occurred despite aggressive efforts (and some success) in the 1960s and 1970s to control predators and increase the quality and quantity of habitat; this suggests that the extinction vortex was set in motion by the isolation of this population during the 1970s. Second, translocations to Illinois of prairie chickens from large populations in neighboring states since 1992 have increased hatching success, without any obvious concurrent changes in environmental variables (unfortunately, the authors do not have data from Illinois × Illinois crosses to control for extrinsic factors affecting hatching success). The prospect that translocations have reduced inbreeding depression in egg hatching success is especially noteworthy because this single demographic rate surpasses all others in its effect on population growth rate in greater prairie chickens (*12*).

Although this study is unique in its comprehensive scope of factors and its temporal and spatial scales, it is consistent with a number of studies implying an important effect of inbreeding depression on population persistence. For example, inbreeding depression arising from small population size has been demonstrated in the wild for plants, vertebrates, and invertebrates (*13*). Furthermore, reduced genetic variation has been shown to reduce population growth (*14*) and increase probability of extinction (*15*).

Many questions remain, of course. Although we know that the costs of inbreeding range widely across species and time (*16*), we do not know much about how different demographic rates (for example, fecundity, egg survival, juvenile survival, adult survival) are affected by inbreeding for most species. We also do not know whether certain populations might become "adapted to inbreeding" as natural selection removes, or "purges," deleterious alleles (*17*).

Although it is becoming increasingly difficult to ignore the relevance of genetics to the extinction vortex, this understanding will not, by itself, address the main threat to biodiversity. This is because the most sinister actor in the extinction melodrama is neither genetics nor random population fluctuations; it is the loss of habitat and habitat quality, accompanied by overexploitation of biological resources, the increasing number of exotic species, pollution, and climate change. This said, researchers and managers can hardly justify a dichotomy that emphasizes one factor to the exclusion of all others (*18*). Small populations on the verge of extinction may well require aggressive acts of genetic intervention, including artificial gene flow and captive breeding.

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