

“knob” is a magnetic field applied perpendicular to the layers. Detailed dynamic and spatial information on the evolution of the electron correlations as a function of the applied field has been obtained. These data should help solve the mystery of the cuprates.

Hoffman *et al.* studied a cuprate superconductor in an applied magnetic field by a novel STM technology of atomically registered spectroscopic mapping. The field induces vortices in the superconducting order. Around each of the vortices, there is a superflow of electron pairs. An innovative analysis of their large amounts of STM data, with very high spatial and energy resolution, enables Hoffman *et al.* to factor out the substantial noise generated by chemical impurities introduced through doping and to test directly for orders other than superconductivity.

Theoretical studies pointed out (5, 19) that the suppression of superconductivity in the vortex cores should induce local magnetic order. This repulsion between the superconducting and magnetic orders also appears in theories of magnetic quantum phase transitions in the superconductor (4, 5, 20). Combining these past works with insights gained from neutron scattering experiments by Aeppli and co-workers (15, 21), Demler *et al.* (22) have pointed out that dynamic spin density wave correlations (like those in panel B, first figure) should be enhanced in the regions of superflow that surround the much smaller vortex cores. Static order in the associated charge density wave has been proposed (23), in coexistence with dynamic spin fluctuations and well-established

superconductivity (see the second figure).

Consistent with these expectations, the STM observations show a clear modulation with a period of four lattice spacings in the electron density of states around the vortices, in regions that also display the characteristic signatures of electron pairing associated with superconductivity. Moreover, the wave vector of this ordering is $2\mathbf{K}$, where \mathbf{K} is the wave vector for spin density wave ordering observed in neutron scattering (15) (albeit in a different cuprate superconductor). The observed field dependencies of the neutron scattering intensities (15, 17, 18) are also consistent with theoretical expectations (19, 22).

These observations are compelling evidence that the order competing with superconductivity is the first of those discussed above: A slight suppression of superconductivity reveals a modulation in observables linked to the electron charge density. This coexistence region between superconductivity and the competing order should yield interesting new insights into the fundamental properties of cuprates. Similar modulations should be observable around other regions of the sample where the density waves can be pinned, for example, near impurities within the Cu plane.

The scope for further studies using the magnetic field as a tuning parameter is also wide. It should be possible to tune the cuprates to the vicinity of quantum phase transition(s) associated with spin and charge ordering. Similar studies can also be carried out in other correlated electron systems, including electron-doped cuprates, organic superconductors, and intermetallic

compounds known as heavy-fermion materials.

The next challenge will be to use our improved understanding of the low-temperature properties of cuprate superconductors to formulate a theory of competing orders above T_c . Here many mysteries remain, particularly the microscopic origin of the “pseudogap” behavior, that is, the appearance of features characteristic of the energy gap of the superconducting state at temperatures well above T_c .

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PERSPECTIVES: ECOLOGY

Inbreeding and Metapopulations

Anthony R. Ives and Michael C. Whitlock

Probably the oldest observation about population genetics is that individuals produced by mating between close relatives are often less healthy than those produced by mating between more distant relatives. This inbreeding depression is so obvious that most human cultures prohibit marriage between close relatives, and animal breeders know to avoid inbreeding their animals. But it is only recently that the importance of inbreeding depression to

natural animal populations has been realized (1, 2). On page 485 of this issue, Ebert, Haag, and co-workers (3) show just how important inbreeding can be.

Ebert *et al.* studied natural populations of the water flea *Daphnia magna*, a small crustacean that lives in temporary rock pools. In a simple but clever experiment, these investigators took advantage of the fact that there are thousands of natural rock pools that potentially sustain *Daphnia* on the islands in the Baltic Sea. For 22 pools, they removed all *Daphnia* and then reintroduced 200 of them (the residents) with 200 from a different pool (the immigrants). There was enough genetic differentiation among pools to be able to distinguish ge-

netically among the residents, immigrants, and hybrids between them. After one round of sexual reproduction, the fate of these three different genotypes was determined by their relative fitness in the following year. During most of the summer *Daphnia* reproduce asexually, which allowed the fitness differences between the genotypes to be magnified by many generations of selection on genetically identical clones.

What they found at the end of the summer was impressive. In all of the replicates in which the hybrid genotypes were found, the frequencies of the hybrids increased, usually substantially, with the average relative fitness of hybrids being 36 times that of nonhybrids. The fact that the different immigrant populations were genetically distinct rules out the possibility that the observed hybrid success was caused by immigrants carrying superior genes. Furthermore, the experiment was performed in parallel in the laboratory with the same genetic pairs of

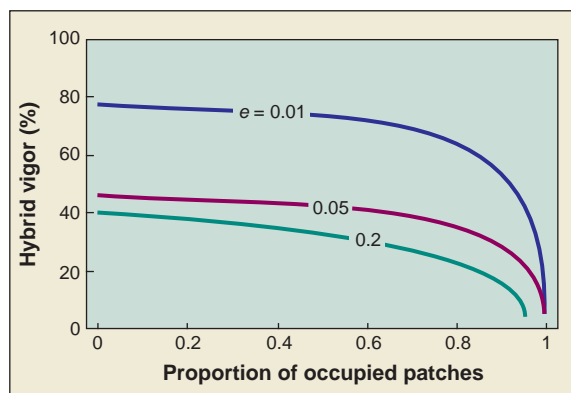
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residents and immigrants, ruling out any influence of interactions between genotypes and the local environment of the rock pools in explaining hybrid success. The remaining hypothesis is that the observed hybrid vigor was a direct result of their escape from inbreeding depression. This confirms that inbreeding depression can be large in natural populations.

The strength of inbreeding depression reveals a puzzle. With fitness costs so high, why hasn't natural selection purged the numerous deleterious alleles that cause inbreeding depression? The answer probably lies in the metapopulation structure of *Daphnia*. A metapopulation is a population of populations: The individuals in the same rock pool constitute a subpopulation, and all rock pools constitute a metapopulation of subpopulations linked by dispersal. If dispersal is low, then subpopulations remain genetically distinct, and weakly selected deleterious alleles can reach high frequencies in local populations (4, 5). The existence of these weakly selected alleles sets the stage for inbreeding depression. The semi-isolation of subpopulations means that they are likely to differ with respect to the deleterious alleles they harbor. Therefore, benefits accrue among the hybrid offspring of residents and immigrants, because the bad effects of any (partly) recessive alleles they receive from one parent are likely to be masked by the alleles from the other parent.

How common are metapopulations and the potential for strong inbreeding depression in other species? One of the hallmarks of metapopulations is the appearance and disappearance of subpopulations from habitat patches (for example, rock pools) as a result of frequent extinction and recolonization. Ebert *et al.* report that *Daphnia* subpopulations in rock pools have a 20% chance of going extinct each year, and because dispersal (recolonization) is low, only 20% of the suitable rock pools are occupied in any given year. Thus, the metapopulation structure of *Daphnia* affects not only its genetic properties but also its demography, as measured by its presence or absence from rock pools.

To compare the effects of metapopulation structure on inbreeding and demography, we calculated the expected hybrid vigor (measured as the percentage gain in relative fitness of individuals whose parents come from different subpopulations compared to individuals produced from parents in the same subpopulation) for a hypothetical species



A matter of inbreeding. Hybrid vigor versus proportion of occupied habitat patches for three different subpopulation extinction rates (e = probability of extinction per sexual generation). We assume that hybrid vigor is caused by many genes with mildly deleterious, partly recessive alleles (7). Migration of individuals into subpopulations and colonization of empty patches are assumed to be governed by the same processes. Although details of the curves depend on the particular assumptions we used in the calculations, the general patterns do not.

sharing many of the population characteristics of *Daphnia*. In the figure, hybrid vigor is plotted against the expected proportion of suitable habitat patches occupied by the species, which is determined by the rates of subpopulation extinction and recolonization. The key point of the figure is that, as the number of occupied patches increases, hybrid vigor remains largely unchanged until almost no empty patches remain. This means

that the genetic importance of metapopulation structure occurs even when recolonization rates are sufficiently high that the metapopulation structure is not apparent from the demography. The explanation for this is simple. From a demographic perspective, only a single disperser is needed to colonize a habitat patch, whereas many dispersers are needed to homogenize the genetics of distinct subpopulations.

These results suggest that “population genetic metapopulations” and the concomitant potential for inbreeding depression may be quite common—perhaps more common than “ecological metapopulations” whose demographies are dominated by extinction and recolonization. Ecological metapopulations might be quite easy to spot in nature; the genetic effects of spatial population structure are likely to be more cryptic. Ebert *et al.* found high inbreeding depression in a species that has a clear ecological metapopulation structure (6), yet it is likely that the same processes that lead to inbreeding depression occur for species that less obviously live in metapopulations.

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PERSPECTIVES: CELL CYCLE

A Trigger for Centriosome Duplication

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The centriosome is the cell's principal organizing center for microtubule assembly. Like DNA, the centriosome must be duplicated once and only once during each cell cycle. Centriosome duplication is important for assembly of the bipolar microtubule spindle to which replicated chromosomes are attached prior to cell division (mitosis). In the absence of centriosomes, the spindle appears to be assembled (1) but cells cannot undergo cleavage (cytokinesis) (2). During normal mitosis, each daughter cell inherits only one centriosome, thus ensuring that the

correct number of centriosomes will be available for the next round of cell division. One intriguing question that still plagues the “centriosome community” is how centriosome duplication is regulated. On page 499 of this issue, Matsumoto and Maller report that a surge of calcium ions followed by activation of calmodulin-dependent kinase II (CaMKII) is the trigger for centriosome duplication (3).

Several years ago, it was discovered that activation of the cyclin E-Cdk2 (cyclin-dependent kinase 2) complex at the G₁-S phase transition (restriction point) of the cell cycle allowed both DNA replication and centriosome duplication to proceed (4, 5). The activated cyclin E-Cdk2 complex together with the Rb tumor suppressor protein enables cells to move from G₁ into S phase. When phosphorylated, Rb

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