softening of a particular kind of crystal vibration, or mode in the phonon spectrum\(^7\). Polturak’s group thinks the same process causes the helium effect. The extraordinary magnitude of the peak in Fig. 1b is associated with the very low formation energy for crystal point defects in helium (\(-1\) meV) compared with b.c.c. metals (\(-1\) eV). This low formation energy for He suggests that both the concentration and the mobility of point defects, such as vacancies, might be greatly enhanced near the peak. Computer simulations by Polturak et al.\(^1\) suggest that the point defects responsible for the very fast diffusion may in fact be a type of interstitial structure in the crystal lattice rather than vacancies.

The acceleration of vacancy creep under a small stress (also called superplasticity by metallurgists) at a phase-transformation temperature is a well-established fact, but in metals the magnitude of such acceleration is nothing like that observed in helium. Polturak and colleagues\(^2\) have evidence that the presence of \(^3\)He enhances superdiffusion in \(^4\)He by further reducing the point defect formation energy. So in isotopic mixtures, the magnitude of the diffusion peak at the transition temperature is even greater than that shown in Fig. 1b.

The significance of these studies in helium is the unprecedented degree of enhancement of point defect concentration and mobility at a phase transformation. These findings are also relevant to melting theory, in that a very high density of point defects combined with a softened phonon mode can lead to melting, by reducing the shear resistance near the transition to the point where the solid becomes mechanically unstable. In their latest work\(^3\), the authors suggest a feedback mechanism in which the point defects in helium soften the phonon (vibrational) spectrum, and this in turn enhances diffusion and creates more point defects. This feedback mechanism, and a very high density of point defects to begin with, are crucial ingredients in producing a mechanical instability sufficient to generate melting; both are missing in rival theories of melting, of which there have been many over the years.

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**Daedalus**

**The insect plane**

Aviation engineers look with envy on birds and especially insects. Their flapping wings lift and propel them far more efficiently than the fixed wings of aircraft. One reason is their ability to exploit the subtleties of stalling.

If the angle of attack of a wing is increased, it ultimately stalls, with sudden, disastrous loss of lift. No fixed-wing aircraft dare risk stalling. But an insect with oscillating wings can exploit an intriguing loophole in the laws of aerodynamics. Accelerated at a high angle of attack into the stalling regime, a wing takes a short while to stall. And until it does, it generates enormous lift. By speeding into stall and out again at each flap, an insect wing develops amazingly high average lift.

So Daedalus is inventing a non-steady-state aircraft wing. A conventional wing could never be made to flap, of course. But it might be covered with a flexible elastic fabric, and this could be flapped by a system of rapid repeated inflation and collapse. It might even be made to flap spontaneously in the slipstream, as a flag does in the wind. But the ideal solution is simpler still. Instead of flapping the wing or its surface, Daedalus plans to flap the airflow around it.

Cunningly, he will generate this non-steady airflow from a non-steady propulsive source, a pulse-jet of the type used to power the old V1 missile. Its primitive motor drew in air through a one-way valve, and mixed it with petrol vapour in its combustion chamber. When the chamber was full, a spark ignited the mixture. The valve closed, directing the propulsive blast out through the tail-pipe. The valve then opened and the cycle repeated. So Daedalus’s new ‘pulse-wing’ aerofoil has a leading edge enclosed in cunningly shaped ducting, which acts as a long, thin pulse-jet combustion chamber stretching the length of the wing.

Each time the chamber fires, a sheet of hot gas blasts from the ducting, entraining the airflow round the wing. It speeds it up dramatically, and veers it upwards to put the wind into brief extreme stall, thus creating a sudden pulse of enormous lift. The craft is both propelled and held aloft by repeated pulses. To minimize noise and vibration, Daedalus hopes to drive his pulsed wing in a continuous, distributed manner. Each explosion will spread from the wing root out to its tip, by which time another explosion will be starting at the root.

David Jones
Speciation without isolation

Tom Tregenza and Roger K. Butlin

There is abundant evidence that new species can arise when a population of organisms is split into isolated elements. The occurrence of sympatric speciation — speciation without isolation — is much more contentious but is now set on firmer theoretical ground.

The rise of biomathematics, which led John Maynard Smith to say, “if you can’t stand algebra keep out of evolutionary biology”, has been a runaway success. In many fields, empiricists continually struggle to keep up with and verify the assumptions and predictions of modellers. An exception is the famously contentious topic of sympatric speciation — the process by which new species arise from coexisting as opposed to geographically isolated populations. There is growing evidence, particularly among ecologists, that sympatric speciation does occur in nature.

At first glance, sympatric speciation looks straightforward. If a lake contains two potential resources — say, large or small prey — then large or small predatory fish will do well while medium-sized fish will be at a disadvantage. This disadvantage to intermediates, termed ‘disruptive selection’, creates pressure for divergence into two populations of distinct ecological types.

In sexual populations, the stumbling block preventing sympatric speciation is that mating between divergent ecotypes constantly scrambles gene combinations, creating organisms with intermediate phenotypes (physical characteristics). This mixing can be prevented only if there is assortative mating, in which pairings between similar individuals are more common. With disruptive selection, this pairing pattern is selectively favoured, because it reduces the production of offspring that are less well adapted to their environment. But there is a barrier to the evolution of assortative mating — the shuffling of genes during gamete formation, which means that genes for mating preference and ecotype (size for instance) may get mixed up whenever an occasional mating between different types occurs. This creates individuals with a preference for the opposite ecotype, increasing gene flow between types and opposing speciation.

Modellers have sought to duck this problem by assuming one of two things — either that the genes responsible for ecological traits and mating preferences are so close together on a single chromosome that they are rarely mixed up by recombination, or that a single gene could both code for the trait and create a preference for partners with that trait. These are plausible assumptions for some situations, such as an insect shifting to a new host plant where it also mates. But in general they are not.

Two new theoretical treatments by Kondrashov and Kondrashov (KK, page 351 of this issue) and Dieckmann and Doebeli (DD, page 354) address these difficulties. Both present models in which there are several separate genetic loci for ecological traits and mating preferences (see Box 1 overleaf for details). With these more realistic assumptions, both predict that sympatric speciation can occur without very strong selection against intermediate forms.

There are two variants of the KK model. In the first, mating probability depends on how similar two individuals are for a single trait (such as colour); in the second, it depends on a match between male trait and female preference. In the DD approach, mating probability is determined by whether the ecological trait or a marker trait, with these loci exerting their influence through a separate set of mating loci. In all of the models, selection increases associations between ecological and marker traits, leading to sexual isolation between ecologically distinct populations (Fig. 1).

In the KK model, disruptive selection is assumed to favour the most extreme phenotypes, regardless of their absolute values. However, this does not fit with the example they give of selection due to two distinct
resources. For instance, if a lake contains large and small food items, and fish are initially all small (as in the KK model), then slightly larger individuals will be less efficient at eating small prey, but still hardly any better at eating large prey. Therefore, with two resources, selection does not simply favour the smallest and the largest individuals. It will favour both extremes only if the population begins at an intermediate size, or if there is competition between individuals.

In the DD model, disruptive selection explicitly arises from competition for a single resource — a potentially more common ecological situation. The resource is assumed to have a unimodal distribution such that its carrying capacity is highest when the entire population has a particular phenotype. Selection leads to the phenotype of all individuals initially converging on this point. This provides an explanation for the nagging problem in other models of how the initial low level of linkage disequilibrium — a greater-than-chance tendency for preferences and traits to be inherited together.

Although the models discussed here agree on the headline prediction that disruptive selection can drive sexual isolation, and result in sympatric speciation, they differ fundamentally in how they arrive at this conclusion. The DD model allows stochastic variation in genetic composition to create associations between preferences and traits. By contrast, the KK model is deterministic, and simply assumes an initial low level of linkage disequilibrium — a greater-than-chance tendency for preferences and traits to be inherited together. This difference changes the models’ predictions about the effect of the number of genetic loci underlying each trait.

In the DD model, the effect of number of loci is considered in terms of its effect on genetic drift. If more loci are involved, speciation tends to take longer because drift is weakened, giving fewer opportunities for chance increases in association between ecological and mating traits to trigger selection for assortative mating. In the KK model, the parameter considered is the strength of disruptive selection required to drive divergence. In this case, larger numbers of loci increase the chances of speciation because they increase the production of disfavoured intermediate phenotypes. The numbers of marker loci have the opposite effect, as fewer marker loci mean more extreme (and hence isolated) marker phenotypes. These differences make a direct comparison between the models’ predictions impossible, which is a pity: it is important to know how robust the predictions of the models are because they point to ways of identifying cases of sympatric speciation. T.Y. & R.K.B.

**Materials science**

**Superhard ceramics**

R. J. Brook

In contrast to the polymer scientist, who has the privilege of calling upon an ever-expanding array of compositions from which to choose, the ceramic scientist has had to devote years of intensive research to the refinement of a relatively limited number of systems. So it is exciting news to hear from Zerr et al. on page 340 of this issue that in one of these systems — silicon nitride — a new form of compound has been found. Moreover, the new cubic compound is potentially much harder than existing phases, offering considerable industrial scope for the material.

Silicon nitride (Si₃N₄) has two long-established crystal forms, α and β. In both, the central silicon is linked to four surrounding nitrogens in a tetrahedral array (Fig. 1a). The different crystal structures are then distinguished by the ways in which the set of tetrahedra are linked to one another. In Si₃N₄ each tetrahedron is linked to each corner to two others, conferring a greater degree of structural rigidity than for silicate systems where the tetrahedra (formed from silicon and four oxygens) are linked one-to-one at the corners.

In the ceramics community, Si₃N₄ has enjoyed an exceptional degree of attention largely because of its potential as a material for high-temperature heat engines. The excitement arises in part from its mechanical properties, such as greater strength and ability to resist mechanical failure when subjected to sudden temperature changes. It is also less brittle than many ceramics, owing to the way in which the crystalline grains in the material become acicular (that is, length ten times greater than width); the resulting interlinking improves the resistance to mechanical failure. Ceramics are traditionally prepared from powdered materials, and Si₃N₄ is no exception: the precursor material is shaped into a powder mass, which is then