Rapid speciation in an arthropod

The likely force behind an explosion of new Hawaiian cricket species is revealed.

Theory predicts that sexual behaviour in animals can evolve rapidly, accelerating the rate of species formation[1,2]. Here we estimate the rate of speciation in *Laupala*, a group of forest-dwelling Hawaiian crickets that is characterized primarily through differences in male courtship song[3]. We find that *Laupala* has the highest rate of speciation so far recorded in arthropods, supporting the idea that divergence in courtship or sexual behaviour drives rapid speciation in animals.

Identifying groups of organisms characterized by high rates of speciation can reveal factors that promote speciation. We used amplified fragment-length polymorphisms (AFLPs) to estimate a phylogenetic tree of *Laupala* (Fig. 1; for methods, see supplementary information). The topology of the tree and precise dating of the Hawaiian islands[4] enabled us to estimate rates of speciation.

The highest speciation rate, 4.17 species per million years, was found in a monophyletic clade from Hawaii Island (Fig. 1). This rate is more than an order of magnitude greater than the average estimated rate of arthropod speciation, calculated as 0.16 per million years[5], and is exceeded only by that of the rapidly speciating African cichlid fish[6].

Our results also reveal a successive reduction in speciation rates with clade age (to 1.26 Myr^{-1} and then 0.80 Myr^{-1}; see supplementary information). Such a decline is expected as older lineages suffer a greater amount of extinction, reducing the apparent number of species formed. Moreover, diversity in island lineages may be limited by island size[7], with speciation rates on older islands declining as islands reach maximum species capacity. In the Hawaiian islands, this effect is magnified as islands have eroded and subsided, becoming smaller over time[4].

By contrast, speciation on the actively growing and youngest island, Hawaii, seems to be in progress, as diversity in *L. cerasina* (Fig. 1) was probably masked by sampling a single population per species. Populations of *L. cerasina* are acoustically diverse[3], and more intensive analysis using AFLPs reveals several distinct genetic groups that correspond to acoustic and geographical variations[8,9]. We conclude that speciation on Hawaii Island is both explosive and ongoing.

Although the causes of speciation are difficult to ascertain experimentally, traits that distinguish closely related species provide important insight. In *Laupala*, closely related species are morphologically cryptic and distinguishable only in the pulse rate of their male courtship song, a secondary sexual trait used in mate attraction. Females prefer pulse rates of their own species[10], so divergence in male song reduces the chances of interbreeding between species.

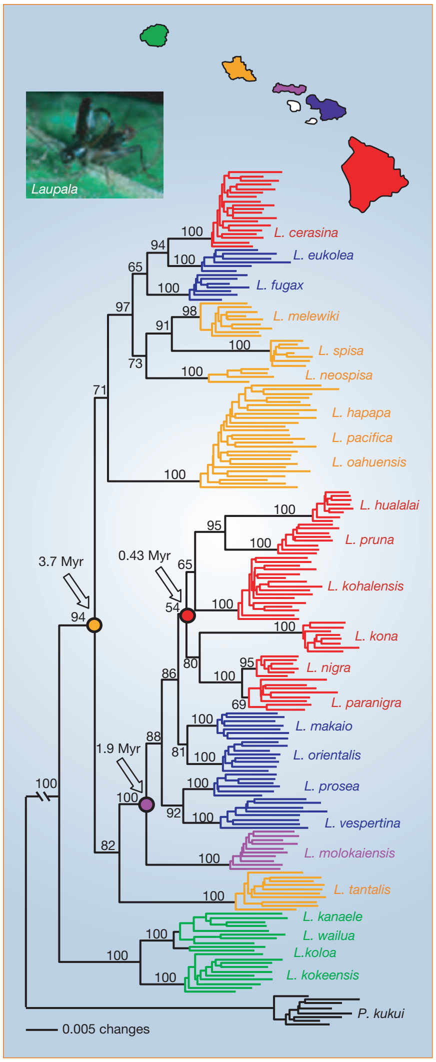

Figure 1 Phylogeny estimate based on analysis of amplified fragment-length polymorphisms for 25 of 38 described species of *Laupala* cricket. Terminal taxa are individuals; branches are colour-coded to indicate Hawaiian island of origin (green, Kauai; yellow, Oahu; purple, Molokai; dark blue, Maui; red, Hawaii). *Prolaupala kukui*, a member of the hypothesized sister genus to *Laupala*[3], was used as the outgroup. Arrows indicate the ages of three most recent common ancestors used to estimate rates of speciation. For further details, see supplementary information.

Closely related species of *Laupala* have no ecologically distinguishable features[3]: they are dietary generalists, without host-plant dependency, and thrive in both native and introduced Hawaiian forests[3,11]. They are frequently syntopic and synchronic, with males of different species often singing next to one another in the wild. It is therefore likely that the forces responsible for speciation in *Laupala* are those that cause the evolutionary divergence of secondary sexual traits.

If secondary sexual traits can evolve rapidly owing to sexual selection, then they could lead to accelerated rates of speciation[1,2]. African cichlid fish exemplify this process, with sister species differing primarily in male coloration, a secondary sexual trait. From this pattern, it has been argued that the spectacular diversification in African cichlid fish is driven by sexual selection[12].

Whether sexual selection has promoted the diversification in song in *Laupala* remains to be proved, and reinforcing selection on the mating system is a possibility; however, other mechanistic explanations can reasonably be ruled out. Ecological speciation, for example, occurs when isolated populations evolve traits that allow them to exploit resources in new environments[13]. By this mechanism, natural selection drives speciation, producing species that differ in ecological traits adapted to novel environments. In *Laupala*, such ecological characters do not distinguish species, so this model is unlikely to explain speciation in this group.

We have shown that the highest rate of speciation recorded so far in arthropods belongs to a group of crickets that differ primarily in secondary sexual traits, indicating that divergence in sexual behaviour may cause this rapid speciation[1,2]. AFLP technology allows high resolution of species relationships and unprecedented insight into the early stages of speciation. The best context in which to investigate the origin of species is provided by the early stages of speciation, before subsequent diversification.

Tamra C. Mendelson*†, Kerry L. Shaw*
**Department of Biology, University of Maryland, College Park, Maryland 20742, USA*
†Present address: Department of Biological Sciences, Lehigh University, Bethlehem, Pennsylvania 18015, USA
e-mail: tamram@lehigh.edu

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Oscillatory motion

Quantum whistling in superfluid helium-4

Fundamental considerations predict that macroscopic quantum systems such as superfluids and the electrons in superconductors will undergo oscillatory motion when forced through a small constriction. Here we induce these oscillations in superfluid helium-4 (^{4}He) by pushing it through an array of nanometre-sized apertures. The oscillations, which are detected as an audible whistling sound, obey the so-called Josephson frequency relation and occur coherently among all the apertures. The discovery of this property in ^{4}He at the relatively high temperature of 2 K (2,000 times higher than the temperature at which a related but different phenomenon occurs in ^{3}He) may pave the way for a new class of practical rotation sensors of unprecedented precision.

The Josephson effects in superconductors have received attention both as an aid to scientific understanding and for their technological importance[1]. Analogous effects, including Josephson oscillations, have been observed[2,3] in superfluid ^{3}He below 1 mK. However, detection of oscillations at the Josephson frequency in superfluid ^{4}He has remained elusive until now, despite almost four decades of attempts[4].

Superconductors and superfluids are both described by a macroscopic wave function that includes amplitude and phase, ϕ. A chemical-potential difference, $\Delta\mu = \mu_2 - \mu_1$, between two baths of superfluid separated by an aperture causes the phase difference, $\Delta\phi = \phi_2 - \phi_1$, to change in accordance with the Josephson–Anderson phase-evolution equation

$$\frac{d\Delta\phi}{dt} = \frac{-\Delta\mu}{\hbar}$$

where $\hbar$ is Planck's constant (h) divided by 2π and where $\Delta\mu/m_4 = \Delta P/\rho - S\Delta T$ (and m_4 is the mass of the ^{4}He atom, ΔP is the pressure difference, ρ is the mass density, S is the entropy per unit mass, and ΔT is the temperature difference). A non-zero $\Delta\phi$ results in a superfluid current, $I(\Delta\phi)$, through the aperture. If $I(\Delta\phi)$ is periodic for 2π, a constant $\Delta\mu$ causes current to oscillate through the aperture at the Josephson frequency $f_j = \Delta\mu/h$. The periodicity in $I(\Delta\phi)$ can occur if the aperture acts like an ideal weak link[3,5], in which case $I(\Delta\phi) \propto \sin(\Delta\phi)$, or by the generation of 2π phase slips[6], in which case $I(\Delta\phi)$ is expected to follow a sawtooth waveform.

The experimental set-up is shown in Fig. 1a (for methods, see supplementary information). We used an electrostatically driven diaphragm[2] to apply an initial pressure step between two baths of superfluid separated by an aperture array. The array consisted of 65×65 nominally 70-nm apertures spaced on a 3-μm square lattice in a 50-nm-thick silicon nitride membrane. After the pressure step, fluid flowed through the array and the chemical-potential difference relaxed to zero. When the output of a diaphragm position sensor, which monitored fluid flow, was connected to a set of headphones, we heard a clear whistling sound that passed from high to low frequency (audio recording in supplementary information).

By using Fourier transform methods, we extracted the frequency and amplitude of this whistle as a function of time throughout the transient. Immediately after the pressure step is applied, the temperatures on either side of the aperture array are equal and the entire $\Delta\mu$ is determined by the initial pressure head, ΔP_0. Figure 1b shows that the initial frequency is proportional to the initial chemical-potential difference. The slope of the line agrees, within the systematic error of our pressure calibration, with the Josephson frequency formula ($f_j = m_4\Delta P_0/\rho h$).

Oscillations resulting from 2π phase slips are expected to have a velocity amplitude $\kappa/2l$, where $\kappa = h/m_4$ is the circulation quantum and l is an effective length for one aperture[7]. If, in addition, the oscillation in each of the N apertures occurs coherently, the amplitude of the diaphragm-displacement Fourier component at f_j is

$$X_0 = \alpha\frac{\rho_s N\kappa a}{4\pi f_j \rho A l}$$

where A is the area of the diaphragm, a is the area of a single aperture, and ρ_s is the superfluid density. The factor α would be $2/\pi$ for a sawtooth waveform, or unity for a sinusoid of the same peak amplitude. We find $\alpha \approx 0.6$, independent of temperature in the range where, if T_λ is the superfluid transition temperature, $T_\lambda - T$ is between 1.7 and 2.9 mK.

We conclude that the oscillation is a coherent phenomenon involving all the apertures in the array, and is possibly sawtooth in waveform. This coherence is remarkable, because earlier work using a single aperture showed that thermal fluctuations in the phase-slip nucleation process destroy time coherence in the rate of phase slippage, so that no Josephson oscillation exists[8]. However, it seems that thermal fluctuations are suppressed for an array — an observation that calls for further investigation[9].

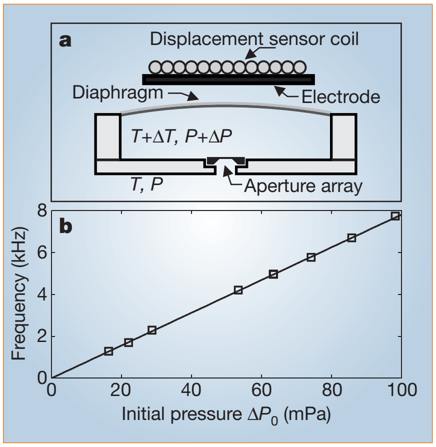

Figure 1 Quantum oscillations in ^{4}He. **a,** Experimental cell (see supplementary information for details). **b,** Whistle frequency plotted against the initial pressure, $\Delta P_0 = \rho\Delta\mu_0/m_4$. Temperature is in the range where, if T_λ is the superfluid transition temperature, $T_\lambda - T$ is 1.7–2.9 mK. A fit (solid line) to the data gives a slope of 78 Hz mPa^{-1}, with a systematic uncertainty of 20% arising from our pressure calibration. This agrees with the Josephson frequency relation $f_j = \Delta\mu/h$ value of 68.7 Hz mPa^{-1}. The oscillation is still present down to at least 150 mK below T_λ, where the healing length is much smaller than the aperture diameter and $I(\Delta\phi)$ is linear. The oscillation is presumably due to periodic 2π phase slips.

We have found that superfluid ^{4}He in an array of small apertures behaves quantum coherently, oscillating at the Josephson frequency. Because these oscillations appear in ^{4}He at a temperature 2,000 times higher than in superfluid ^{3}He, it may be possible to build sensitive rotation sensors using much simpler technology than previously believed[10–13]. This could find application in rotational seismology, geodesy and tests of general relativity.

E. Hoskinson, R. E. Packard, Thomas M. Haard
Physics Department, University of California, Berkeley, California 94720, USA
e-mail: packard@socrates.berkeley.edu

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