

and preferred traits of their parents. Such mating behaviour can arise through a process called sexual imprinting, in which young offspring learn to recognize their parents during a period of parental care and later use this learnt information to select a mate similar to their parents.

Sexual imprinting is common in bird species, and also in some species of mammal and fish. It provides a way of preventing recombination from breaking the association between mating preference and the preferred trait genes⁴. Imprinting can speed the establishment of reproductive isolation, which might lead to speciation. To identify factors governing the establishment of a variety of colour polymorphisms in *O. pumilio*, Yang and colleagues investigated whether imprinting occurs in this species, a behaviour that hasn't previously been reported in amphibians.

Females of *O. pumilio* lay eggs on the ground, on a leaf covered by other foliage, where they are fertilized by the male. During the following week, the male ensures that the eggs stay wet, and after the eggs have hatched, the female takes over the parental care. She carries each tadpole on her back (Fig. 1) to a water-filled bromeliad plant, and then returns to feed the tadpole with her unfertilized eggs until it is sexually mature.

The authors studied three colour types of *O. pumilio*, and carried out laboratory experiments involving three set-ups: tadpoles were raised by their biological parents, which were both the same colour; they were raised by their parents, which were of different colours; or they were raised by foster frogs that were not the same colour as the tadpoles' parents. For all three scenarios, when the female tadpoles became adults, female offspring preferred to mate with males of the same colour as the mother that had reared them.

Yang and colleagues demonstrated that male offspring had an imprinted behaviour, too. These frogs biased their territorial aggression towards males of the same colour as the mother that had reared them. Using simulations, the authors showed that, over many generations, the effect of imprinting on male and female behaviour has opposite effects on the fitness, and thus the prevalence, of a frog of its mother's colour in the population. If a male is the same colour as a female's mother, the probability that the female will mate with the male is boosted. However, when that colour becomes the most common type in the population, such males incur a survival penalty by being subject to competitive aggression from other males of the same colour. This aggression could explain how an alternative rare colour could persist in a population because, compared with males of the common colour, males of the rare colour would instead spend less time and energy on territorial defence, and presumably expend this energy and time on attracting females, increasing their chances of mating. Such 'rare-male advantage' can help to

maintain multiple forms of a particular trait in a population⁵.

A factor not considered by Yang and colleagues in their work is the role of natural selection owing to the frogs' bright colours. These frogs might be targeted by a range of predators. Predators often learn to recognize and associate particular colour patterns with toxicity through personal experience with a toxic prey. Thus, variation in such colours could limit the ability of a given colour to act as a warning because predators would need to learn to recognize each different warning colour⁶. Predation is therefore likely to boost the selection of the most common colour. Nevertheless, several forms of these frogs are equally toxic and conspicuous to their predators⁷. There is a hypothesis⁸ that when populations are sufficiently toxic and conspicuous, predators will be able to generalize across such bright colours and recognize them as being toxic. Sexual selection would then be free to drive the evolution of other bright colours.

It is interesting that both natural selection and sexual selection are affected by learning in the various interacting individuals — the frogs and the predators. Future experiments might investigate to what extent predators have a role in affecting the prevalence of the different frog colours.

The mechanisms that Yang and colleagues reveal to be acting in *O. pumilio* populations show how intricately natural and sexual selection affect processes that might drive

speciation, and indicate that neither process can necessarily be considered separately⁹. In this frog species, imprinting inextricably links both female mate preferences and interactions between males, ensuring that the prevalence of these imprinted behaviours tracks extremely closely to the frequency of the particular parental colour form in the population. Previous work has shown that sexual imprinting favours leading a population on a path towards reproductive isolation⁴. The evidence obtained by Yang and colleagues now shows how imprinting can also affect intra-sexual aggression and might help to maintain polymorphisms, thereby giving an extra boost for conditions that favour speciation. ■

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1. Yang, Y., Servodio, M. R. & Richards-Zawacki, C. L. *Nature* **574**, 99–102 (2019).
2. Reynolds, R. G. & Fitzpatrick, B. M. *Evolution* **61**, 2253–2259 (2007).
3. Felsenstein, J. *Evolution* **35**, 124–138 (1981).
4. Verzijden, M. N. *et al. Trends Ecol. Evol.* **27**, 511–519 (2012).
5. Tinghitella, R. M. *et al. Behav. Ecol.* **29**, 783–797 (2018).
6. Mappes, J., Marples, N. & Endler, J. A. *Trends Ecol. Evol.* **20**, 598–603 (2005).
7. Maan, M. E. & Cummings, M. E. *Am. Nat.* **179**, E1–E14 (2012).
8. Cummings, M. E. & Crothers, L. R. *Evol. Ecol.* **27**, 693–710 (2013).
9. Maan, M. E. & Seehausen, O. *Ecol. Lett.* **14**, 591–602 (2011).

CONDENSED-MATTER PHYSICS

Exotic state seen at high temperatures

The phenomenon of Bose–Einstein condensation is typically limited to extremely low temperatures. The effect has now been spotted at much higher temperatures for particles called excitons in atomically thin semiconductors. SEE LETTER P.76

ANDREY CHAVES & DAVID NEILSON

At sufficiently low temperatures, large assemblies of particles that are classified as bosons condense into a single quantum state. This remarkable phenomenon, known as Bose–Einstein condensation (BEC), can allow the particles to become a superfluid, whereby they flow without friction. Superfluidity has been seen in gaseous helium-4 and in ultracold atoms, but only at extremely low temperatures (a few kelvin). In the past few decades, there have been many attempts to achieve high-temperature BEC in semiconductors using electrically neutral composite particles called excitons, which

are bound states of a negatively charged electron and a positively charged hole (electron vacancy). On page 76, Wang *et al.*¹ report compelling experimental evidence that charge-separated excitons in a pair of atomically thin semiconductors can exhibit BEC at temperatures as high as 100 K.

When an electron is excited from the 'valence' energy states of a semiconductor material to higher-energy conducting states, it leaves behind a hole. The electrostatic attraction between electrons and holes can bind them into excitons. Separately, electrons and holes are particles that are classified as fermions, which cannot form Bose–Einstein condensates. But because a bound state of two

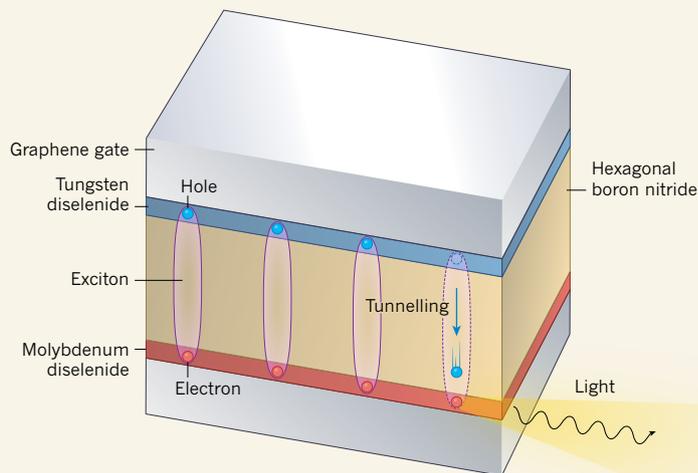


Figure 1 | Excitons in a semiconductor device. Wang *et al.*¹ study monolayers of the semiconductors tungsten diselenide and molybdenum diselenide that are separated by sheets of the two-dimensional electrical insulator known as hexagonal boron nitride. The two ends of this device consist of electrodes called gates that are made from graphene (a 2D form of carbon). The device contains composite particles known as excitons, which are bound states of an electron vacancy (a hole) and an electron. A hole in one monolayer can tunnel to meet an electron in the other monolayer, and merge with it, releasing energy in the form of light. The authors demonstrate that, at temperatures up to about 100 kelvin, several features of this light depend only on the exciton density. This observation suggests that the excitons are in a single quantum state — a phenomenon known as Bose–Einstein condensation.

fermions is a boson, excitons can condense.

The effective masses of electrons and holes (the masses that these particles seem to have when responding to electrical forces) are much smaller than those of atoms. As a result, excitons can condense at much higher temperatures than can ultracold atoms. In addition, the energies needed to split excitons into electrons and holes are greater than the thermal energy of the excitons even at room temperature, so excitons can be stable at this temperature.

When electrons and holes are in the same spatial region of a semiconductor, there is a high chance that they will recombine (merge), releasing energy in the form of light through a process called electroluminescence. Such electron–hole recombination usually happens so quickly that BEC cannot occur, but recombination can be avoided by separating the electrons and holes into two adjacent semiconductor layers. However, despite expectations, experiments over the past few decades that have searched for high-temperature BEC of excitons have been largely unsuccessful.

In 2002, charge-separated excitons were produced by confining electrons and holes in two disconnected slabs (quantum wells) of the semiconductor gallium arsenide, separated by a slab of another semiconductor, aluminium gallium arsenide². However, the electron–hole pairing interactions in such systems are weak because it is difficult to get the quantum wells close to each other and because the interactions are screened (weakened) by the presence of the other charges.

It was later recognized that, by replacing

the quantum wells with atomically thin sheets of the semiconductor graphene (a two-dimensional form of carbon), the separation between the layers could be dramatically reduced, thereby greatly strengthening the electron–hole pairing interactions³. To decrease the detrimental effects of screening, researchers proposed alternative atomically thin semiconductor layers; namely, two sheets of bilayer graphene⁴ or of molybdenum disulfide⁵. For the bilayer graphene, strong experimental signatures of BEC were reported last year⁶, but at temperatures of only about 1 K.

Wang and colleagues studied charge-separated excitons in a device that comprises two semiconducting monolayers (one of molybdenum diselenide and the other of tungsten diselenide), separated by a few atomic layers of the 2D electrical insulator known as hexagonal boron nitride (Fig. 1). This material limits the tunnelling of charges between the two monolayers to suppress electron–hole recombination. The two ends of the device consist of electrodes called gates that are made from graphene. By combining voltages applied to the two gates and a voltage applied to the tungsten diselenide layer, the electron and hole densities in each monolayer can be tuned independently.

The authors detected a large electric current associated with tunnelling of charges between the layers. This current depends only on the exciton density, suggesting that the excitons coordinate strongly with each other. The electron–hole recombination induces strong electroluminescence, the intensity of which has a critical threshold that depends on

the exciton density. This intensity also has a large enhancement that is strongly peaked at equal electron–hole densities. Such sensitivity of the electroluminescence enhancement to charge imbalance is consistent with exciton condensation.

These tunnelling and electroluminescence characteristics persist up to temperatures of about 100 K. Wang *et al.* therefore interpret this temperature as the transition temperature for BEC in this system, consistent with previous predictions⁷. Earlier this year, a theoretical investigation of superfluidity specifically for this molybdenum diselenide–tungsten diselenide system⁷ reported properties that quantitatively align with those in the current experiment, lending further credence to the authors' conclusions.

In 2D systems, the transition temperature for BEC is generally higher than that for superfluidity. Above the superfluid transition temperature, there are disconnected regions of superfluidity that persist up to the BEC transition temperature. Both of these temperatures increase linearly with exciton density, at rates that depend on the electron and hole effective masses, but the BEC temperature increases much more quickly than does the superfluid temperature. For this reason, Wang and colleagues' measurements, which are sensitive to BEC, reveal condensation at high exciton densities (of about 10^{12} per square centimetre) at temperatures up to 100 K.

Superfluidity could not be probed directly in the current experiment. But this is an exciting challenge for future work. Conclusive evidence for superfluidity could come from direct measurements of electric current flowing in opposite directions along the two layers, using independent electrical contacts for these layers.

The authors' molybdenum diselenide–tungsten diselenide double layer is a straightforward semiconductor system. As a result, it is suitable for future condensate-based optoelectronics and ultrafast devices, and paves the way for the search for exciton-mediated high-temperature superconductivity. ■

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1. Wang, Z. *et al.* *Nature* **574**, 76–80 (2019).
2. Butov, L. V., Lai, C. W., Ivanov, A. L., Gossard, A. C. & Chemla, D. S. *Nature* **417**, 47–52 (2002).
3. Min, H., Bistrizter, R., Su, J.-J. & Macdonald, A. H. *Phys. Rev. B* **78**, 121401(R) (2008).
4. Perali, A., Neilson, D. & Hamilton, A. R. *Phys. Rev. Lett.* **110**, 146803 (2013).
5. Fogler, M. M., Butov, L. V. & Novoselov, K. S. *Nature Commun.* **5**, 4555 (2014).
6. Burg, G. W. *et al.* *Phys. Rev. Lett.* **120**, 177702 (2018).
7. Conti, S., Van der Donck, M., Perali, A., Peeters, F. M. & Neilson, D. Preprint at <http://arxiv.org/abs/1909.03411> (2019).