Figure 1 | The strawberry poison frog *Oophaga pumilio*. Yang *et al.*[1] reveal that a learning process called imprinting occurs in this species, in which the behaviour of offspring is influenced by the colour of their mother. Imprinting occurs during the period of parental care of the developing offspring. An example of maternal care is the transport of tadpoles on their mother's back, as shown in this image of *O. pumilio* from Costa Rica.

EVOLUTION

Frog mothers' powerful influence

It has now been found that mothers of a species of frog affect the behaviour of their offspring — influencing female mating preferences and aggression between males. Such behaviours might lead to the formation of new species. SEE LETTER P.99

MACHTELD VERZIJDEN

The ability of a species to maintain many different types of individual in a population, known as polymorphisms, is intriguing because rarer forms must have some selective advantage to be preserved. Establishing diversity in a species through the presence of polymorphisms can provide a step towards speciation (the formation of new species). On page 99, Yang *et al.*[1] reveal a surprising mechanism that affects the maintenance of colour polymorphisms in the strawberry poison frog (*Oophaga pumilio*). The finding has implications for our understanding of evolution.

Oophaga pumilio (Fig. 1) lives in Central America, and frogs of this species have many widely differing types of skin colour. These bright colours warn predators that the frogs are toxic. The colours have another important role, in that females have strong preferences for the colour of males when choosing their mate[2]. Usually, for any given species, females' mating preference for a type of male drives a rise in the prevalence of the most popular female-preferred polymorphism (such as a male colour). Thus, colour selection by female mating preference is probably not sufficient to explain how multiple colour polymorphisms are maintained in *O. pumilio*.

Polymorphisms that are perpetuated over many generations could be a route to the formation of a separate species if males and females choose to mate only with their own type. However, one issue that affects the chances of such reproductive isolation arising is the pattern of co-inheritance of the genes that affect mating preference and the genes responsible for the preferred trait. A process that shuffles genes, termed recombination, occurs when egg and sperm cells are formed, and this results in each egg and sperm cell having a unique combination of the parental versions of genes. Recombination could disrupt the co-inheritance of the versions of genes affecting mating preferences and those that affect the preferred trait[3], thereby influencing the success with which the genes giving rise to the preference and to the preferred trait might be co-inherited.

One mechanism that could help to boost the likelihood of co-inheriting the preference and the trait together is if individuals learn to prefer to mate with individuals that are similar to their parents, because the individuals' offspring would inherit the mating preferences 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 genes[4]. 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 population[5].

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 colour[6]. 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 predators[7]. There is a hypothesis[8] 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 separately[9]. 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 isolation[4]. The evidence obtained by Yang and colleagues now shows how imprinting can also affect intrasexual aggression and might help to maintain polymorphisms, thereby giving an extra boost for conditions that favour speciation. ■

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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