that closely resembled one another, but it was left to his contemporary Fritz Müller to provide a complete explanation. Müller's argument was based on 'strength in numbers' — unpalatable species may evolve similar appearances simply because this allows them to share the cost of teaching predators to avoid them[3].

Textbooks generally treat these two forms of mimicry as distinct phenomena, with deceitful batesian mimics exploiting the signals of unpalatable models, and honest müllerian mimics mutually reinforcing the meaning of their shared signals. However, generations of researchers have debated what type of mimicry occurs when the two or more unpalatable mimetic species do not have equal palatability[4,5], and whether batesian and müllerian mimicry represent endpoints of a continuum (Fig. 1). In particular, could a parasitic form of müllerian mimicry (quasi-batesian mimicry) arise, with weakly unpalatable mimics undermining the effectiveness of the signals of the more unpalatable prey[4,6]?

Rowland *et al.*[1] now provide some empirical answers, but also highlight a complication long anticipated by theorists. In their experiments, the authors allowed individual wild-caught great tits (*Parus major*) to forage for prey in the form of pieces of almond. The pieces of nut were wrapped in paper marked with a simple symbol, and were distributed at random over an aviary floor. Sixty palatable prey were always provided. The rest of the prey consisted of systematic mixes of highly unpalatable 'models', moderately unpalatable mimics and entirely palatable mimics. High and moderate levels of unpalatability were generated by soaking the almonds in concentrated and dilute chloroquine phosphate solution, respectively. Like the models, the palatable mimics were always wrapped in paper marked with a solid black square, whereas the moderately unpalatable mimics carried either a solid black square (perfect mimics) or a curvier, diamond-shaped black symbol (imperfect mimics) (see Table 1 on page 64). In all instances, individual birds were allowed to forage for 50 prey items before a trial was complete.

Rowland *et al.* found that increasing the number of moderately unpalatable mimics reduced the overall proportion of highly unpalatable models that were attacked, whether the mimic was perfect or imperfect. Likewise, the presence of the highly unpalatable model reduced the 'mortality' of moderately unpalatable mimics. From these results, it might at first seem that all types of unpalatable prey are engaged in a mutually beneficial müllerian relationship. Yet when the number of palatable mimics was increased, the mortality of the highly unpalatable model stayed approximately constant — thus, even the batesian mimic was non-parasitic.

What drives this tendency towards mutualism? Adding more mimics to the system inevitably reduces the per capita mortality of the entire prey population because a fixed number of prey items were always attacked. The impact of these simple dilution effects has rarely been explored experimentally, but has long been predicted by theory[7]. For example, mathematical calculations predict that increasing the density of a palatable (or moderately unpalatable) mimic while keeping the model density constant (as did Rowland *et al.*[1]), can increase both the mimic and model survivorship simply because more food is available[8].

In contrast to the findings of Rowland *et al.*, the only other experiment[9] to investigate quasi-batesian mimicry found that increasing the density of moderately unpalatable mimics actually increased the mortality of the more unpalatable model. Yet in this earlier experiment the overall prey densities were kept constant, so any increased tendency of predators to attack models would not have been masked by increases in food availability. Nevertheless, this cannot be the whole story because, by statistically controlling for the likely effects of dilution, Rowland *et al.* found that an increase in the density of moderately unpalatable prey had no significant effect on the probability that the birds would attack an individual model on encounter.

So, like well-behaved intermediates, the moderately unpalatable mimics neither reduced nor enhanced the attack rates of predators on the models following encounter, but increasing mimic availability did reduce the overall death toll. Perhaps the educational benefits of two unpalatable prey types sharing the same signal were roughly cancelled out by hungry or insensitive birds attempting to eat moderately unpalatable, yet nutritious, mimics. If so, then mimicry can indeed be considered as a continuum. Whether real mimics exhibit such moderate levels of unpalatability to predators is another question, but it seems reasonable to suppose that some do.

Certain unconventional theories of mimicry have been based directly on dilution phenomena[10], but to understand the evolution of mimetic signals I believe it is generally more informative to control for its effects. For example, one reason for the interest in quasi-batesian mimicry is that it can potentially explain the co-occurrence of several distinct forms of the same species of a moderately unpalatable mimic[6]. Rowland *et al.*[1] did not compare the survival of a moderately unpalatable mimic with a rare mutant form that resembles a different unpalatable model. However, the fact that predator behaviour towards models was largely independent of the density of unpalatable mimics indicates that no selection for multiple forms of the mimic would occur in this system.

Whatever the underlying mechanism, Rowland and colleagues' results suggest a process of 'advergent' evolution[5], in which the more weakly defended mimic evolves to resemble the better defended model, without markedly changing the way predators treat the model. I suspect that many müllerian mimicry systems

50 & 100 YEARS AGO

50 YEARS AGO

La Gomera is one of the Canary Islands, lying in the Atlantic off the west coast of North Africa... Apart from a single road, which links San Sebastian, the capital, with the other three towns, the only means of travel between most points on the island is by rough paths which are little better than goat tracks; communication on the island is a great problem. But the Gomeros do communicate freely, across their ravines and from the valleys to the mountaintops... Long ago the Gomeros contrived an elegant solution to their problem; namely, a whistled language by which they speak to each other across miles of disjoined terrain. The *silbo*, as this language is called, is not a mere code or signal system, but a version of Spanish. It has extraordinary carrying power: it can be heard and understood clearly over far greater distances than shouted talk. On a windless day any practised *silbador* can be heard more than a mile away. A good performer can whistle messages three miles or more.
From *Nature* 6 July 1957.

100 YEARS AGO

Resort to experiment must be had in order to trace more accurately the circumstances associated with the spontaneous occurrence of cancer both in individuals and in families. The removal by surgical means of cancerous tumours occurring spontaneously in mice prolongs their lives and has enabled us to breed from them; we have, therefore, now the means of observing descendants of mice of known cancerous parentage, and by successively crossing other spontaneously affected animals with the offspring of cancerous parents, we can concentrate the hereditary tendency, if it exists. This concentration in large numbers of animals of a known age and in a known amount should enable us, in the course of a few years, to determine whether there is a family or only an individual tendency to the disease.
From *Nature* 4 July 1907.