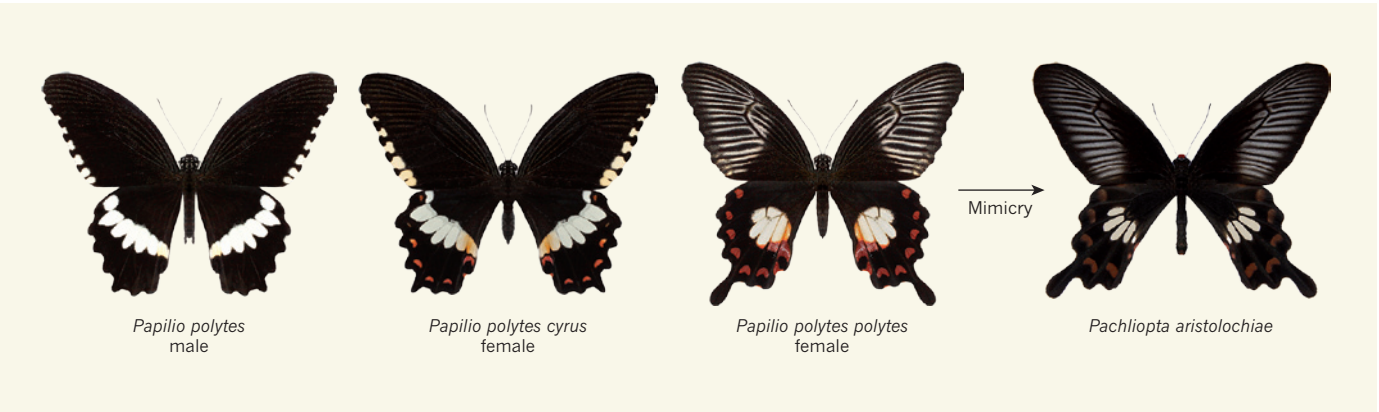
EVOLUTIONARY BIOLOGY

Sex, lies and butterflies

Variation in an evolutionarily conserved sexual-differentiation gene, *doublesex*, has been found to explain how females of one species of butterfly mimic the colour patterns of several toxic species to avoid predation. SEE LETTER P.229



KRUSHNAMEGH KUNTE

Figure 1 | Female-specific mimicry. Males of the swallowtail butterfly species *Papilio polytes* exist in one form, but several female forms co-occur in the same population. Females with the *cyrus* form look like males, whereas other female forms mimic the colour patterns of distantly related toxic species, such as the *polytes* form, which resembles *Pachliopta aristolochiae*.

DAVID W. LOEHLIN & SEAN B. CARROLL

Biological mimicry, in which one species gains an advantage by closely resembling another, unrelated species, is one of the most spectacular phenomena in nature. Expert impostors such as the cuckoo, milk snake and bee orchid have long fascinated naturalists and have played an important part in the development of evolutionary theory. Indeed, in the years immediately after the publication of Charles Darwin's *On the Origin of Species*, Henry Walter Bates[1] and Alfred Russel Wallace[2] recognized that butterfly mimicry was an obvious adaptation that could be explained only by natural selection. For the next 150 years, however, the mechanisms that generate these striking patterns eluded biologists.

But no longer — there has been a burst of breakthroughs[3,4] in this long-standing mystery. On page 229 of this issue, Kunte *et al.*[5] reveal that the remarkable ability of females of a swallowtail butterfly species to closely match the colour patterns of several unrelated butterflies is due to variation at a single genetic region: the butterfly version of the well-studied *doublesex* regulatory gene.

In the classic case of 'Batesian' mimicry[1], the warning colours of unpalatable or toxic butterflies are co-opted by non-toxic free-rider species. Among some swallowtail butterflies (genus *Papilio*), Wallace described an intriguing twist in which mimicry is limited to females[2]. Further studies showed that several discrete female forms, each resembling the warning colour pattern of a different toxic butterfly, often co-occur in a population alongside non-mimetic females and males[6] (Fig. 1). Although it is still not known why one species can maintain several different mimetic and non-mimetic patterns, the inheritance of this variation is surprisingly simple[2]: female colour patterns stay intact in genetic crosses within, but not between, populations, with each pattern assorting as one of two possible variants from a single genetic locus[6].

Kunte *et al.* bring swallowtail Batesian mimicry into the molecular era by showing that the differences between female mimetic forms in *Papilio polytes* are tightly associated with genetic variation around the *doublesex* locus. This gene is a particularly satisfying explanation for the evolution of sex-specific colour patterns, because genes of the *Dmrt* family (which includes *doublesex*) control aspects of sexual differentiation in most animals[7]. The *doublesex* gene basically acts as a switch. Specifically, in the best-studied *doublesex* gene (that of the fruit fly *Drosophila melanogaster*), different RNA transcripts are produced in males and females by a process known as alternative splicing. The male and female transcripts encode distinct protein isoforms that are thought to activate or repress different sets of genes, leading to sex-specific differentiation[7,8].

How could intricate wing-pattern variation derive from this single genetic signal? In principle, different female wing-pattern gene variants could derive from mutations that alter *doublesex* transcription, splicing or protein structure. Kunte and colleagues report that the swallowtail *doublesex* transcripts are also alternatively spliced in different sexes, but they find no evidence for splicing differences between mimetic forms. Rather, they find several mutations in protein-coding sequences, and speculate that these could alter the structure and activity of the Doublesex protein.

However, the authors also make the intriguing observation that colour stripes in the forewings of mimetic females are accompanied by a striped pattern of Doublesex expression. This raises the strong possibility that changes to this pattern of *doublesex* expression are the cause of the different mimetic forms. This inference is grounded in insight into the mechanics of the *doublesex* gene in other insects. Specifically, rather than signalling 'male' or 'female' in every cell, *doublesex* is elaborately regulated and active in only certain cell populations, including those that make structures that differ between the sexes[8,9]. Indeed, evolutionary changes to regulatory sequences of the *doublesex* locus have reshaped the wings of male wasps[10], and shifts in *doublesex* expression have changed the position of sexually dimorphic structures in flies[9]. Therefore,

broadening of *doublesex* expression in the swallowtail to a different part of the wing might be sufficient to expand a pre-existing female-specific colour pattern and generate a new mimetic form that could then persist owing to the selective advantage it conveys.

The intricate patterns of *doublesex* expression also help to explain how such apparently complex morphological variation could map to a single genetic locus. The mimicry loci in *P. polytes* and other butterflies have been proposed to be 'supergenes' — linked clusters of trait-altering genes — because of the complexity of the colour pattern and the rare occurrence of individuals with mixed mimetic patterns[8]. Like other developmental regulatory genes, *doublesex* probably has multiple transcription-regulating elements (enhancers). In principle, different elements could control *doublesex* expression in different parts of the swallowtail wing, and genetic variation at two elements should occasionally separate when chromosomes cross over during gamete formation. It is possible that other supergenes are also well-known developmental regulatory genes that have accumulated multiple functional mutations in evolution.

By accomplishing the arduous task of gene mapping in a butterfly, Kunte *et al.* open the door to understanding the mechanics of how the insect's mimetic pattern is generated and how each wing variant is maintained in a population. Identifying the precise molecular mechanism behind this spectacular mimicry switch promises to be exciting, whether it is due to regulatory mutations, protein alterations or a combination of the two, especially in light of the central role of *Dmrt* genes in sexual dimorphism across the animal kingdom. ■

David W. Loehlin *and* **Sean B. Carroll**
are in the Howard Hughes Medical Institute and Laboratory of Molecular Biology, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA.
e-mails: loehlin@wisc.edu; sbcarrol@wisc.edu

1. Bates, H. W. *Trans. Linn. Soc. Lond.* **23,** 495–566 (1862).
2. Wallace, A. R. *Trans. Entomol. Soc. Lond.* **2,** 14–15 (1864).
3. Reed, R. D. *et al. Science* **333,** 1137–1141 (2011).
4. Martin, A. *et al. Proc. Natl Acad. Sci. USA* **109,** 12632–12637 (2012).
5. Kunte, K. *et al. Nature* **507,** 229–232 (2014).
6. Clarke, C. A. & Sheppard, P. M. *Phil. Trans. R. Soc. B* **263,** 431–458 (1972).
7. Kopp, A. *Trends Genet.* **28,** 175–184 (2012).
8. Robinett, C. C., Vaughan, A. G., Knapp, J.-M. & Baker, B. S. *PLoS Biol.* **8,** e1000365 (2010).
9. Tanaka, K., Barmina, O., Sanders, L. E., Arbeitman, M. N. & Kopp, A. *PLoS Biol.* **9,** e1001131 (2011).
10. Loehlin, D. W. *et al. PLoS Genet.* **6,** e1000821 (2010).

This article was published online on 5 March 2014.

ASTROPHYSICS

Cosmic lens reveals spinning black hole

The power of a cosmic lens to magnify and split the light from a distant, mass-accreting giant black hole into four components has allowed researchers to measure the black hole's spin. SEE LETTER P.207

GUIDO RISALITI

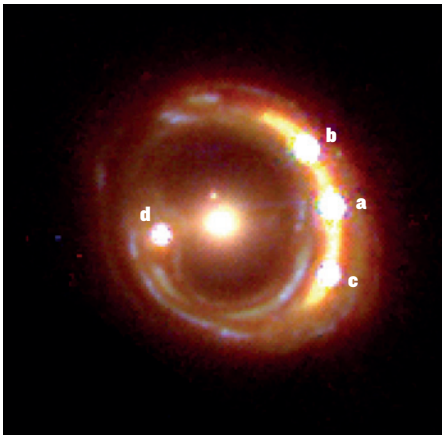
Quasars are the most powerful, continuously emitting sources of radiation in the Universe. They reside at the centre of a small fraction of galaxies, and are powered by supermassive black holes, which have masses millions to billions times greater than that of the Sun. Although giant black holes are present in most — possibly all — galaxies, not all of them are in an active state, in which they accrete gas from a surrounding disk. In fact, most of these objects are in a quiescent phase. It is the active type of supermassive black hole that drives quasars. The formation history of supermassive black holes is thought to be closely tied to that of their host galaxies, but how exactly they form and grow remains unclear. In this issue, Reis *et al.*[1] (page 207) describe how a cosmic lens has enabled them to find that a supermassive black hole powering a distant quasar has grown through coherent, rather than random, episodes of mass accretion.

Astronomers believe that supermassive black holes formed in the early Universe from small 'seeds' with masses of up to 10,000 solar masses. These seeds would have then grown to reach millions to billions of solar masses either through multiple mergers during galaxy collisions or through gas accretion from their host galaxies; this accretion would have consisted either of many short, unrelated accretion episodes or of fewer, longer and ordered accretion phases. Different models of galaxy evolution predict a different mix of these processes, so reconstructing the formation history of giant black holes would provide a way for us to understand how galaxies evolved.

Supermassive black holes are simple systems. They are characterized by just two quantities, their mass and their angular momentum (spin). Whereas the total amount of accretion and any mergers that a supermassive black hole undergoes are encoded in its mass, how this mass was assembled is encoded in its spin[2]. A few ordered accretion events or mergers of large black holes produce high spins, and short, random accretion processes produce low spins. Measuring these spins is therefore a major goal of extragalactic astronomy: the spins of supermassive black holes hold a key to understanding the evolution of their host galaxies.

But how can we measure the spins? According to Einstein's general theory of relativity, a black hole's gravitational field twists space-time around it. Such twisting depends on the black hole's spin, so measuring the twisting allows the spin to be estimated. The signature of space-time distortion is imprinted on the emission of radiation from regions close to the black hole's event horizon — the surface beyond which no radiation can escape. In quasars, the bulk of the huge, observed luminosity is emitted by the accretion disk at optical and ultraviolet wavelengths. However, this primary emission is nearly featureless, so, despite its vicinity to the event horizon, it does not provide an easy means to detect space-time distortions. The best way to perform such a measurement is to observe X-rays reflected by the disk.

The main source of X-ray emission in quasars is believed to be a compact cloud of hot electrons in the inner part of the black hole's accretion disk. Some of this radiation illuminates the accretion disk and is reflected towards the observer's line of sight. This reflected emission usually accounts for less than 1% of the total energy produced by quasars, but contains narrow spectral features — most notably, an iron spectral line at the object's



ACS & NICMOS/ESA/HST/STSCI/AURA/NASA/REF. 10

Figure 1 | A quadruple quasar. Reis and colleagues' analysis[1] of a distant quasar, whose light is magnified and split into four components (**a**–**d**) by the gravitational field of a foreground galaxy (central object), has enabled them to calculate the spin of the supermassive black hole that powers the quasar.