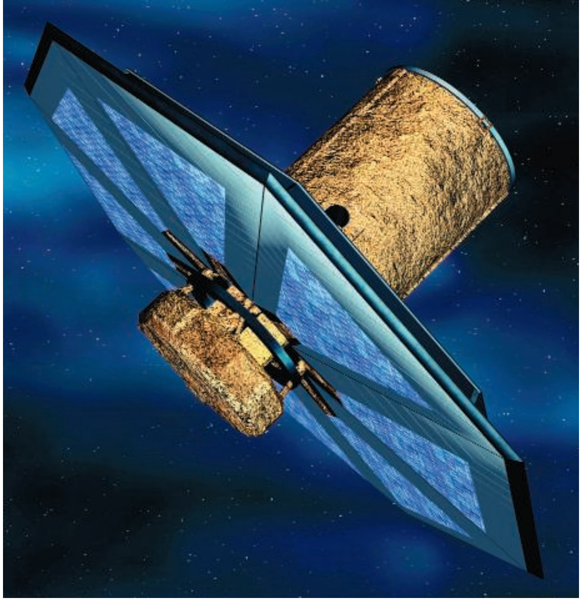
astronomy and moved us into an era of observing the invisible. Out of proportion with its modest budget, ESA's many missions have contributed to discoveries that poured in over the decades as detectors covering the full wavelength spectrum were launched from different continents. X-rays, for example, helped us understand the mechanisms of the solar corona. Stars, young and old, sometimes shine much brighter in x-rays than in the optical spectrum, and x-ray detectors provided a new look at their evolution and death. X-rays have shown us how stars collapse when they die and leave behind cores of a new state of matter, such as neutron stars. More important, x-rays from space gave the first evidence for black holes, objects so dense that not even light can escape them. Giacconi shared a Nobel prize for physics in 2002 for these and other discoveries.

Gamma-ray astronomy, another science of the invisible, has shown us objects emitting radiation that, on Earth, is produced only by radioactivity and particle accelerators. ESA's first mission, COS-B (1975), for example, showed the reality of "gamma-ray stars," that is, neutron stars that are only visible in gamma-rays (*2*).

Gamma-rays were also the protagonists of a unique success story in space science. During the Cold War, gamma detectors were launched to ferret out covert nuclear tests. Sure enough, the Vela spy satellites (a "secret" code name from the Spanish "velar," to monitor) launched by the United States detected suspicious bursts of gamma-rays. However, they came from the sky and not from the USSR (*3*), as was first disclosed at a 1973 conference where Soviet scientists admitted observing something similar. Gamma-ray bursts represented one of the top astronomical enigmas for a quarter of a century until the Italian/Dutch satellite BeppoSax (*4*), launched 10 years ago, showed that the bursts originated from enormous explosions in galaxies at cosmological distances, when galaxies were being born into a young Universe.

No one had observed stars being born before the development of satellite-based infrared astronomy, which yielded the first images of star "nurseries." These are "warm" (by interstellar standards, actually –200°C) dust cocoons, collapsing to form tens of new baby stars. Space infrared telescopes, such as ESA's Infrared Space Observatory (*5*), have also shown that water is abundant wherever stars are conceived and, in general, that water is everywhere in the sky. Water, we have learned, is the second most abundant molecule, after hydrogen, in the Universe. Think of it when you go swimming: You are floating in molecules that had probably been around for some time before raining on the newly formed Earth.



Other worlds. The proposed Darwin mission is a group of four satellites that will search for Earth-like planets and analyze their atmospheres for chemical signatures of life.

Where should we look in the next half-century? Europe has set for itself a long-term "Cosmic Vision" (*6*) to carry space science to 2025. Alas, we have discovered, like everyone else has, that choosing is hard. We want to study gravitational waves and we want to understand dark energy; we want to travel to Mars and we want to explore Jupiter. We need large interferometric telescopes in space to discover new planets (see the figure) and we need large orbiting collectors to catch more photons. To make a "concord out of this discord" is the challenge being faced by the new generation of European researchers.

References and Notes

1. Sounds of Sputnik are available at www.amsat.org/amsat/features/sounds/firstsat.html.
2. www.esa.int/esaSC/120375_index _0_m.html
3. R. Klebesadel *et al*., *Astrophys. J*. **182**, L85 (1973).
4. www.asdc.asi.it/bepposax/
5. http://isowww.estec.esa.nl/
6. http://sci.esa.int/science-e/www/area/index.cfm?fareaid=100

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EVOLUTION

Feathers, Females, and Fathers

Sex linkage of genes involved in adaptation and speciation extends to birds, explaining why females prefer males of their own species.

Michael G. Ritchie

Alfred Wallace, Darwin's contemporary and rival, argued that when species hybridize, natural selection favors individuals who are more fussy about whom they mate with, which therefore increases female discrimination of males from different species (*1*). Modern evolutionary genetics has questioned the importance of the "Wallace effect" (also known as "reinforcement") because genetic recombination between female discrimination and male trait genes would scramble combinations of loci that favor speciation. Several solutions to this have been proposed, including close genetic linkage of such loci. A simpler possibility is sexual imprinting, which causes a female to prefer males that resemble her father. A study of flycatchers by Sæther *et al*. on page 95 of this issue (*2*) has taken advantage of natural hybridization that occurs between species of this bird, and demonstrates that female preference for father-like males is due to sex linkage of genes for female preferences rather than to sexual imprinting. The linkage of genes that influence speciation to sex chromosomes may turn out to be a common influence on the origin of species.

The evolutionary biologist J. Felsenstein (*3*) famously argued that because of genetic recombination, there might be fewer species of animals than we expect. In other words, if sexual species hybridize, recombination jumbles up their genes such that independent sets of loci coding for hybrid unfitness, male sexual traits, and female preferences are unlikely to crystallize out into new species. Exceptions may occur if the genes are all tightly genetically linked on one chromosome. Felsenstein also recognized that a "single-allele" solution could facilitate speciation. In this case, allelic replacement at one locus simultaneously causes selective mating between individuals

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that are genetically related or have similar characteristics (known as assortative mating), but it was difficult to imagine the mechanism for this. Sexual imprinting is one possibility (*4*, *5*); if a gene makes a female prefer males that are like her father, then the same allele could increase assortative mating between populations. It has been proposed that sexual imprinting may be involved in rapid speciation in the face of gene flow in birds (*6*) and fish, including the dramatic radiations of African cichlids (*7*).

Unlike most animals, female birds are the heterogametic sex, having the equivalent of a human Y chromosome, called the W chromosome (so females are ZW, males ZZ). Collared and pied flycatchers meet and occasionally hybridize along a contact zone in central and northern Europe. Hybrid females are sterile but hybrid males are fertile, an example of "Haldane's rule" in that the heterogametic sex (having two different sex chromosomes) shows greater dysfunction. It also indicates that fertility dysfunction probably involves genes on the sex chromosomes. In these hybrid zones of contact, male sexual plumage differences are accentuated and hybridization levels reduced, providing evidence that the Wallace effect has occurred (*8*). What accounts for this? Female sexual imprinting on paternal traits such as plumage differences, or genetic linkage between preference and trait loci?

Only up to 5% of mating pairs of flycatchers in the hybrid zone are between species, but Sæther *et al*. realized that the resulting offspring offered an excellent opportunity to test the mechanism underlying the inheritance of mate preferences. If preference genes are autosomal, hybrid females should have intermediate preferences, but if the preferences depend on the father, then hybrid females should prefer males that are like their father. This was unambiguously the case: Only 4 of 31 hybrid females mated with a male other than their paternal type (and hybrid males mated randomly). This pattern is consistent with Z linkage of mate preference loci (females receive their single Z chromosome from their father, whereas males get a copy from each parent), but it is also consistent with paternal sexual imprinting in females. Very neatly, Sæther *et al*. disentangled Z linkage and imprinting by examining the choice of females that had been cross-fostered. Offspring sometimes result from extra-pair copulations (females mating with males of another species, or heterospecific males), leading to females that are reared by heterospecific males. The authors also successfully cross-fostered some chicks between parents of either species. As adults, these females mated with males of their own species even if they had been reared by heterospecific males, ruling out sexual imprinting. Although sample sizes were understandably low (Sæther *et al*. must have been particularly anxious when awaiting the return of migratory females the season after the cross-fostering), the results strongly support Z linkage. There are perhaps alternative explanations (such as genomic imprinting, in which gene expression is influenced by which parent the allele comes from), but they seem much less likely.

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Father-like traits preferred. A male collared flycatcher feeds its chicks. Collared and pied flycatchers occasionally hybridize in central and northern Europe. Females develop a sexual preference for males of their own species as a result of sex-linked genes, not sexual imprinting.

It has been argued that sexual imprinting is a widespread phenomenon that can increase speciation rates (*6*, *9*), particularly by reinforcement (*10*). However, some models give only ambiguous support for this (*11*, *12*), and another empirical study failed to demonstrate any role in speciation (*5*). Genetic linkage may be more straightforward (*13*). Previous studies of flycatchers implied that the Z chromosome also carries loci that influence male plumage and hybrid unfitness (*14*); therefore, all these loci will have reduced genetic recombination, facilitating the Wallace effect. Linkage may be a more common factor to promote this than "single-allele" solutions. One potential case of a single-allele system has recently been described in the fruit fly *Drosophila melanogaster* (*15*), but the locus is unidentified and very tight linkage cannot be unambiguously discounted. A series of hybridization studies in a variety of organisms suggest that chromosomal rearrangements such as inversions may be another means of reducing genetic recombination between favored gene arrangements (*16*). The fact that traits involved in sexual isolation (male traits and female preferences) are sex-limited may mean that sex linkage of loci is favored, as gene expression must be influenced by the sex chromosomes. Lepidoptera, the other major animal group in which females are heterogametic, are particularly likely to show sex linkage of genes involved in adaptation and speciation (*17*), so it is very interesting that Sæther *et al*. suggest that this phenomenon extends to birds.

More studies with the experimental ingenuity of Sæther *et al*. will be required to test whether this is a general phenomenon, but an intriguing hypothesis is that female heterogamety and strong sex linkage might mean that the Wallace effect is more common in birds and butterflies than in other groups.

References

1. A. R. Wallace, *Darwinism* (Macmillan, London, 1889).
2. S. A. Sæther *et al.*, *Science* **318**, 95 (2007).
3. J. Felsenstein, *Evolution* **35**, 124 (1981).
4. M. R. Servedio, M. A. F. Noor, *Annu. Rev. Ecol. Evol. Syst.* **34**, 339 (2003).
5. A. Y. K. Albert, *Evolution* **59**, 927 (2005).
6. D. E. Irwin, T. Price, *Heredity* **82**, 347 (1999).
7. M. N. Verzijden, C. ten Cate, *Biol. Lett.* **3**, 134 (2007).
8. G.-P. Sætre *et al.*, *Nature* **387**, 589 (1997).
9. I. P. F. Owens, C. Rowe, A. L. R. Thomas, *Trends Ecol. Evol.* **14**, 131 (1999).
10. M. R. Servedio, S. A. Sæther, G.-P. Sætre, *Evol. Ecol.*, 10.1007/s10682-007-9188-2 (2007).
11. M. N. Verzijden, R. F. Lachlan, M. R. Servedio, *Evolution* **59**, 2097 (2005).
12. K. Aoki, M. W. Feldman, B. Kerr, *Evolution* **55**, 25 (2001).
13. D. W. Hall, M. Kirkpatrick, *Evolution* **60**, 908 (2006).
14. G.-P. Sætre *et al.*, *Proc. R. Soc. London Ser. B* **270**, 53 (2003).
15. D. Ortiz-Barrientos, M. A. F. Noor, *Science* **310**, 1467 (2005).
16. L. H. Rieseberg, *Trends Ecol. Evol.* **16,** 351 (2001).
17. M. G. Ritchie, S. D. F. Phillips, in *Endless Forms: Species and Speciation*, D. A. Howard, S. Berlocher, Eds. (Oxford Univ. Press, Oxford, 1998), pp. 291–308.

10.1126/science.1149597