ing glacial and interglacial periods. During warm interglacials, ISM rainfall appears to vary with CO_2 concentrations because of the dominance of thermodynamic mechanisms and northern pulling. During colder glacials, however, ISM rainfall does not appear to vary with CO_2, due to the dominance of southern pushing. Because rising CO_2 tends to enhance northern pulling but weaken southern pushing, the future net dynamic forcing on the ISM remains uncertain. In the current climate, models suggest that rising CO_2 will enhance ISM rainfall but not winds (*6*), likely because of the dominance of enhanced evaporation and moisture supply. Were we in a colder climate, however, the ISM's response to global warming could be very different.

References and Notes

1. Z. An *et al.*, *Science* **333**, 719 (2011).
2. R. Tomas, P. Webster, *Q. J. R. Meteorol. Soc.* **123**, 1445 (1997).
3. M. Rodwell, B. Hoskins, *J. Atmos. Sci.* **52**, 1341 (1995).
4. P. Webster, J. Fasullo, in *Encyclopedia of Atmospheric Sciences*, J. Holton, J. A. Curry, Eds. (Academic Press, Waltham, MA, 2003), pp. 1370–1864.
5. W. R. Boos, Z. Kuang, *Nature* **463**, 218 (2010).
6. IPCC, *Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the International Panel on Climate Change* (Cambridge Univ. Press, Cambridge, 2007), chaps. 9 and 10.
7. J. Jouzel *et al.*, *Science* **317**, 793 (2007).
8. L. E. Lisiecki, M. E. Raymo, *Paleoceanography* **20**, PA1003; 10.1029/2004PA001071 (2005).
9. D. Pollard, R. M. DeConto, *Nature* **458**, 329 (2009).
10. **Acknowledgments:** Figure courtesy of Z. An and J. B. Dong.

10.1126/science.1210019

EVOLUTION

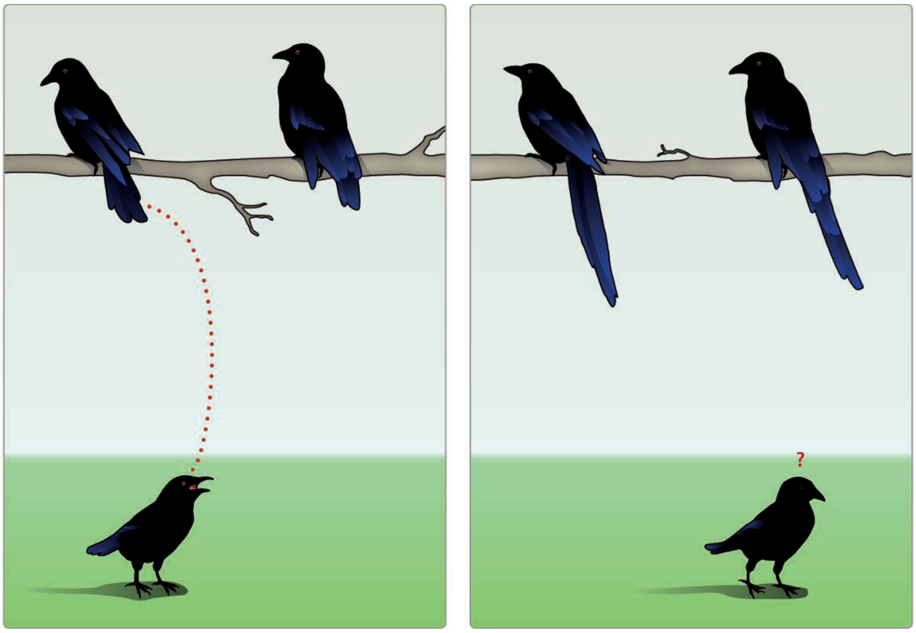
Is Bigger Always Better?

Female perceptual limitations may explain why sexual selection doesn't always lead to exaggerated male traits.

Candy Rowe[1] and Susan D. Healy[2]

Darwin was famously puzzled by the length of a peacock's train—what made it so big and so elaborate? The theory of sexual selection provided us with the answer: Females choose males with more exaggerated traits, such as a bigger tail, because they signal benefits for their offspring (*1*). Recent studies, however, have suggested that this is an oversimplification because the perceptual and cognitive mechanisms underlying female choice may not always lead to larger and more extravagant male traits (*2*, *3*). On page 751 of this issue, Akre *et al.* offer further evidence that female perception can make a big difference. They show that although female frogs prefer male frogs with longer calls, the females are less able to discriminate between males as their calls become longer, perhaps constraining the evolution of call length. The finding is consistent with Weber's law (*4*), which holds that as the magnitude of two stimuli increases, a greater difference is required to distinguish between them.

When an animal compares two stimuli, it must be able to perceive a difference between them in order to make a choice. Psychophysical experiments show that animals do this based on relative, not absolute, differences (*5*). For example, if a female bird is presented with two males with tails that are relatively short but of different lengths, Weber's law suggests she will more easily perceive even a slight difference (see the figure). As the tails get longer, however, the difference must be bigger for the female to detect the longer tail. This observation suggests that females may become less choosy as traits get bigger, because they become less able to discriminate between males with large traits. Therefore, sexual selection would get weaker as male ornament size increases, leading to a cessation in trait exaggeration.



Perceiving a difference. Weber's law suggests that females should choose males based on the relative, rather than the absolute, difference in their traits. A female bird considering two males with tails of different but relatively short lengths (**left**) should perceive the difference more readily than if she is comparing two males with longer tails (**right**). This perceptual limitation may help to explain why sexual selection does not lead to ever bigger and showier male traits.

CREDIT: P. HUEY/*SCIENCE*

Akre *et al.*'s data are the first to provide experimental support for this idea. They studied túngara frogs (*Physalaemus pustulosus*). Males gather in choruses and produce calls that consist of a whine followed by a number of "chucks" (0 to 7, although typically no more than 2) (*6*). Females are attracted to the chorusing males and tend to choose to mate with males that produce the calls with the most chucks (*7*). In Akre *et al.*'s experiment, the researchers played male calls of different lengths from two speakers, and then measured a female frog's discrimination ability by recording which speaker she chose to approach. Contrary to their

---

[1]Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, NE2 4HH, UK. [2]Schools of Biology and Psychology, University of St Andrews, St Andrews KY16 9JP, UK. E-mail: candy.rowe@ncl.ac.uk, sdh11@st-andrews.ac.uk

Downloaded from www.sciencemag.org on August 4, 2011

Published by AAAS

expectation, females did not always prefer to approach the speaker producing the most chucks. Instead, female preference strongly depended upon the "chuck ratio" between the two calls: Although females strongly preferred calls with three chucks compared to those with one chuck, they cared little more for three-chuck calls than they did for two-chuck calls. The findings suggest that female discrimination constrains the production of longer calls.

Where does that leave predators—which are often seen as the opposing selective force to female preference—in the evolution of male traits? Although males benefit from bigger or more conspicuous traits that attract more mates, these traits can also make it easier for predators to find and catch males (*8*). Akre *et al*. explored this question by observing the behavior of frog-eating bats. Remarkably, the bats, like female frogs, preferred males that produced calls with more chucks, but their preference also decreased as the chuck ratio became larger. This suggests that male calls may not become more conspicuous to the bats as the calls get longer. Instead, the risk associated with adding an extra chuck declines: A male producing three chucks next to a male producing two exposes himself less to predation than does a male producing two chucks next to a male producing one. As a result, in the case of male túngara frogs, both the additional benefits of attracting a female and the costs of being eaten decrease as chuck number increases. This adds weight to the idea that female discrimination is acting as a brake on lengthening calls.

These findings raise an intriguing question: Why do some males produce calls with up to seven chucks, despite evidence showing that increasing chuck number by more than two is pointless for attracting unaware females? Males respond to the calls of other males by increasing their chuck number by one (*7*). This suggests that, during competitions with neighboring males, male frogs can distinguish chuck number, even beyond those differences distinguishable to females. Do male túngara frogs differ from females in their discriminatory abilities? Or do they just have more time to listen to their neighbors' calls than do females looking for a mate?

One way to approach these questions is to consider the female's point of view. Females, after all, are caught in a bind: They need to choose a good male before being eaten. The female who chooses a good male quickly is likely to produce offspring, while the female who sits listening to a chorus trying to determine which male is best may become a bat's dinner. A female in a hurry might discriminate between males only when the chuck ratio is small and detecting a difference is easy. The difference might also mean that the selected male's neighbor can't keep up, so the female really has chosen the best male (at least locally). Although psychophysics might describe how a choice can become increasingly difficult, it does not explain whether a female is prepared to pay the cost of solving that increasing discrimination problem (*9*). Might this explain why elaboration of male traits varies across species: Female peacocks are prepared to take their time to compare and contrast males, whereas túngara females are not?

References

1. S. Andersson, *Sexual Selection* (Princeton Univ. Press, Princeton, NJ, 1994).
2. M. Bateson, S. D. Healy, *Trends Ecol. Evol.* **20**, 659 (2005).
3. S. R. Pryke, S. Andersson, *Behav. Ecol.* **19**, 1116 (2008).
4. K. L. Akre, H. E. Farris, A. M. Lea, R. A. Page, M. J. Ryan, *Science* **333**, 751 (2011).
5. M. Treisman, *Psychol. Rev.* **71**, 314 (1964).
6. X. E. Bernal, R. A. Page, A. S. Rand, M. J. Ryan, *Am. Nat.* **169**, 409 (2007).
7. X. E. Bernal, K. L. Akre, A. T. Baugh, A. S. Rand, M. J. Ryan, *Behav. Ecol. Sociobiol.* **63**, 1269 (2009).
8. M. Zuk, G. R. Kolluru, *Q. Rev. Biol.* **73**, 415 (1998).
9. L. Chittka, P. Skorupski, N. E. Raine, *Trends Ecol. Evol.* **24**, 400 (2009).

10.1126/science.1210723

PHYSICS

Spotlight on Plasmon Lasers

A plasmonics-based design approach is enabling coherent light sources to be built at the nanometer scale.

Volker J. Sorger and Xiang Zhang

Lasers are the workhorse of the information age, sending massive amounts of light packets through vast networks of optic fibers. Demands for ever-increasing speed and functionalities call for scaling down of photonic devices, similar to the trend in electronics. However, photonic devices face the fundamental challenge of the diffraction limit of light—a limitation that prevents squeezing light into spaces smaller than half of its wavelength. This barrier limits traditional optical components to sizes that are hundreds of times larger than that of their electronic counterparts. Surface plasmons are collective electronic oscillations on a metal-dielectric interface with a much smaller wavelength than the excitation or emitted photons, and have emerged as a promising solution to overcome such a barrier (*1*). In 2003, the surface plasmon laser or "spaser" was theoretically proposed. The idea was to tightly confine light in the form of localized plasmons into deep subwavelength dimensions overlapping with a gain medium to achieve stimulated emission and light amplification or lasing, creating a coherent light source at the nanometer scale (*2*). That proposal is now being realized with several plasmonics-based design approaches being used to fabricate nanometer-scale coherent light sources.

The "gold-finger" laser was the first experimental attempt using metals to confine the optical energy to lasing (*3*). A tiny compound semiconductor pillar was used as a gain medium and wrapped in a thin gold layer. This small laser was electrically pumped though it was diffraction limited because of its nonplasmonic nature. Later, a nanolaser showing plasmonic character with one-dimensional confinement was demonstrated (*4*). The large resistive losses associated with the metal required cryogenic temperatures for laser operation. In a different approach, core-shell colloidal particles suspended in water were optically pumped with localized plasmons bound to the surface of a metal particle (*5*). The 40-nm core-shell particle consisted of a gold core as a plasmonic cavity covered by a shell of silica decorated with dye molecules that provided the gain. Although this nanoparticle approach provides the ultimate scaling down in all three dimensions, its optical mode extends appreciably outside the structure, and electrical connections are difficult to implement.

One of the major challenges confronting

NSF Nanoscale Science and Engineering Center, 3112 Etcheverry Hall, University of California, Berkeley, CA 94720, E-mail: xiang@berkeley.edu

Downloaded from www.sciencemag.org on August 4, 2011

Published by AAAS