brief communications

- Côté, I. M. & Cheney, K. L. Proc. R. Soc. Lond. B 271, 2627–2630 (2004).
- Smith-Vaniz, W. F. Acad. Nat. Sci. Philadelphia Monogr. 19, 1–196 (1976).
- 6. Randall, J. E., Allen, G. R. & Steene, R. Fishes of the Great Barrier Reef and Coral Sea (Crawford House, Bathurst, Australia, 1997).

Supplementary information accompanies this communication on *Nature*'s website.

Competing financial interests: declared none.

Behavioural ecology

Transient sexual mimicry leads to fertilization

exual mimicry among animals is widespread^{1,2}, but does it impart a fertilization advantage in the widely accepted 'sneak–guard' model³ of sperm competition? Here we describe field results in which a dramatic facultative switch in sexual phenotype by sneaker-male cuttle-fish leads to immediate fertilization success, even in the presence of the consort male. These results are surprising, given the high rate at which females reject copulation attempts by males, the strong mate-guarding behaviour of consort males, and the high level of sperm competition in this complex mating system^{4,5}.

The giant Australian cuttlefish, Sepia apama, is a solitary cephalopod mollusc that forms large aggregations to mate and lay eggs⁴. Females lay one large egg at a time (5–39 per day) and mate up to 17 times with 2-8 males daily. The operational sex ratio averages four males to one female, but ranges up to eleven males to one female. Females reject 70% of mating attempts and the competition between males for mates is intense; mate guarding is almost continuous. Consort males obtain 64% of matings, the remainder being by small, unpaired or extrapair males. Small males (with male coloration and of similar size to females) obtain extrapair copulations by 'open' stealth (approaching a guarded female as the consort is repelling other males), by 'hidden' stealth (meeting females under rocks) or — the subject of this investigation— by mimicking the appearance and behaviour of females^{4,6}.

Visual deception is achieved when small males suddenly hide their sexually dimorphic fourth arms, acquire the mottled skin patterning typical of females, and shape their arms to mimic the posture of egg-laying females, who are not receptive to mating⁴ (Fig. 1; for video, see supplementary information). This facultative change in appearance is instantaneous and occurs at a rate of about 10 changes per 15 min during intense behavioural interactions (demonstrated in 12 video subsamples (data not shown); mimic duration, 10–184 s). We found that female mimickers could successfully deceive the consort male and that they were able to position themselves near the female in 30 out of 62 attempts. Other males attempted to







Figure 1 Female mimicry by 'sneaker' male cuttlefish leads to extrapair copulations and fertilization. **a**, An unpaired male (m) assumes female coloration and posture and approaches the paired female (f) while the consort (c) displays to an approaching large male (top right); note the conspicuous, large white arms, a sexually dimorphic male character. **b**, The female accepts a mating attempt by the female mimic as the consort continues to display to the other large male. **c**, The consort male allows the mimic to finish mating without interruption, even when he is not distracted (for video, see supplementary information); the other small 'sneaker' male has swiftly transformed into a female mimic as well.

mate with the mimics 41 times (25 attempts by large males and 16 by small males, two of which were by other female mimics).

We observed five initiations of mating by mimics. One mimic was rejected, one was interrupted by the consort male, and three resulted in successful spermatophore transfer. Consorts did not mate with females immediately after being cuckolded by the mimic. We tested the paternity of the next laid egg by using five microsatellite DNA fingerprints⁵ on tissue samples from the females and any male that mated with them during the focal samples (up to four in 30 min; females had up to 5 male genotypes in their sperm sources, which included recently attached spermatangia and stored sperm⁷). Two of the three successful inseminations by mimics resulted in fertilization. Both guarders and sneaks are able to father subsequent eggs⁵, so the matings by mimics may

have fertilized later eggs, but we could not test this possibility because SCUBA-diving constraints curtailed our sampling efforts.

Cuttlefish have keen vision but poor social recognition8, which favours visual sexual mimicry. In contrast to taxa in which alternative mating tactics are either fixed or vary ontogenetically^{1,9,10}, cuttlefish use neural control to change their skin patterning, posture and tactics instantly. To our knowledge, this is the first demonstration of immediate fertilization success in an animal using facultative mimicry as part of a conditional mating strategy11. These field results, combined with those on bluegill sunfish¹⁰ (Lepomis macrochirus), which are 'broadcast' spawners, lend genetic and behavioural support to Parker's predictions that some sneaks can win sperm competition and steal³ fertilization from guarders.

Roger T. Hanlon*, Marié-Jose Naud†‡, Paul W. Shaw†, Jon N. Havenhand‡§

*Marine Resources Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA e-mail: rhanlon@mbl.edu

†School of Biological Sciences, Royal Holloway College, University of London, Egham TW20 0EX, UK

‡School of Biological Sciences, Flinders University, Adelaide 5001, Australia

§Tjarnö Marine Biological Laboratory, Gothenburg University, S45296 Strömstad, Sweden

- Andersson, M. Sexual Selection (Princeton Univ. Press, Princeton, New Jersey, 1994).
- Saetre, G. P. & Slagsvold, T. Am. Nat. 147, 981–995 (1996).
- Parker, G. A. in Sperm Competition and Sexual Selection (eds Birkhead, T. R. & Møller, A. P.) 3–54 (Academic, London, 1998).
- 4. Hall, K. C. & Hanlon, R. T. Mar. Biol. 140, 533-545 (2002).
- Naud, M. J., Hanlon, R. T., Hall, K. C., Shaw, P. W. & Havenhand, J. N. Anim. Behav. 67, 1043–1050 (2004).
- Norman, M. D., Finn, J. & Tregenza, T. Proc. R. Soc. Lond. B 266, 1347–1349 (1999).
- 7. Naud, M. J., Shaw, P. W., Hanlon, R. T. & Havenhand, J. N. *Proc. R. Soc. Lond. B* (in the press).
- 8. Boal, J. G. Anim. Behav. **52**, 529–537 (1996).
- Boal, J. G. Anim. Benav. 32, 329–357 (1996).
 Shuster, S. M. Evolution 43, 1683–1698 (1989).
- Fu, P., Neff, B. D. & Gross, M. R. Proc. R. Soc. Lond. B 268, 1105–1112 (2001).
- 11. Gross, M. R. Trends Ecol. Evol. 11, 92-98 (1996).

Supplementary information accompanies this communication on *Nature*'s website.

Competing financial interests: declared none.

brief communications arising online

www.nature.com/bca

Evolutionary genomics: Codon bias and selection on single genomes

M. W. Hahn, J. G. Mezey, D. J. Begun, J. H. Gillespie, A. D. Kern, C. H. Langley, L. C. Moyle (doi:10.1038/nature03221)

Evolutionary genomics: Detecting selection needs comparative data

R. Nielsen, M. J. Hubisz (doi:10.1038/nature03222)

Evolutionary genomics: Codon volatility does not detect selection

Y. Chen, J. J. Emerson, T. M. Martin (doi:10.1038/nature03223)

Reply: J. B. Plotkin, J. Dushoff, H. B. Fraser (doi:10.1038/nature03224)