

Male displays adjusted to female's response

Macho courtship by the satin bowerbird is tempered to avoid frightening the female.

Models of sexual selection generally assume that behavioural courtship displays reflect intrinsic male qualities such as condition, and that males display with maximum intensity to attract females to mate¹. Here we use robotic females in a field experiment to demonstrate that male satin bowerbirds (*Ptilonorhynchus violaceus*) do not always display at maximum intensity — rather, successful males modulate their displays in response to signals from females. Our results indicate that sexual selection may favour those males that can produce intense displays but which know how to modify these according to the female response.

The courtship of the male satin bowerbird consists of a dramatic, coordinated display of feather-puffing, extending the wings suddenly, and running accompanied by a loud buzzing vocalization. The intensity of this display necessitates trade-offs for males and females. Males must display intensely to be attractive, but these displays involve sudden movements and are similar to male–male aggression displays^{2,3} and so may be perceived as threatening by females². Females may be attracted by intense displays that indicate genetic or proximate benefits^{1,4–6}, but they risk being startled repeatedly when threatened by intense displays, which can disrupt or end courtship⁷. This startling may be costly if females cannot efficiently assess potential mates or if they lose the opportunity to mate with more intensely displaying, preferred males. These trade-offs should favour communication because both sexes will benefit if females are not threatened unnecessarily by intense male displays.

During the process of mate selection, the average female satin bowerbird approaches several males for courtship, returns to a

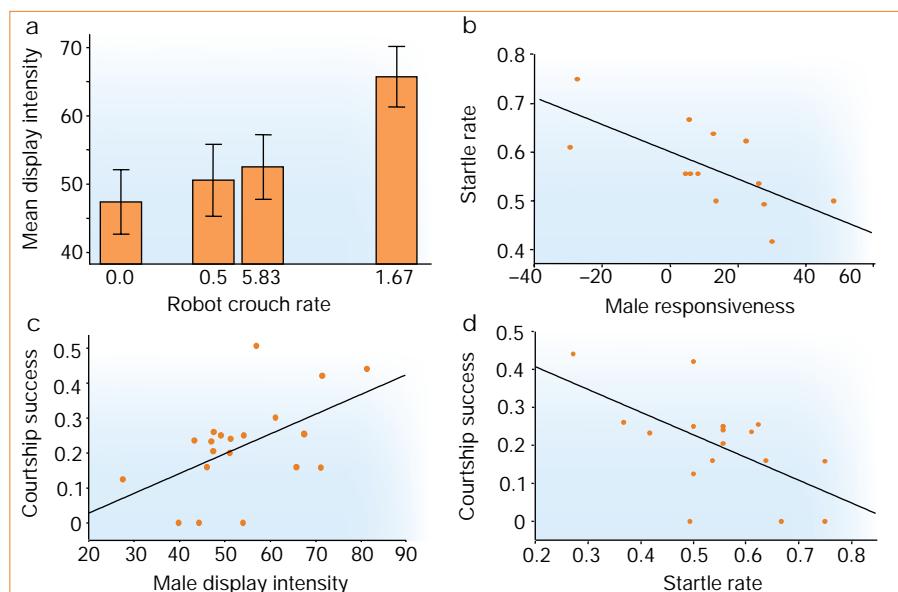


Figure 2 Response of male satin bowerbirds to female signals. **a**, Positive relationship between mean male display intensity (\pm s.e.) and robot crouch rate (ANOVA linear contrast, each male a random block: $F_{1,36}=8.69$, $P<0.006$; display intensity was scored as an index incorporating aspects of male display that affected the threat to females: the degree of feather puffing, the distance run, and male location relative to the female). **b**, Males who are more responsive to female signals are less likely to startle females with intense displays ($n=13$, $r^2=0.47$, $F_{1,11}=9.93$, $P<0.009$; responsiveness is the slope of the male's intensity regressed on robot crouch rate; startle rate was estimated from natural bower activity³ as the average proportion of intense displays that startle females in first courtships between the male and each female he courts). **c**, Males with a higher average display intensity in experimental courtships were more successful in natural courtships ($n=20$, $r^2=0.29$, $F_{1,18}=7.23$, $P<0.015$; male courtship success was measured as the proportion of courted females who mated with the male). **d**, Males who startle females with intense displays less frequently are more successful in natural courtships ($n=17$, $r^2=0.35$, $F_{1,15}=8.10$, $P<0.012$). Further details are available from the authors.

subset of males, and finally copulates with a single male⁸. In each courtship, a female typically ‘crouches’, lowering herself down and tilting forwards towards the mating position, fluffing her wings when she is fully crouched. Crouching is highly variable, and females may crouch in courtships occurring a week or more before copulation and for males that are not finally chosen as mates. As crouching increases, a female is less likely to be startled by intense male displays, so crouching may

indicate the degree of intensity that she will tolerate without feeling threatened, and signals increasing tolerance during sequential courtships with a male (details of the relationship between crouching and startling are available from the authors). By increasing the intensity of his display as a female's crouching increases, a male should thus be able to maintain his attractiveness without threatening the female.

We tested this hypothesis by measuring the male response to the controlled crouching of robotic female bowerbirds (Fig. 1). Males should respond to increased female crouching by increasing their display intensity, so that high-intensity displays are given when females are likely to be less easily startled. In support of this prediction, we found a highly significant, positive correlation between male display intensity and robot crouch rate (Fig. 2a).

In addition, males that respond more effectively to female signals should threaten females less frequently with intense displays, and we found that there is indeed a negative relation between male responsiveness to robot crouching and the startling of females by male displays in natural courtships (Fig. 2b). When we controlled for responsiveness,



Figure 1 Robotic female satin bowerbird. Robots were capable of three movements, controlled by servo motors: crouching (simultaneous lowering and forward-tilting of the body), looking around during courtship (lateral head movement), and wing-fluffing upon reaching the mating position (lateral wing movement). Robots were enclosed in female satin-bowerbird skins, placed in the bower of the male under test (where females are typically courted⁹) at our field site in Australia, and controlled remotely. The responses of 20 males were tested with robots that crouched from the upright position to the mating position (pictured) at four different rates: fast (3 min total, 1.67 position changes per min), moderate (6 min, 0.83 changes per min), slow (9 min, 0.55 changes per min), and no crouching (0 changes per min), with order randomized between males.

we found a positive relationship between male display intensity and startle rate ($\beta_{\text{response}} = -0.92$, $P < 0.001$; $\beta_{\text{intensity}} = 0.51$, $P < 0.028$; $r^2 = 0.68$, $F_{2,10} = 10.71$, $P < 0.003$).

We predicted that the most successful males would be those who produce high-intensity displays without startling females. Indeed, we found a positive correlation between male display intensity in robot courtships and male success in natural courtships (Fig. 2c), and a negative relationship between startle rate and male courtship success (Fig. 2d), with both factors contributing to male courtship success when considered together ($\beta_{\text{intensity}} = 0.55$, $P < 0.004$; $\beta_{\text{startle}} = -0.57$, $P < 0.003$; $r^2 = 0.65$, $F_{2,14} = 13.23$, $P < 0.0006$).

Our results indicate that although female satin bowerbirds prefer intensely displaying males, successful males do not always display at maximum intensity — instead, they modulate the intensity of their display in response to female signals, to remain attractive without threatening the females. In satin bowerbirds — and perhaps in other species in which variation in sexually selected traits

has not yet been examined in detail — male courtship success may depend on both an attractive display and the intrinsic ability to modify these in response to female signals.

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ponents of the emitted laser harmonics were measured by using high-dynamic-range, charge-coupled-device arrays as detectors.

When an electromagnetic wave propagates in a magnetized plasma with its \mathbf{k} vector perpendicular to \mathbf{B} , the extraordinary wave (x -wave; that is, with an electric field vector perpendicular to the magnetic field) can experience cut-offs and resonances (Fig. 1a). Cut-offs occur when the plasma index of refraction is equal to zero, and resonances when the index approaches infinity. The x -wave is reflected when it encounters a cut-off and is absorbed in a resonance. For example, the cut-offs for the fifth, fourth and third harmonics occur at 460, 340 and 220 megagauss, respectively, for a density of $n_e = 2.4 \times 10^{21} \text{ cm}^{-3}$ (the relativistically corrected critical density). Resonances occur at higher magnetic fields than cut-offs. The ordinary (o) wave (with \mathbf{E} parallel to \mathbf{B}) is unaffected by the magnetic field — implying that if a field larger than the cut-off field exists in the plasma, then only the ordinary wave is able to propagate to the detector and therefore is the only one observable.

This is what we find for the highest-intensity shots. Figure 1b shows the ratio of p -component (x -wave) to total emission (x -wave plus o -wave) for both the third and fourth harmonics for various incident laser intensities. At high intensities, the x -wave cut-offs are definitely observed, implying the existence of a minimum magnetic field of 340 megagauss in the plasma; no cut-offs were seen for the fifth harmonic. This indicates that the peak magnetic field is below 460 and above 340 megagauss at intensities of about $9 \times 10^{19} \text{ W cm}^{-2}$. Such fields are more than an order of magnitude larger than any previously observed in the laboratory^{7–9}. These cut-offs were consistently reproducible in our experiments — but only at the highest laser intensities.

The magnitude of the magnetic fields generated in this way could soon approach those needed for testing astrophysical models of neutron stars and white dwarfs¹⁰.

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Laser technology

Measuring huge magnetic fields

Huge magnetic fields are predicted^{1–4} to exist in the high-density region of plasmas produced during intense laser-matter interaction, near the critical-density surface where most laser absorption occurs, but until now these fields have never been measured. By using pulses focused to extreme intensities to investigate laser-plasma interactions⁵, we have been able to record the highest magnetic fields ever produced in a laboratory — over 340 megagauss — by polarimetry measurements of self-generated laser harmonics.

Because harmonics of the laser are generated at the critical-density surface and subsequently propagate isotropically out of the

dense region⁶, we have found that measuring the final polarization of these harmonics is a powerful way to find out the magnitude of the magnetic fields through which they travel. The use of self-generated laser harmonics is particularly convenient because these are produced at precisely the same time as the magnetic fields are generated and propagate so that their \mathbf{k} vectors are perpendicular to azimuthal magnetic fields in the plasma — which greatly simplifies data interpretation. In our experiments, we use the propagation properties of lower-order harmonics (that is, the third, fourth and fifth harmonics).

These results were obtained with the Vulcan laser system (wavelength 1.054 μm , pulse energy up to 90 J, pulse duration about 1 picosecond). The beam was p -polarized and focused to a maximum intensity of $9 \times 10^{19} \text{ W cm}^{-2}$ onto a thin solid target (0.1–1.0 mm). The polarization com-

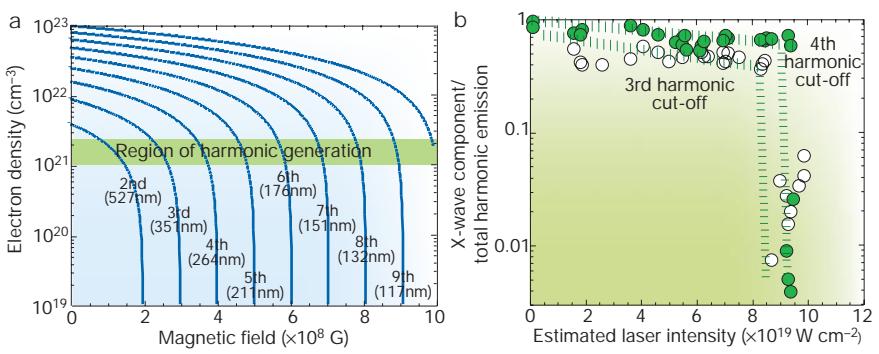


Figure 1 Laboratory measurement of magnetic fields greater than 340 megagauss. **a**, Plot of x -wave cut-offs for various harmonics (second, third, and so on) of 1.054- μm radiation in terms of plasma electron density and magnetic field. **b**, X -wave/total harmonic emission of third harmonic (hollow circles) and fourth harmonic (filled circles) for a series of laser shots.