Flashing males win mate success

SIR — The spectacular bioluminescent displays of male fireflies (Coleoptera: Lampyridae) are widely regarded as advertisement signals under sexual selection pressures[1]. However, despite extensive work on species identity[2], mimicry[3] and synchrony[4] in bioluminescent signalling systems, potential influences of intra- and intersexual selection on the evolution of flash characters have never been demonstrated in any species. Here, we report the first evidence for intersexual selection on a bioluminescent signal character. Using a novel photic playback experiment, we determined that females of the Nearctic firefly species *Photinus consimilis* prefer flash rates that exceed the mean rate in the male population but prefer flash lengths that approximate the mean. This combination of directional and stabilizing selection indicates that females do not simply choose signals containing high photic power.

The *P. consimilis* signalling system includes elements typical of many Lampyridae[5]. Males signal while slowly flying 1–3 m above the ground. A stationary female on the ground which detects a male's signal may reply with a dimmer signal after a characteristic delay; this often attracts the male to her vicinity. A signalling dialogue may ensue and culminate in courtship and mating.

Male signals are 0.7–3.1-s flash 'trains' given at 2.5–4.0 trains per min. The males fly 3–6 m between producing successive flash trains, but usually hover while flashing. Each flash in a train is approximately 70 ms long (F). Radiant intensity during a flash rises gradually to a plateau, then slowly decays. Flash period (T) and interflash interval (T–F) within a train are influenced by temperature and may be predicted by least-squares linear models; the average male flash rate ($\bar{T}^{-1}$) at

23.3 °C is 3.3 s^{-1} (n=61). Female signals consist of 1–12 flashes which begin 6–10 s after the end of a male's flash train. At 23.3 °C, the female flash rate is approximately 2 s^{-1} (n=28).

Contrary to the conventional wisdom that flash characters are fixed entities within firefly species[6], we found that temporal characters in *P. consimilis* signals varied considerably between males. We video-recorded flash trains from 61 males flying at Roaring River State Park, Missouri, corrected their flash rates, and consequently their inter-flash intervals, to values predicted for 23.3 °C, and calculated mean values for all characters of each individual (Fig. 1).

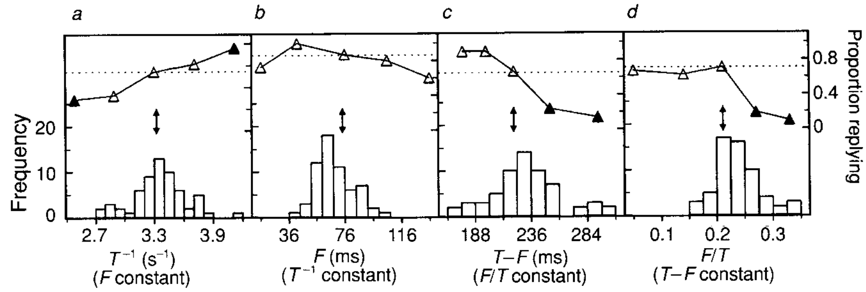

FIG. 1 Between-male variation and female preference for 4 male signal characters in *Photinus consimilis*: *a*, Flash rate, T^{-1} (T=flash period) (n = 22); *b*, flash length, F (n = 15); *c*, inter-flash interval, T–F (n = 21); *d*, duty cycle, F/T (n = 21). Histograms, proportions of males whose mean temperature-corrected values for a signal character fell within the given bins. Arrows, population means. Triangles, proportions of females (n = 15–22) that exhibited one or more flash replies to simulated male signals with the given level of the character; proportions that differed significantly (P<0.05; G-test, with Holm correction for multiple tests) from proportion responding to the mean level (dotted line) are shown solid. Simulated signals were created and edited by computer, transferred to digital audio tape (DAT), and played back through a frequency-to-voltage converter at 3.5 trains per min; their voltage was used to drive photic output of a light-emitting diode (LED = 580 nm) positioned 1.5 m above the female.

Because of the marked variation in all temporal characters, we investigated whether female *P. consimilis* evaluate the flash characters of potential mates and thereby discriminate among them. Using a photic analogue of the acoustic playback experiment, we tested the responses of females to simulated male signals in which intensity, and spectral and temporal characters were controlled (Fig. 1). We held peak radiant intensity and wavelength constant for every trial, and adjusted values of temporal characters to one of five levels spanning the range displayed by the male population at the temperature of the trial.

To test the influence of number of flashes per train (N) on female response, we fixed all other temporal characters at levels average for the population and recorded replies to the five selected N levels: 2, 4, 6, 8 and 10 flashes. We detected no differences between the proportions of females replying to the various N levels. However, the mean frequency with which females replied to the lowest N level and the number of flashes included in those replies are significantly lower than in replies to the mean N level.

Testing the influences of the other temporal characters was more difficult. Only one character could be fixed at a time, because flash rate, inter-flash interval, flash length and duty cycle (F/T) are interdependent. If, for example, flash length were fixed, a heightened response to shorter inter-flash intervals might reflect preference for higher flash rate or higher duty cycle. Thus, in order to determine the influence of any single character on female response, it was essential to combine results from tests of all four characters. We therefore conducted four series of trials, in each series fixing one character (and N = 6) at the level average for the population. We presented 1 character in each series at five selected levels; the two remaining characters varied necessarily. Our tests revealed significant differences between the proportions of females replying to the levels of each variable character except flash length (Fig. 1). Flash rate was the fixed character in the series of trials wherein flash length was the designated variable (Fig. 1*b*); absence of differential responses only in this series indicated that females were influenced primarily by flash rate. But female replies to very brief and long flashes are both less frequent and include fewer flashes than do replies to the mean male flash length (Fig. 2).

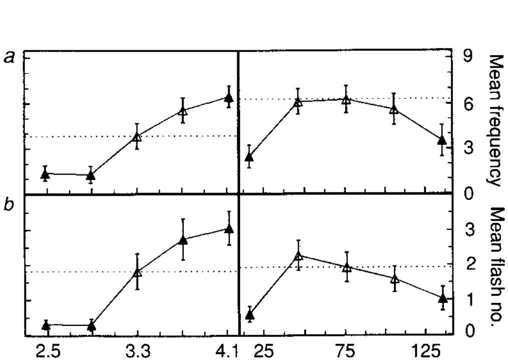

FIG. 2 Frequency and number of flashes in female *P. consimilis* replies shown in Fig. 1 (*a*, *b*). *a*, Mean (± s.e.) frequency of the nine successive flash trains presented to a female that were followed by her reply; frequencies that differed significantly (P<0.05; Wilcoxon matched-pairs signed-rank test, with Holm correction for multiple tests) from the frequency of replies to the mean level are shown shown solid. *b*, Mean (± s.e.) of the average number of flashes in a female's replies; flash numbers that differed significantly (P<0.05) from flash numbers in replies to the character's mean level are shown solid.

Results from the photic playback experiment demonstrate strong directional selection favouring rapid male flash rates in *P. consimilis*. Females are more likely to reply to simulated male flashes delivered at faster rates, and their replies to the faster rates include more flashes (Fig. 2). Because visible female replies are an essential prelude to pair formation, a male's mating success and fitness should be proportional to his flash rate, provided that his flash number exceeds a minimum value and his flash length approximates the mean.

Neither flash number nor flash length is correlated with flash rate (P>0.10) in signals recorded from the male population. Consequently, female preference for high flash rate is unlikely to select indirectly for other signal features. Although the striking discrepancy between the average and preferred male flash rates (Fig. 2) indicates that such female preference is strong, our data alone cannot support any one sexual selection model over another.

The finding that female *P. consimilis* identify male flashes based on their rate but not their power indicates the operation of a perceptual filter yielded by phasic neural responses to flash onsets, followed shortly thereafter by adaptation and inhibition[7]. Such neural processing may be an ancestral feature. Moreover, this feature could represent an evolutionarily conservative mechanism in neural systems[8], which could account, in part, for some astonishing similarities in female choice for rapid rhythms observed among diverse species in pulsing visual, acoustic[9] and now photic signals.

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