Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*

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THE sensory bases of species and population mate preferences are well known[1–3]; in frogs properties of the female auditory system influence such preferences[2,3]. By contrast, there is little understanding of how sensory characteristics could result in sexual selection within a population. One possible mechanism is that females are more sensitive to male courtship signals that deviate from the population mean. We document this mechanism in the frog *Physalaemus pustulosus*. Female basilar papilla tuning is biased toward lower-than-average frequencies in the 'chuck' portion of the male's call, explaining female preference for the lower-frequency chucks produced by larger males. The tuning does not differ between *P. pustulosus* and its close relative *P. coloradorum*, a species in which males never evolved the ability to produce chucks; thus the female tuning evolved before the chuck and therefore the chuck played no role in the evolution of the preference. This allows us to reject two popular hypotheses for the evolution of this female preference (runaway sexual selection and natural selection) in favour of a third: sexual selection for sensory exploitation.

Male *P. pustulosus* produce an advertisement call consisting of a 'whine', which is necessary and sufficient for species recognition, followed by 0–6 'chucks', which increase the attractiveness of the call to females[4–8]. Chucks have a fundamental frequency of ~220 Hz with 15 harmonics. Most of the energy ($\bar{X} = 90\%$, s.e. = 0.02, $N = 110$) is above 1.5 kHz, and thus mainly stimulates basilar papilla receptors rather than the lower-frequency amphibian papilla receptors[9,10]. In phonotaxis experiments, females prefer synthetic calls having chucks with lower fundamental frequencies. Larger males produce lower-frequency chucks and have greater mating success in nature. Thus preferential female phonotaxis generates sexual selection[4–8].

This preference could result from the upper harmonics of lower-frequency calls eliciting greater neural stimulation of the high-frequency basilar papilla receptors due to differences in peak frequency or harmonic structure[11]. Similar mechanisms appear to guide interspecific and interpopulational mate choice[3,10,12]. In all studies to date in which female mate preferences based on call frequency are expressed, tuning of the peripheral auditory system predicts the preference by indicating frequencies that would most strongly stimulate the auditory system. There are no reported examples of any mechanisms overriding this peripheral bias. We tested whether differences in auditory stimulation could account for interspecific mate choice by obtaining acoustically-evoked multiunit activity from the torus semicircularis (inferior colliculus) to estimate the frequency sensitivities of the amphibian and basilar papillae[3,13]. Resulting audiograms were averaged and truncated below 1.5 kHz to yield a mean basilar papilla audiogram (Fig. 1). We then determined the Fourier spectrum (energy versus frequency)[3] of chucks from 54 males randomly sampled from a population on Barro Colorado Island, Panama[4–8] (Fig. 1). The mean dominant (peak energy) frequency of the chucks (2.55 kHz) was higher than the mean best frequency of the basilar papilla (2.13 kHz).

We quantified each chuck's stimulation of an average basilar papilla using a computer model that treated the audiogram as a filter and measured how much energy in a chuck would pass through it. We then determined how a change in the frequencies

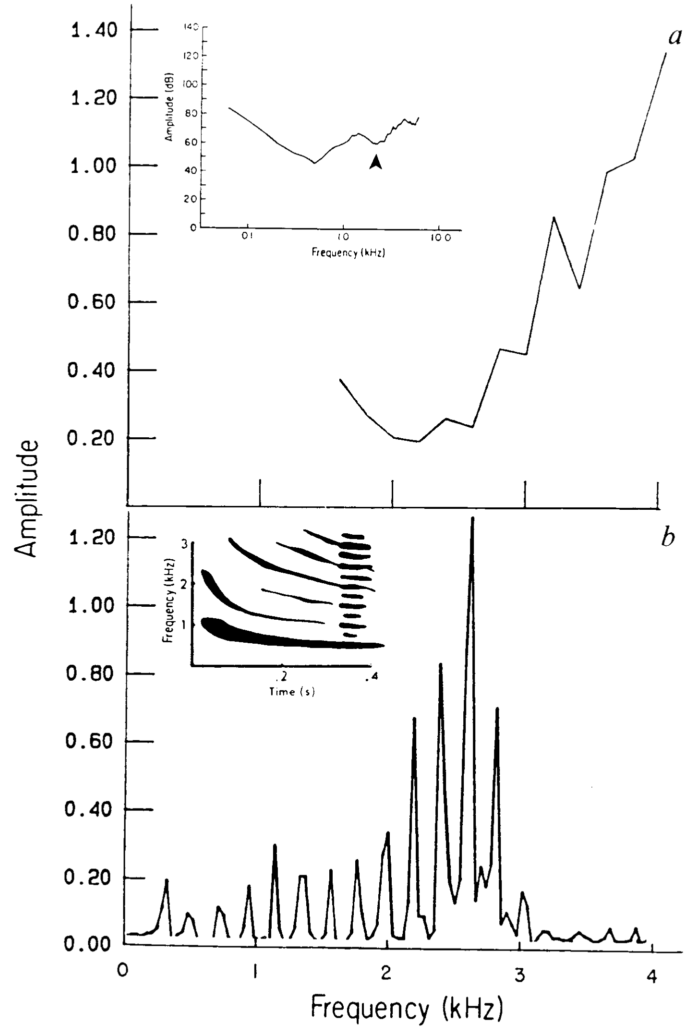

FIG. 1 *a*, The mean audiogram of the basilar papilla of *P. pustulosus* derived from five individuals. Audiograms represent thresholds as a function of frequency, determined for sinusoidal, closed-field stimuli using 1–2 MΩ glass electrodes. The truncation of the audiogram below 1.5 kHz to eliminate influences of amphibian papilla neurons and the slight broadening of the tuning curve resulting from averaging biases the results toward the null hypothesis. Insert, audiogram from a single frog; basilar papilla best frequency is marked by arrow. Male and female audiograms did not differ. *b*, Representative Fourier spectrum of a chuck. Insert, sonogram of a whine plus a chuck.

of each chuck would influence the amount of neural stimulation. Each chuck's Fourier spectrum was multiplied by a series of numbers ('frequency multipliers') in 0.01 increments between 0.95 and 1.05, and resultant spectra corrected so that total power remained constant. For the chuck of each male, we determined the optimal frequency multiplier, that is, one resulting in a chuck that elicited the greatest neural stimulation (the 'optimal chuck').

Our hypothesis that chucks with lower fundamental frequencies elicit greater neural stimulation predicts that the average optimal frequency multiplier is less than 1.0 (the unmanipulated chuck). Our data support this hypothesis: the average optimal frequency multiplier is 0.98 (s.e. = 0.009), and is significantly less than 1.0 (one-tailed Student's t test; $t = 2.0$, d.f. = 53, $P = 0.025$; Fig. 2). Also consistent with our hypothesis, the mean dominant frequency of the optimal chucks ($\bar{X} = 2.489$ kHz, s.e. = 0.05) is significantly lower than that of the unmanipulated chucks ($\bar{X} = 2.552$ kHz, s.e. = 0.058; one-tailed paired t test; $t = 2.48$, d.f. = 53, $P = 0.02$). Therefore, the patterns of mate choice reported in nature[4–7] and the response of females in phonotaxis experiments[4–7] are predicted by the relationship

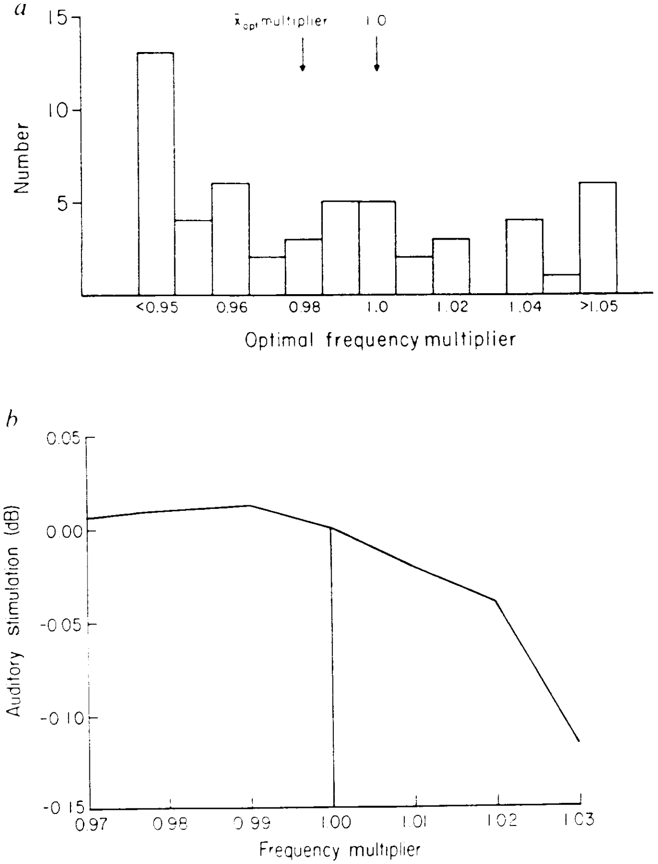

FIG. 2 *a*, The distribution of frequency multipliers resulting in chucks that maximize stimulation of the basilar papilla. Stimulation by a call was assessed by summing call pressure squared divided by auditory threshold squared at 10-Hz intervals through the basilar papilla audiogram, then taking 20 × log of the square root of this sum to yield the energy passing through the basilar papilla filter function. *b*, Average amount of neural stimulation, in dB, is 20 × log of the ratio of energies passing through an average basilar papilla audiogram from a manipulated chuck and an unmanipulated chuck, as a function of frequency multiplier across all calls tested.

between peripheral tuning and chuck frequencies. Furthermore, the disadvantage of producing a nonoptimal chuck is asymmetric (Fig. 2). As the chuck falls below optimal frequency, neural stimulation decreases only slightly, but there is a greater decrement in stimulation when the frequency of the chuck is increased above the optimal chuck. The asymmetry indicates stronger selection against chucks that are too high relative to chucks that are too low in frequency.

Three alternative hypotheses address the evolution of female preferences. Fisher's runaway sexual selection hypothesis[14-16] suggests that female preferences and male traits are genetically correlated, and that preferences will evolve as a correlated response to selection on the male trait. The natural selection hypothesis[17,18] postulates that female preferences evolve due to reproductive benefits accrued by choosing certain males. Sexual selection for sensory exploitation[11,19-22] hypothesizes that males evolve traits that exploit preexisting biases in the female's sensory system. Only the sensory exploitation hypothesis predicts that the evolution of the female trait (basilar papilla tuning) precedes the male trait (the chuck). Fisherian and natural selection hypotheses require the male trait to precede or coincide with the female trait. We assessed these hypotheses by measuring basilar papilla tuning in seven individuals of the closely related species *P. coloradorum*. This species does not produce chucks, and the ability to produce chucks was derived in *P. pustulosus* after these species diverged[23,24].

There was no significant difference between the average basilar papilla best frequencies of *P. pustulosus* ($\bar{X} = 2.13$ kHz, s.e. = 0.07) and *P. coloradorum* ($\bar{X} = 2.23$ kHz, s.e. = 0.13; two-tailed Students $t = 0.63$, $P = 0.54$; Bartlett test for homogeneity of variances, $F = 2.31$, d.f. = 1, $P = 0.13$). It is most parsimonious to assume that the identical basilar papilla tuning in the two species is a trait shared by a common ancestor, and therefore existed before the chuck evolved in *P. pustulosus*. Female *P. pustulosus* do have more eggs fertilized when they mate with larger males[4]. Although this advantage could help maintain the preference once it is expressed, it cannot be argued that females evolved their tuning characteristics to gain this reproductive advantage. Rather, the existence of identical tuning before and after the evolution of the chuck supports the sensory exploitation hypothesis, that in *P. pustulosus* lower frequency chucks exploit preexisting biases in the female's sensory system, but not the Fisherian or natural selection hypotheses. □

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