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## Research Letters / Navorsingsberigte

### Stabilizing or directional selection in signalling systems: Investigations in a population of painted reed frogs, *Hyperolius marmoratus*

Numerous studies in sexual selection have been interpreted as showing that components of the signalling system involved in mating are under strong directional selection due to female preferences for elaborate traits. Conversely, the recognition concept of species predicts strong stabilizing selection on the specific-mate recognition system. We document directional preferences in a population of the African painted reed frog, *Hyperolius marmoratus*, in two-choice phonotaxis experiments, utilizing synthesized calls. Females failed to respond consistently to population mean values of specific-mate recognition system signal components in choice experiments presenting mean and extreme value stimuli. Even the least-preferred extremes of coupled signal components were still effective in eliciting phonotactic responses. Our results provide no evidence for stabilizing selection within the tested range. However, there is also no evidence for an open-ended directional preference spanning the natural range of male stimuli. The claims of the recognition concept are examined. We believe that it is incorrect to argue whether or not the recognition concept is 'correct'. Rather, it provides an explicit null hypothesis. Studies in sexual selection are concerned with instances in which the assumptions of the recognition model are violated (e.g. where males signal variation in the benefits that they provide females). Understanding this issue should reduce the amount of confusion in the literature, and clarify our objectives when it comes to investigating the selective forces manifest in signalling systems.

There is a continuing debate about the relative importance of directional and stabilizing selective forces in shaping signalling systems. Numerous studies in sexual selection have been interpreted as showing that components of the signalling system involved in mating are under strong directional selection due to female preferences for elaborate traits.<sup>1</sup> In contrast, the recognition concept of species (RC) predicts strong stabilizing selection on the specific-mate recognition system (SMRS).<sup>2</sup> Paterson's concept emphasizes the co-adaptation between signalers and receivers; in the species' preferred habitat, individuals with aberrant signal or receiver traits have reduced fitness and consequently the system is subject to strong stabilization.

These two views seem contrary, and the research approaches in dealing with the integration of these two schools of thought differ substantially. Several workers have attempted to reconcile them.<sup>3,4</sup> Others have attempted to deride one or the other (sexual selection;<sup>2,5,6</sup> the RC<sup>7,8</sup>), and many researchers in sexual selection continue to cite Paterson's work in a manner which appears to ignore the inherent contradictions.<sup>9-12</sup> This confusion requires clarification and we believe that a conceptual house-cleaning is in order. In this paper we report on investigations into directional

female preferences in the painted reed frog, *Hyperolius marmoratus*. We use coupled components of synthesized calls for which the direction of female preference is known. Our results are then discussed in the light of the RC and sexual selection theory.

#### Materials and methods

Phonotaxis experiments were conducted during December 1993 and January 1994, on female *H. marmoratus* in Zululand, South Africa. Amplexing pairs were collected in the field between 21:00 and 22:30 and transported to the test site. Females were tested on the night of capture. They were separated from males before testing and placed individually in the centre of an outdoor arena (3 × 3-m canvas floor with 0.5-m-high canvas walls) beneath a perforated plastic release box. Two loudspeakers were positioned facing one another, at opposite ends of the arena, each 1 m from the release box. Acoustic stimuli were broadcast through the loudspeakers. After an acclimatization period (5 min for the first trial, and 2 min for subsequent trials) the release container was lifted and removed from the arena. A positive response was scored if the female approached to within 10 cm of the loudspeaker and turned to face it, or made physical contact with it. A 'no response' was scored if females failed to respond within a 10-min period or left the arena. Females were discarded after three no responses. Female snout-vent lengths (SVL) were measured. Air temperature was measured with a Digitemp DT2010 digital thermometer, and ranged between 18.8°C and 24.9°C over the study period.

Stimuli were broadcast using a Uher 4200 stereo tape-recorder, a Klein and Hummel SB280/II stereo amplifier and two Philips AD50600 5-inch diameter loudspeakers. The peak sound pressure levels (SPL) of all stimuli were set at 104 dB at 50 cm (natural call intensity) using a Brüel and Kjaer 2209 sound-level meter. The arena was dimly lit by a 40-W red light bulb suspended 1.5 m above ground level.

Four stimuli were broadcast in pairwise combinations (six combinations). Three of the stimuli were synthetic *H. marmoratus* calls that differed in frequency and call repetition rate (Table 1), but were identical in all other respects. These stimuli were named normal, fast/low and slow/high. The frequency and call repetition rate of the normal stimulus were close to the mean population values. The fast/low and slow/high calls had frequencies and call repetition rates that fall at the extremes of the natural population range (see Table 1). The fourth stimulus consisted of a 100-ms burst of white noise (0–24 kHz) with a duration of 50 calls min<sup>-1</sup>. Previous work has shown that female *H. marmoratus* prefer calls with frequencies below the mean<sup>13</sup> and above average call rates.<sup>14</sup> Call duration was not manipulated since the direction of female preference for this parameter is unknown. Although females of this species preferentially approach the louder of two stimuli,<sup>15</sup> the correlation between sound pressure levels and distance could confound data interpretation.

Each female was tested in up to six trials, but only once in any single pairwise stimulus combination. Trial order was

Table 1. Synthesized and natural call parameters.

	Frequency range [centre frequency] (kHz)	Mean call repetition rate (calls min <sup>-1</sup> )
Natural call	2.24–4.05# [2.98]#	56* [range 40–75]*
Synthesized stimuli		
Slow/high	3.05–3.55 [3.30]	25
Normal	2.65–3.15 [2.90]	50
Fast/low	2.25–2.75 [2.50]	100

#Natural frequency parameters obtained by pooling data from Dyson<sup>26</sup> and Telford.<sup>27</sup>  $n = 151$ .

\*Mean call repetition rate and range from Dyson.<sup>26</sup>  $n = 47$ .

randomized and loudspeaker positions were switched between trials. We assume that a female's choice in one trial did not influence her choice in subsequent trials. Ten stimulus–noise trial combinations were performed to assess whether the synthesized stimuli were effective in eliciting female responses relative to the control (noise) stimulus. For fast/low–slow/high and normal–slow/high combinations, 20 trials were conducted. Fast/low–normal trials were continued until the end of this species' breeding season (for reasons discussed below). The response data were analysed using exact binomial tests.<sup>16</sup> Non-parametric analyses (Mann-Whitney  $U$  tests) were used when data could not be normalized. Parametric tests were used on normally distributed data. Results are adjusted for significance using the sequential Bonferroni test.<sup>17</sup> Unless otherwise stated, two-tailed test statistics are presented. The alpha significance level was set at  $P = 0.05$ .

## Results

Noise stimuli did not elicit phonotactic responses (Table 2). Females preferentially responded to fast/low stimuli when given a choice between fast/low and slow/high calls ( $P = 0.009$ ), and to normal stimuli when given a choice between normal and slow/high calls ( $P = 0.00004$ ). There was no significant difference in female responses to fast/low or normal calls when they were pitted against one another ( $P = 0.34$ ) (Table 3). This trial combination was continued until the end of the breeding season in order to establish if a significant preference may have become evident at larger sample sizes. The direction of female responses was not influenced by temperature or response time, but was influenced by female size. Females that approached the fast/low stimuli

were significantly larger than those approaching either normal or slow/high stimuli [fast/low–normal:  $t = 2.05$ ; d.f. = 26;  $P$  (one tailed) = 0.03; fast/low–slow/high; Mann-Whitney  $U$ ;  $Z = -2.22$ ;  $P$  (one tailed) = 0.03]. One-tailed tests were used due to prior predictions.<sup>18,19</sup>

Where the influence of temperature and response time could be tested for, they showed no significant influence (Mann-Whitney  $U$  tests; temperature; fast/low–slow/high,  $P = 0.14$ , fast/low–normal,  $P = 0.94$ ; response time; fast/low–slow/high,  $P = 0.48$ , fast/low–normal,  $P = 0.23$ ). Female responses were examined for a consistent preference for either side of the testing arena. No significant end bias was present (binomial exact,  $P = 0.759$ ).

## Discussion

We failed to show female *H. marmoratus* responding consistently to population mean values of signal components of the SMRS in phonotactic choice experiments presenting mean and extreme value stimuli. Our stimulus–noise experiments showed that even when the least-preferred extremes of these signal components were combined, the stimulus (slow/high) was still effective in eliciting a phonotactic response. Two-choice experiments with the two extremes tested against the mean showed that females preferred the mean stimulus to the slow/high stimulus, whereas there was no preference for or against the fast/low stimulus. Our results provide no evidence for stabilizing selection within the tested range. However, there is also no evidence for an open-ended directional preference spanning the natural range of male stimuli.

Although both frequency and call repetition rates were combined, these results are similar to those expected on the basis of female frequency tuning curves alone, as documented in *Acris crepitans* and *Physalaemus pustulosus*.<sup>18</sup> In both species, the tuning curve of the female basilar papilla is such that the best excitatory frequency is slightly below the mean dominant frequency of male calls in the population. Furthermore, the tuning curve is asymmetric such that the rate of decrease in neural stimulation is more rapid for calls that lie above the optimal frequency than for those that are below this frequency. Behaviourally, such a tuning curve should translate into a preference for the mean when the alternative is a high-frequency call. Depending on the magnitude of the difference between the mean and a low-frequency stimulus, females will show either no preference or will prefer the mean. These tuning curves could be described as allowing females to preferentially mate with males with low-frequency calls (large males). Alternatively, given the asymmetry in the tuning curve, it might be more accurately described as decreasing the probability that females mate with small males.

The RC has been closely associated with claims that the mean male signal value should coincide with the mean female receiver tolerance; this is a consequence of stabilizing selection. In

Table 2. Stimulus–noise phonotactic responses of *H. marmoratus* females (exact binomial test).

Stimulus 1	Number of responses	Stimulus 2	Number of responses	Binomial probability *(adjusted Bonferroni probability)	Number of non-responses
Fast/low	8	noise	0	0.008 *(0.024)	2
Normal	10	noise	0	0.002 *(0.006)	0
Slow/high	10	noise	0	0.002 *(0.006)	0

Table 3. Two-choice phonotactic responses of *H. marmoratus* females (exact binomial test).

Stimulus 1	Number of responses	Stimulus 2	Number of responses	Binomial probability *(adjusted Bonferroni probability)	Number of non-responses
Fast/low	11	normal	17	0.34 *(1.000)	0
Fast/low	16	slow/high	4	0.009 *(0.027)	0
Normal	19	slow/high	1	< 0.000 *( < 0.000)	0

anurans, we suggest that these claims are only partly correct. Here we consider only call frequency. First, tuning curves suggest an optimal frequency which elicits a maximal female response. However, the mean dominant frequency of males does not coincide with this value in the two species where data are available (*A. crepitans* and *P. pustulosus*).<sup>18</sup> Hence, any stability in the male signal through time in these two species cannot be attributed solely to an internal equilibrium generated by the coadaptation of male signallers and female receptors.

Simple physical constraints mean that receptors can only perceive a limited range of stimuli, the extremes of which will be less effective in stimulating the neural system. Therefore, at a trivial level, it is true that all mating signals are subject to stabilizing selection. However, the stronger claim that they are stabilized by current interactions between males and females is only true if females discriminate against the extremes of the natural range in variation. Only a few studies have shown this (e.g. in *Hyla cinerea*).<sup>20</sup> Moreover, even when a preference for the mean is seen, this translates into actual stabilizing selection only if the preference also effects male mating success in the field.

It has been suggested that one can reconcile the RC and sexual selection studies by separating mating signals into essential (SMRS) and non-essential (sexual selection) components.<sup>3</sup> However, this approach is flawed because large variation in essential components (also described as those involved in species recognition) often causes variation in mating success and hence may be attributed to sexual selection.<sup>21</sup> We believe that the distinction between mate recognition and mate selection is fallacious.

Most neuroscientists agree that a preference among alternate stimuli results from enhanced neural stimulation at some level of the nervous system.<sup>22</sup> Anuran sensory systems are often biased towards species-specific information, with the spectral tuning of the auditory system tending to match the spectral composition of the conspecific advertisement call. Signals having frequencies higher or lower than the frequency band to which the auditory system is tuned will not stimulate the nervous system as effectively as a signal with a frequency that matches the optimum band. This would explain why conspecific calls generally elicit phonotactic responses more readily than heterospecific calls.<sup>20</sup> However, heterospecific signals cannot be regarded as mere noise (*sensu* Littlejohn).<sup>23</sup> Most anurans probably do not have advertisement calls that are able to stimulate heterospecific females' auditory systems sufficiently to elicit a response and interspecific interactions are probably negligible in most anurans.<sup>20</sup> Even in cases where the heterospecific call is capable of eliciting a response, conspecific calls have been found to be more effective than, and preferred to, the heterospecific signal. Females, under natural conditions, will almost certainly be faced with a conspecific-heterospecific choice, and female response to heterospecifics will probably never be naturally manifest or have evolutionary consequences. Mate recognition will almost always appear, superficially, to be an all-or-none quantum process (as predicted by the RC). However, there appears to be no 'appropriate' signal that stimulates a female to respond, but rather a gradient of signals that provide varying levels of stimulation to the females' auditory systems. Therefore, what appears superficially as a quantum process need not be so. Heterospecific calls can elicit a response in the absence of conspecifics.<sup>21,24,25</sup> The interpretation borne from the recognition concept of species has a tendency to conceal the proximate basis in the act of recognition – that conspecific calls are responded to because of the increased level of stimulation that these calls provide, relative to that of heterospecifics. The field for gene recombination can therefore be thought of as an incidental consequence of the underlying receiver sensory properties, that is, be delimited by the manifes-

tations of female mating preferences. At the proximate, mechanistic level, the processes of mate selection and mate recognition are essentially identical.

We suggest that it is more correct to view the RC as holding a position in sexual selection or speciation studies analogous to that of the Law of Hardy-Weinberg in population genetical studies. Two assumptions of the RC are: (1) that the only cost to females is the time associated with searching for a mate, hence a preference for the mean is most beneficial; and (2) that males do not signal variation in the benefits that they provide females (either direct or genetic). Clearly, these assumptions are unrealistic in many species. Most sexual selection studies aim to investigate the effect of violation of these assumptions. Why don't mean male signal and mean female preference coincide? Why do females have effectively open-ended preferences for some signal components? If our view is accepted, then it becomes meaningless to argue whether or not the RC is correct, or to dispute its importance in the field of evolutionary biology. The RC should be seen as representing an explicit null-hypothesis in sexual selection studies, providing a necessary basis for investigating the evolution of signalling systems.

Thanks to Phil Bishop and Rob Veale for preparing the stimulus tapes and to Ian and Jean Garland for permission to work on their property. Rob Brooks, Chris Byl, Tim Halliday, Neville Passmore, Steven Snyman and an anonymous referee provided helpful comments on previous drafts of this paper. This project was funded by FRD (South Africa) and the CBRG (University of the Witwatersrand). M.D.J. is funded by the Rhodes Trust (Oxford).

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Received 19 October 1994; accepted 9 March 1995.

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## Coupled chaotic oscillators and control of chaos

Chaotic attractors typically have embedded within them an infinite number of unstable periodic orbits. This observation can be used to control chaos. Long-period orbits can be stabilized. Here we show that chaos can be controlled by a weak coupling of two identical chaotic systems.

Recently, many authors have discussed the controlling of chaos in nonlinear dynamical systems.<sup>1–9</sup> The control of chaos can be realized by applying a proportional feedback at a Poincaré section<sup>1–5</sup> as proposed by Ott, Grebogi and Yorke.<sup>1</sup> Alternatively, the control of chaos can be obtained by using conventional set point feedback,<sup>6</sup> by using perturbations to drop their system into Arnold tongues of periodic behaviour,<sup>7</sup> or by using weak periodic oscillations to drive one of the control parameters.<sup>8,9</sup> In this paper we show that chaos can also be controlled by a weak coupling of two chaotic oscillators. Several couplings are discussed.

It is well known that anharmonic systems with an external periodic perturbation

$$\frac{d^2x}{dt^2} + \mu \frac{dx}{dt} + bx + cx^3 = k \cos(\Omega t), \quad (1)$$

( $\mu > 0$ ,  $c > 0$ ) can show chaotic behaviour for certain ranges of the parameters  $\mu$ ,  $b$ ,  $c$ ,  $\Omega$  and  $k$  (compare refs 10–17 and references therein). For example, from numerical calculations we find that the one-dimensional Lyapunov exponent  $\lambda_L$  (where we select the biggest rate) is given by  $\lambda_L = 0.55$  for the values  $\mu = 1$ ,  $b = -10$ ,  $c = 100$ ,  $\Omega = 3.5$  and  $k = 1.55$ . The quantity  $\lambda_L$  measures the sensitivity to initial conditions and is therefore an indicator of the degree of chaos.

When (1) is written as a system according to

$$\frac{dx}{dt} = y, \quad \frac{dy}{dt} = -\mu y - bx - cx^3 + k \cos(\Omega t), \quad (2)$$

an attractor can be defined, since (2) is invariant under  $x \rightarrow x$ ,  $y \rightarrow y$  and  $t \rightarrow t + 2\pi n/\Omega$  ( $n \in \mathcal{N}$ ). Here  $\mathcal{N}$  denotes all the natural numbers. We mark all points in  $\mathcal{R}^2$  with the coordinates

$$(x(2\pi n), y(2\pi n)).$$

This is called the Poincaré map.<sup>15–17</sup> This map now allows the detection of periodic, quasiperiodic and chaotic solutions. This means it leads to the attractor of the dynamical system. Numerical results from this map indicate that there is chaotic behaviour. Moreover, we find that the autocorrelation functions  $C_{xx}$  and  $C_{yy}$  decay. Thus there is no correlation between  $x(t)$  and  $x(t+T)$  for a large time interval  $T$ . The same holds for  $y(t)$ . Notice that for  $\mu = k = 0$ ,  $b < 0$  and  $c > 0$  there is a homoclinic orbit.<sup>15–17</sup> Thus we can apply the theory of Melnikov.<sup>15–17</sup> This is a perturbation theory (the unperturbed case is  $k = 0$  and  $\mu = 0$ ) to calculate the onset of chaos.

We study two linearly coupled anharmonic oscillators with an external periodic force [see (2)] and the bifurcation parameters given above. The two oscillators are identical. In addition we consider two linearly coupled limit cycle systems with an external periodic force. For both systems, which behave chaotically without coupling, we find that the coupled system can behave regularly for certain values of the coupling constant. We let digital time integrations run for a long time so that all transients have decayed and then allow a single trajectory to wander over the final attractor. It is important to notice that the behaviour of nonlinear dynamical systems also depends on the initial conditions. For different initial conditions we could find different domains of attractions.

Our coupled anharmonic system is of the form

$$\frac{d^2x}{dt^2} + \mu \frac{dx}{dt} + bx + cx^3 = k \cos(\Omega t) + g \frac{du}{dt} \quad (3a)$$

$$\frac{d^2u}{dt^2} + \mu \frac{du}{dt} + bu + cu^3 = k \cos(\Omega t) + g \frac{dx}{dt}, \quad (3b)$$

where  $g$  is the coupling constant. We introduce the quantities  $y = dx/dt$  and  $v = du/dt$  and therefore (3) can be written as a non-autonomous system of the first order. We choose the parameter values  $\mu$ ,  $b$ ,  $c$ ,  $\Omega$  and  $k$  in such a manner that there is chaotic behaviour for  $g = 0$ . In the following we use the values given above. Now we study (3) in relation to the coupling constant  $g$ . In particular we are interested in whether or not regular behaviour can arise for certain values of  $g$ . To characterize the chaotic motion we have calculated the one-dimensional Lyapunov exponent (we select the biggest rate), the autocorrelation functions, and the attractor.

We consider the initial values:  $x(0) = 0.8$ ,  $dx(0)/dt = 1.0$ ,  $u(0) = 0.5$ ,  $du(0)/dt = 1.2$ . Figure 1 shows the phase portrait for the uncoupled system where  $g = 0$  (chaotic case). From our numerical studies we find the following: For  $g = 0.40$  we find periodic