Modeling Neural Circuits to Understand Incipient Speciation in Chorus Frogs

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Introduction

- Species interactions propel biodiversity and can shape evolutionary trajectories among populations
- Species interactions can promote speciation when unfit hybridization results in the selection of traits that promote divergence of mating behavior to prevent hybridization
- Divergence of mating behaviors leads to reproductive isolation among populations of the same species
- The current study probes at the genetic drivers of reproductive isolation in the upland chorus frog (Pseudacris feriarum) through analyzing the variation in female preference for male mating calls
- The variation in male acoustic signaling is primarily observed in P. feriarum sympatric populations, which have diverged due to interactions with other species (e.g. P. nigrita). The male acoustic signal varies little in allopatry, where no closely-related species exist

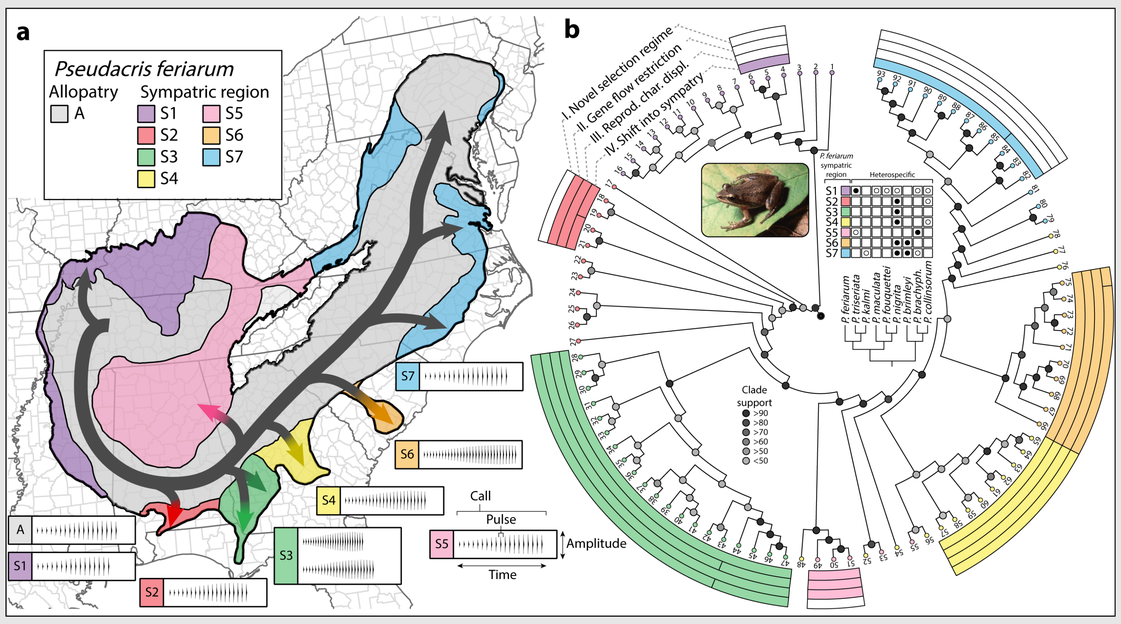

Figure 1. Diversification of mating signals in the upland chorus frog (P. feriarum). (a) The upland chorus frog has expanded from an ancestral region (gray) into the ranges of heterospecifc species (sympatry, colored ranges) multiple independent times. In many of these cases, the male mating call has diverged (see oscillograms representing the calls) in response to selection on females to avoid hybridization. (b) Phylogenetic relationships among P. feriarum sampled across the range, showing the independent expansion into sympatric regions. The inset shows the phylogenetic relationships among the trilling chorus frogs and the interactions of P. feriarum with those species.

Behavioral Data

- In a previous study (Lemmon 2009), male calls were recorded across the geographic range of the species. In addition, the preferences of females for different call types were assessed using binary choice experiments.

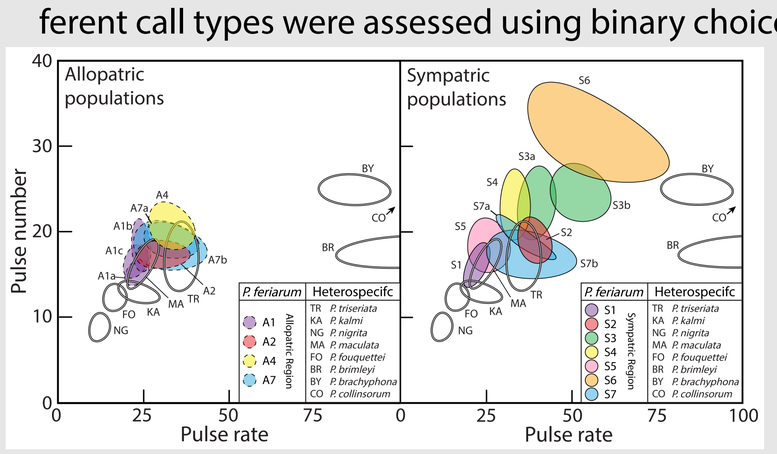

Figure 2. Distributions of male calls recorded in different allopatric (left) and sympatric (right) populations. Distributions are represented by 50% confidence envelopes. Note the increased diversity of calls among sympatric populations, compared to allopatric populations.

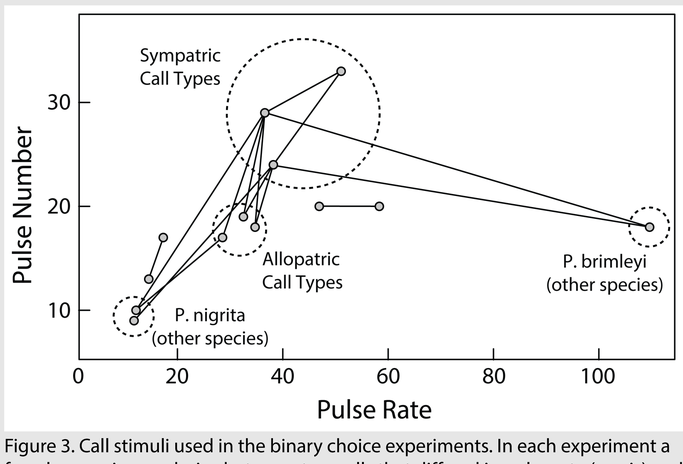

Figure 3. Call stimuli used in the binary choice experiments. In each experiment a female was given a choice between two calls that differed in pulse rate (x-axis) and pulse number (y-axis). Each call is represented by a grey point. Each line in the graph connects two calls that females were asked to choose between.

PopID	Call 1	Call 2	#pref1	#pref2
S6	S6	A2	25	4
S6	S6	S3a	19	7
S6	$S6^{BR}$	BR^{S6}	10	11
S6	$S6^{NG}$	NG^{S6}	19	7
S6	S6	S7b	20	8
S6	S6	NG	16	7
S6	S6	BR	21	5
S6	S6	*	8	11
S3a	S3a	S6	34	15
S3a	S3a	A2	27	27
S3a	$S3a^{BR}$	BR^{S3a}	18	11
S3a	$S3a^{NG}$	NG^{S3a}	11	10
S3a	S3a	S7b	14	8
S3a	S3a	NG	12	2
S3a	S3a	BR	9	1
S3a	*	S6	5	15
S3a	*	A2	16	4
S3a	*	S7b	19	1
S3a	*	BR	18	2
S3a	*	#	47	7
S3a	+	#	38	5
S3a	*	+	48	11
A7a	A2	S6	12	11
A7a	A2	S3a	14	8
A7a	$A2^{BR}$	BR^{A2}	18	10
A7a	$A2^{NG}$	NG^{A2}	15	7
A7a	A2	S7b	16	6
A7a	A2	NG	16	3
A7a	A2	BR	18	1
A7a	A2	*	11	8
A2	A2	S6	19	12
A2	A2	S3a	15	10
A2	$A2^{BR}$	BR^{A2}	20	6
A2	$A2^{NG}$	NG^{A2}	15	8
A2	A2	S7b	14	8
A2	A2	NG	16	4
A2	A2	BR	18	2
A2	*	#	33	16
A2	+	#	32	19
A2	*	+	31	20

Table 1. The raw behavioral data to which neural models were fit. Behavioral data were collected in two allopatric populations (A2 in Alabama and A7a in North Carolina), and two two sympatric populations (S3a in Florida, and S6 in South Carolina).

Neural Circuit

- Previous work in neurophysiology (Naud et al. 2015; Aluri et al. 2016) has identified a neural mechanism by which female frogs can distinguish among male calls differing in the number and rate of pulses within the calls
- The neural computational model describing this mechanism incorporates the activities of neurotransmitter receptors, which determine the magnitude and duration of effect that each neuron has on the downstream
- Neurotransmitter receptor activities are controlled by the expression level and structure of protiens that make up the neurotransmitter receptor
- By comparing (among populations) the neural model parameters that best fit the behavioral data, we hope to identify the genes that have evolved as the female preferences have diversified across populations

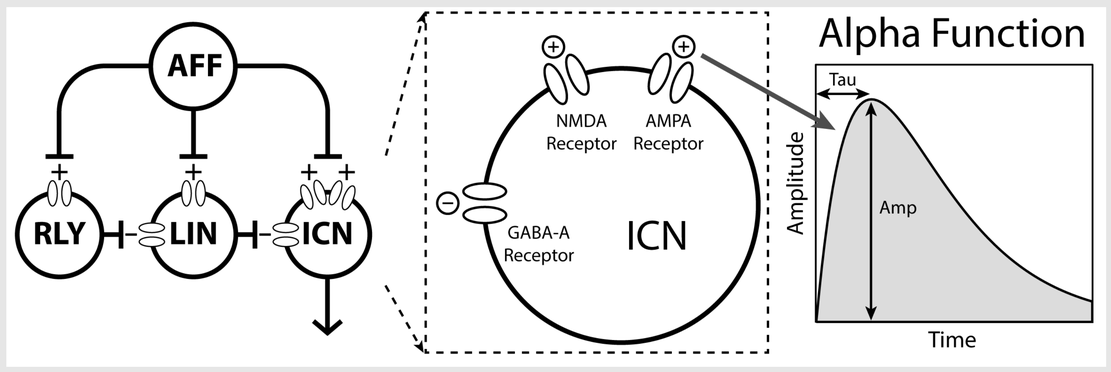

Figure 4. The female preference for male mating signals is modeled using a dis-inhibition circuit involving four neurons, the afferent neuron (which trasmitts a signal from the ear to the mid-brain), a relay neuron (RLY), a long interval neuron (LIN), and an interval counting neuron (ICN). The LIN inhibits the activity of the ICN until a sufficient number of call pulses cause the LIN itself to be inhibited by the relay neuron. At that point, the ICN is released from inhibition and can send a signal downstream. This signal is eventually expressed as a preference of the female for the male producing the call signal. At each synapse, the upstream neuron has either an excitatory (+) or an inhibitory (-) effect on the downstream neuron, controlled through neurotransmitter receptors goverened by an alpha function. This function has two parameters, tau and alpha, reflecting the composition and abundance of the protein that forms the neurotransmitter receptor.

Results

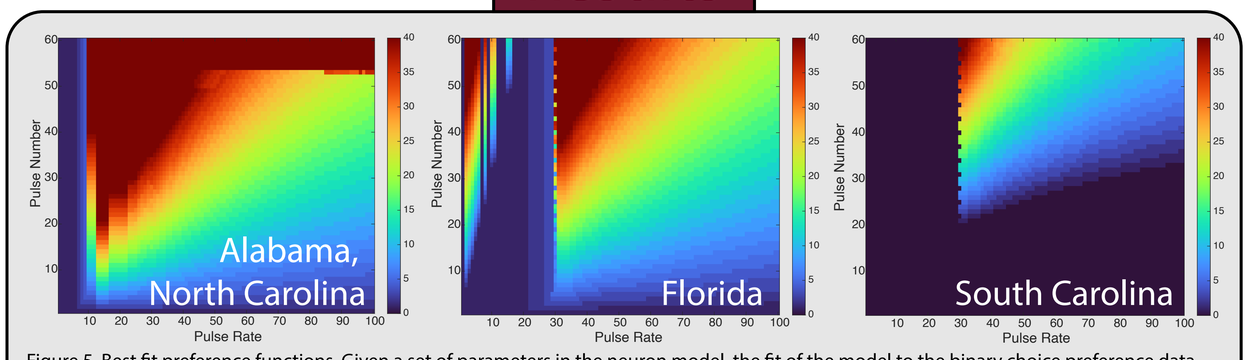

Figure 5. Best fit preference functions. Given a set of parameters in the neuron model, the fit of the model to the binary choice preference data can be assesed using a likelihood function. For each population the parameters were optimized such that the likelihood of the preference data was maximized. Here we show the relative preference of females for different male calls assuming the optimized model. The color represents the number of times the ICN neuron fires in when the circuit is presented a call stimulus with a certain pulse rate and pulse number combination.

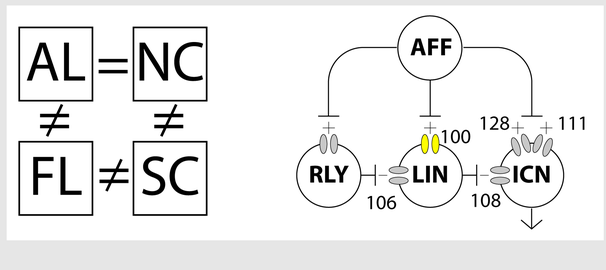

Figure 6. Model testing. Performing analyses using constraints allows us to identitfy whether pairs of populations have significantly different preference functions (left), and allows us to determine which neurotransmitter receptor has evolved between populations (right). In the best supported overall model the two allopatric populations (Al, NC) have the same preference function, whereas the two sympatric popualtions (FL, SC) have unique preference functions. In the optimal neural models the excitatory neurotransmitter receptor (AMPA, yellow) have evolved between sympatry and allopatry. This model is significantly models evoking evolution of other receptors. Numbers in right panel indicate AIC scores.

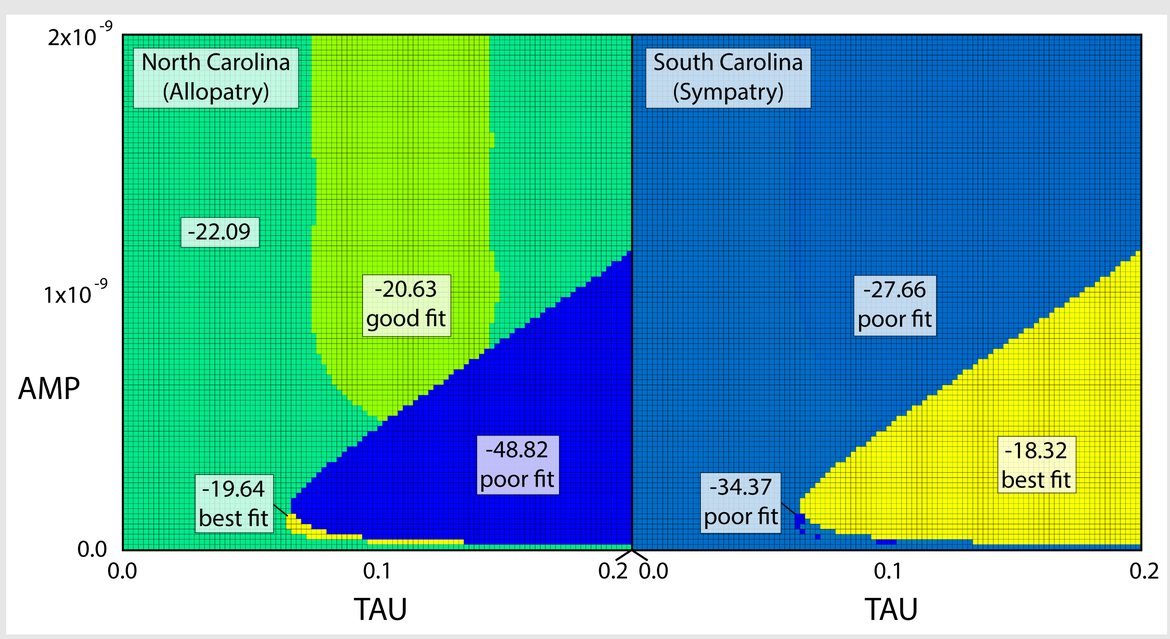

Figure 7. Likelihood surfaces showing how the fit of the neuron model to the preference data changes when the TAU (x-axis) and AMP (y-axis) parameters are changed (excitatory LIN connection). Surfaces for the South Carolina (Sympatry) and North Carolina (Allopatry) populations are shown. All other parameters are constrained to be the same in the two populations. Note that the parameter combinations producing a good fit for one population produces a poor fit to the other population, and vice versa. The likelihood surfaces suggest that a small change in expression of the AMPA neurotransmitter in the LIN neuron could result in a shift from the preference function seen in allopatry (NC population) to that seen in sympatry (SC population). The likelihood surfaces also indicate that a broad range of parameter values can produce the same preference function, suggesting that cryptic variation may exist in allopatry and/or sympatry.

References: Lemmon 2009. Evolution 63: 1155-1170. Naud et al. 2015. J. Neurophysiology 114: 2804-2815. Alluri et al. 2016. PNAS E1927-2935.