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Non-parallel coevolution of sender and receiver in the acoustic communication system of treefrogs

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Advertisement calls of closely related species often differ in quantitative features such as the repetition rate of signal units. These differences are important in species recognition. Current models of signal–receiver coevolution predict two possible patterns in the evolution of the mechanism used by receivers to recognize the call: (i) classical sexual selection models (Fisher process, good genes/indirect benefits, direct benefits models) predict that close relatives use qualitatively similar signal recognition mechanisms tuned to different values of a call parameter; and (ii) receiver bias models (hidden preference, pre-existing bias models) predict that if different signal recognition mechanisms are used by sibling species, evidence of an ancestral mechanism will persist in the derived species, and evidence of a pre-existing bias will be detectable in the ancestral species. We describe qualitatively different call recognition mechanisms in sibling species of treefrogs. Whereas *Hyla chrysoscelis* uses pulse rate to recognize male calls, *Hyla versicolor* uses absolute measurements of pulse duration and interval duration. We found no evidence of either hidden preferences or pre-existing biases. The results are compared with similar data from katydids (*Tettigonia* sp.). In both taxa, the data are not adequately explained by current models of signal–receiver coevolution.

Keywords: call recognition; phonotaxis; coevolution; speciation; acoustic communication

1. INTRODUCTION

Because most communication systems function in the context of reproduction, communication behaviour is a major determinant of reproductive fitness. Moreover, the rapid diversification of communication systems (Gleason & Ritchie 1998) may lead to morphological or ecological divergence, enabling communication systems to play a major role in speciation (e.g. Otte 1989). Therefore, the question of how communication systems diversify, for example, how new traits or characters in communication systems evolve, is of fundamental importance for evolutionary biology, and has recently received much attention.

Current models explaining the coevolution of sender and receiver in communication systems can be divided into two groups (see a review in Endler & Basolo 1998): (i) classical sexual selection models (Fisher process, good genes/indirect benefits, direct benefits models), and (ii) receiver bias models (pre-existing bias, sensory exploitation, hidden preferences). One major difference between the two groups is the temporal relationship of the appearances of preference and signal trait: in the classical sexual selection models, the signal character evolves before, or concomitantly with the receiver preference, while in receiver bias models, the preference exists before the preferred signal character evolves. Both groups allow for changes in both sender and receiver traits.

The vast majority of evolutionary studies of communication systems have considered female *preference* for a specific signal parameter as the important characteristic of the receiver (e.g. Bush *et al.* 1996; Gerhardt *et al.* 1996; Ryan & Rand 1993; but see Ryan *et al.* 1990). The preference is the agent that causes selective pressures on the signal, and thus largely determines signal evolution. In this respect, the preference is an important cue for understanding signal design and the evolution of signal traits.

In order to understand the coevolution of signal and receiver, however, it is important to consider the actual trait or phenotype of the receiver, rather than just its consequences. That is, we need to know the call recognition mechanism (i.e. the phenotype) that generates a preference, rather than only the preference itself (i.e. the phenotype's consequence). Two species that prefer a call of 30 pulses s^{-1} over calls with the same duty cycle, but of higher or lower pulse rate might use different mechanisms: one species might evaluate pulse rate, the other species pulse duration. By simply looking at the preference, we would conclude that the receivers are the same and that receiver traits have not changed between the two species. Understanding the underlying mechanisms would lead to a very different conclusion: the receiver traits (or phenotypes) in the two species are different and have diverged.

In the present study, we tested female call recognition mechanisms in two sibling species of treefrogs (*Hyla chrysoscelis* and *H. versicolor*) of known evolutionary history (Ptacek *et al.* 1994). The calls of both species differ primarily in pulse rate (*H. chrysoscelis* 50 pulses s^{-1}, *H. versicolor* 20 pulses s^{-1}, at 20 °C), while most other parameters (pulse duty cycle, call duration and spectral composition) are similar (Gerhardt & Doherty 1988). With all other parameters held constant, the differences in pulse rate are sufficient for females of both species to discriminate conspecific from heterospecific calls (see a review in Gerhardt 2001; Bush *et al.* 2002). Although the calls of the two species also differ in pulse rise time, this difference is of minor importance for call recognition relative to the difference in pulse rate (Diekamp & Gerhardt 1995; Bush *et al.* 2002).

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Female call recognition mechanisms were tested in behavioural experiments, quantifying phonotactic responses as a measure of the attractiveness of a stimulus. We show that qualitatively new call recognition mechanisms evolved in sibling species in which male calls vary quantitatively in the value of one parameter, the pulse repetition rate.

2. MATERIAL AND METHODS

We collected *H. versicolor* of the northwestern mitochondrial lineage (Ptacek *et al.* 1994) from breeding sites in Boone County, Missouri, USA. Although currently allopatric, it is probable that these populations of *H. versicolor* are descended from populations that interacted with *H. chrysoscelis*, populations of which occur within 30 km (Ptacek *et al.* 1994). *Hyla chrysoscelis* were collected from a syntopic population in Phelps County, Missouri. In order to ensure receptivity, we collected females in amplexus, removed the males, and held the females at *ca.* 2 °C until 30 min before use in an experiment, at which time they were acclimatized in an incubator until the cloacal temperature reached 20 (± 1) °C. Between trials, the females were kept in the incubator to ensure a constant body temperature, which was checked periodically throughout the experiments. All individuals were released at their breeding sites at the end of the experiments. Experimental procedures were evaluated and approved by the Laboratory Animal Care and Use Committee of the University of Missouri, Columbia.

Phonotaxis experiments took place in a temperature regulated, single-walled, sound-proof chamber (Industrial Acoustics) at 20 (± 1) °C. The walls, ceiling and other sound-reflecting objects in the chamber were covered with anechoic foam (Illbruck, 10 cm thick), and the floor outside of the arena was covered with thick carpet or anechoic foam.

The phonotaxis arena was circular in shape and 2 m in diameter; the walls (height of 50 cm) consisted of hardware cloth covered with black fabric and placed on a 'Resopal' floor. The loudspeaker (Analog–Digital Systems 200) was placed at floor level on the outside of the arena wall, facing the centre of the ring. The position of the loudspeaker was varied throughout the experiments. An infrared light source and video camera were suspended over the centre of the arena, and enabled us to monitor the behaviour of the frogs from outside the chamber. No optical cues were available for the frogs' orientation.

(a) *Stimulation*

Synthetic advertisement calls were generated using a custom made DA-converter system (12 bit resolution, 50 kHz sampling rate). The signals were amplified and their amplitude was controlled with the aid of a computer. The amplitudes of the signals were monitored with a Larson Davis sound level meter (model 720). The amplitudes of the control stimuli (see below) were adjusted to a sound pressure level of 85 dB SPL (re 20 µPa) fast RMS at the position of the release box; all other stimuli were adjusted to equivalent peak amplitudes. All stimuli used in this study consisted of two phase-locked sinusoids of 2.2 kHz and 1.1 kHz (at −6 dB relative to the amplitude of the 2.2 kHz component), which simulates the spectral structure of the natural calls of both species. The computer-synthesized signals had a signal-to-noise ratio of at least 40 dB.

For *H. chrysoscelis*, the control stimulus (i.e. the model of the conspecific call) consisted of 45 pulses with 10 ms duration, repeated at 50 Hz (pulses per second), i.e. the silent interval between the pulses was 10 ms. Each pulse had an inverse exponential rise time and an exponential fall time, each equal to 50% of the pulse duration (figure 1*a*). In this species, we synthesized calls in which the pulse and interval duration each ranged from 2 to 38 ms. The pulse shape was held constant as in the control, and pulse number per call was varied to maintain a minimum call duration of *ca.* 900 ms and a minimum pulse number of 30.

For *H. versicolor*, the control stimulus consisted of 18 pulses with 25 ms duration, repeated at 20 Hz, i.e. the silent interval between the pulses was 25 ms. Here, we varied the pulse duration from 2 to 155 ms and the interval duration from 0 to 115 ms. Pulse number per call was adjusted to maintain a minimum call duration of *ca.* 900 ms and a minimum pulse number of 10. Each pulse had linear rise and fall times, with the rise time always 80% of the pulse duration, the fall time 20% (figure 1*a*). Female *H. versicolor* discriminate in choice experiments against pulse rise times shorter than those in natural male calls (Gerhardt & Schul 1999). Therefore, the change in pulse rise time may have contributed to the decreased attractiveness of the short pulse durations (5, 10 and 15 ms) used in the experiments with *H. versicolor*. However, single-speaker experiments demonstrated that changes in pulse rise time alone, i.e. when the pulse duration was held constant, had only a minor influence on the attractiveness of the calls (Bush *et al.* 2002): rise times of 9 ms and 3 ms resulted in phonotactic scores (see below) of above 0.8 and 0.4. Thus, the near-zero responses we report here for such short pulses (figure 1*c*) were due mainly to the short pulse duration rather than the short rise time.

The call period (i.e. duration from one call beginning to the next) was 5.5 s for all experiments.

(b) *Experimental protocol*

At the start of each trial, we placed the female in the acoustically transparent release box in the centre of the arena. After four repetitions of the stimulus, we removed the lid of the release box and measured the time until the female touched the wall of the arena, directly in front of the speaker. We recorded a score of 'no response' if the female remained in the release box for 3 min, left the release box but did not reach the speaker within 5 min, or arrived at the wall of the arena in the semi-circle opposite the speaker.

Each female began an experimental session with two control trials in which she was presented with the model of the conspecific call 'control stimulus' (see above). Only her data from the second of the control trials were used as a control time in the data analysis. Following these initial trials, we presented each female with two different test trials, another control trial, two different test trials, a control trial, etc., until the female's response to the control trial began to weaken, as evidenced by an increasing response time. At this point the female was removed from the experiment and her previous two test scores were discarded. In order to abolish possible memory effects between trials, we returned each female to the incubator for a minimum of 5 min between trials. We presented the test trials in random order, which differed among females, until each test stimulus had been presented to 10 different females.

(c) *Calculation of the phonotaxis score*

We calculated a phonotaxis score (PS) for each trial completed by each female. It was calculated as the ratio of her response time during the control trials to her response time during the test trial ($PS = t_{control}/t_{test}$). The control time was the aver-

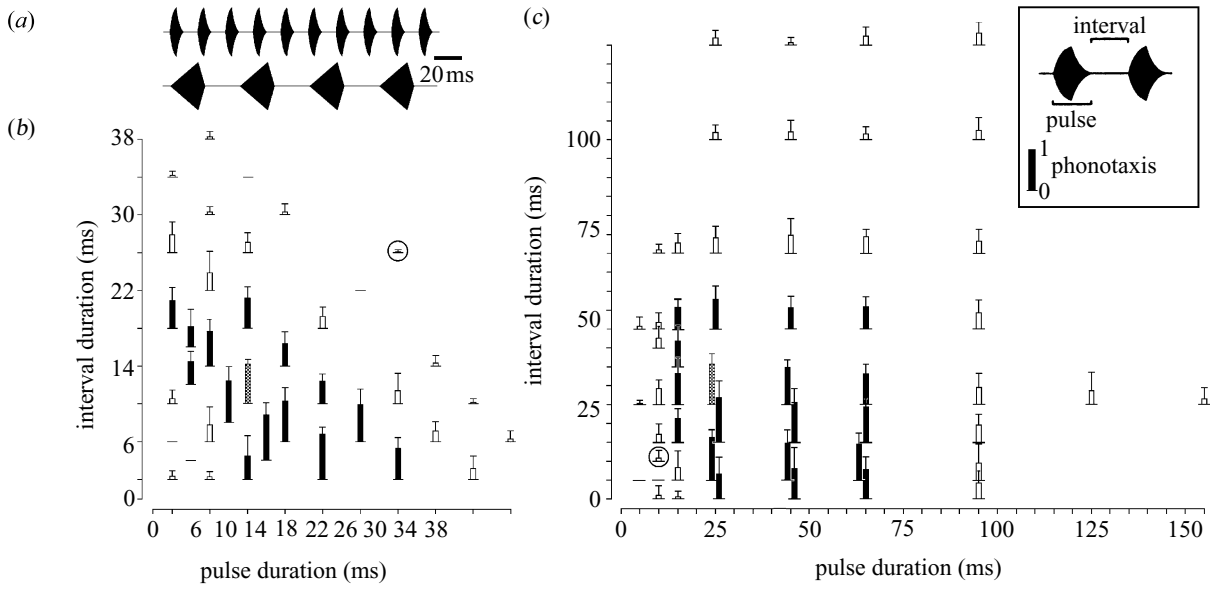

Figure 1. (*a*) Temporal patterns of the control stimuli used for *Hyla chrysoscelis* (top trace) and *H. versicolor* (bottom trace). The calls consisted of 45 pulses (*H. chrysoscelis*) or 18 pulses (*H. versicolor*) with pulse periods of 20 ms and 50 ms, respectively. The durations of the pulses and the intervals were varied independently for use in the various test situations (see inset). The specific pulse shape was held constant for each species. (*b*,*c*) Importance of pulse duration and interval duration for phonotactic responses of female *H. chrysoscelis* (*b*) and *H. versicolor* (*c*). The bars indicate the PS (mean ± s.d.) for the respective parameter combination. (See inset for the scale of the phonotactic response.) The baseline of each bar is positioned on the interval duration. Filled bars indicate significant responses to stimuli of the given parameter combination. White bars indicate non-significant responses, and grey bars indicate the responses to the control stimulus (model of conspecific calls). The call parameters of the sibling species are indicated by a circle in (*b*) and (*c*). Note the different axis-scaling in (*b*) and (*c*). $n = 10$ for all tests in (*b*) and (*c*).

age of the control trials immediately before and after the test trial of interest. A PS of 1, therefore, indicates that the female approached the test stimulus with the same response time as the average of the two surrounding control stimuli; a score of less than 1 indicates that she approached the test stimulus more slowly than she approached the control. A PS of zero was assigned to all trials in which the female received a 'no response' (see above). Note that the PS can exceed 1 if the female approached the test stimulus more rapidly than the control stimulus. Female responses were considered significant if two criteria were met: (i) the distribution of PSs was significantly greater (one-sided *t*-test; $p < 0.05$) than a hypothetical population of zero responses of the same size (Schul 1998), and (ii) the average response was at least 50% of the response to the control stimulus. Note that the distinction of significant responses was not meant to classify stimuli as 'recognized' and 'not recognized'. Call recognition is a gradual process, with a continuum of relative response scores (a detailed discussion in Bush *et al.* (2002)). The application of a significance criterion merely emphasizes the shape of the response fields to clarify the mechanisms used for song recognition (see § 3).

The method of calculating the PS is described in detail and evaluated elsewhere (Bush *et al.* 2002).

3. RESULTS

The pulse rate of a call is a composite parameter determined by the sum of the durations of both the pulses and the silent intervals between the pulses. Any change in pulse rate inherently causes a change of one or both of these durations. Thus, in order to identify the criterion used for call recognition, i.e. identify the recognition mechanism, we varied pulse duration and interval duration independently of each other in our test stimuli. Because the pulse duration and interval duration were manipulated independently, the data can be plotted in a response field indicating the ranges of attractive stimuli (e.g. stimuli that are recognized as conspecific). The shape of the field reveals which temporal parameters are used for call recognition, as described below.

Females of *H. chrysoscelis* showed reliable phonotaxis to call models when the sum of pulse duration and interval duration (i.e. the pulse period) was close to 20 ms, which is equivalent to 50 pulses s^{-1}, the conspecific pulse rate. These responses appear in figure 1*b* along a diagonal from top left to bottom right. Response magnitudes decreased sharply to both higher and lower pulse rates. This selectivity was almost independent of pulse duration: pulses from 2 to 18 ms were attractive, as long as the pulse period was close to 20 ms. The response pattern of the females indicates a dominant role for the pulse rate in call recognition. Thus, in *H. chrysoscelis* we interpret the underlying mechanism as pulse rate recognition.

The situation was markedly different in *H. versicolor*. If females were using the same recognition mechanism as in *H. chrysoscelis*, one would predict a response field with a diagonal line parallel to that of the *H. chrysoscelis* field, but shifted towards the lower pulse rate of *H. versicolor*. Female responses did not occur along a diagonal of constant rate, but rather outlined a rectangular response field (figure 1*c*). This field was limited by a minimum pulse duration of 15 ms, by a maximum pulse duration of 65 ms, and a maximum interval duration of 45 ms. No minimum interval duration was detected, as females

responded to stimuli with pulses directly abutting each other, i.e. amplitude modulation was limited to the ramped shape of the pulses. Female phonotaxis in *H. versicolor* thus relied on the measurement of absolute pulse and interval duration, which had to fall within the limits described above in order to elicit phonotaxis. These limits were absolute, in that the acceptable range for each parameter was largely independent of the value of the other parameter. Only for very short interval durations (0 and 5 ms) was the minimum pulse duration slightly longer than for other interval durations (figure 1*c*).

The independence of pulse rate in the call recognition of *H. versicolor* becomes obvious when significant responses to pulse rates far from the conspecific pulse rate (e.g. 9 Hz = 65 ms pulse duration/45 ms interval duration, or 40 Hz = 25 ms pulse duration/0 ms interval duration) are compared with very weak responses at the conspecific pulse rate of 20 Hz (e.g. 10 ms/40 ms or 5 ms/45 ms pulse duration/interval duration, respectively). Also, by comparing the responses to stimuli with equal rate but different durations, it becomes obvious that for call recognition in *H. versicolor,* filtering of pulse rates was subordinate in function to the combined measurements of pulse and interval durations.

The independent evaluation of pulse and interval durations in *H. versicolor* was in striking contrast to the situation in *H. chrysoscelis*, in which the pulse rate, i.e. the combination of pulse and interval duration, was most important for eliciting a response. Neither species showed secondary maxima in the response fields, nor could we detect any considerable responses to the call parameters of the sibling species (circled call parameters in figure 1*b*,*c*).

4. DISCUSSION

(a) *Preference for call characters versus call recognition mechanisms*

In this study, we examined the receiver mechanisms underlying female preferences for pulse rate in *H. chrysoscelis* and *H. versicolor*. The preferences themselves have been studied in detail using call models with a constant duty cycle (reviews in Gerhardt 2001; Bush *et al.* 2002), which would correspond to the stimuli along the diagonal from bottom left to top right in our response fields. Such preference functions have similar shapes in the two species and differ only in the value of the preferred pulse rates: females show a preference for the conspecific pulse rates over lower and higher pulse rates. Considering only the preference functions would lead one to infer that the receivers of the two species diverged quantitatively, while the general receiver mechanisms were conserved.

Although the data presented here do not conflict with the previously determined preference functions, they do demonstrate that testing female preferences alone might lead to an incomplete and possibly misleading picture. Our results indicate that the similar preference functions are generated with different mechanisms; thus, the divergence between the two species was not limited to the tuning frequency of rate recognition, but involved the evolution of a new call recognition mechanism. This example emphasizes the importance of considering the receiver mechanisms as well as the preferences, when studying the coevolution of sender and receiver in a communication system.

(b) *Non-parallel coevolution of sender and receiver*

During speciation, the calls of the two *Hyla* species diverged primarily in pulse rate (Gerhardt 2001). The call recognition mechanisms of the two species, however, did not diverge in a parallel fashion. While females of *H. chrysoscelis* recognize the conspecific pulse rate, females of *H. versicolor* do not use their conspecific, lower pulse rate for call recognition, but rather rely on a different mechanism requiring pulse duration and interval duration to fall within certain independent values. Thus, whereas the general call structure was preserved during speciation, the mechanisms for call recognition diverged between the two extant forms and rely on different temporal qualities of the calls.

One might argue that the lack of parallel changes in call structure and call recognition in this system is due to the unusual mechanism of speciation: *H. versicolor* arose by auto-tetraploidization from the diploid *H. chrysoscelis* (Wasserman 1970). The reduced pulse rate of *H. versicolor* is associated with polyploidy: artificially produced triploids and tetraploids have significantly slower pulse rates than their diploid ancestors (Ueda 1993; Keller & Gerhardt 2001). However, the pulse rate of the tetraploid *H. versicolor* has probably been further modified by selection (Keller & Gerhardt 2001). This strongly indicates that call recognition was also under selective pressure during speciation of these two forms, rather than being a consequence of the cytological changes due to polyploidy.

A shift in the mode of call recognition has also been described in a species complex that arose without polyploidy. Recognition mechanisms have been studied in detail in three sibling katydid species (Tettigoniidae) in which acoustic communication plays a major role in species isolation (Schul 1998). In this system, as in *Hyla*, male calls vary primarily in pulse rate and are perceived by the females to have pulse rates of *ca*. 28 pulses s^{-1} (*Tettigonia cantans*), 11 pulses s^{-1} (*T. viridissima*) and 45 pulses s^{-1} (*T. caudata*) (Heller 1988; Schul 1998). As in this study, the mechanisms of female call recognition in these species were evaluated by varying pulse duration and interval duration independently. *Tettigonia cantans* uses pulse rate recognition, as indicated by female responsiveness only to stimuli with pulse periods equivalent to its conspecific pulse rate. Female *T. viridissima* use a mechanism that relies on independent evaluation of a minimum pulse duration and minimum and maximum interval durations. In *T. caudata*, a third mechanism was identified in which females use pulse duty cycle: the pulse duration must cover at least 60% of a pulse period to elicit a response, regardless of the absolute value of the pulse period. Figure 2*a* depicts the fields of attractive stimuli of the three *Tettigonia* species. The recognition mechanisms are indicated by the shapes of the fields. Pulse rate recognition is indicated by responses along a diagonal from top left to bottom right. The irrelevance of pulse rate in the fields of *T. viridissima* and *T. caudata* is clear.

The situation in the *Tettigonia* system is similar to that in the *Hyla* system described here (figure 2*b*). Within each system, the calls of the sibling species vary primarily in

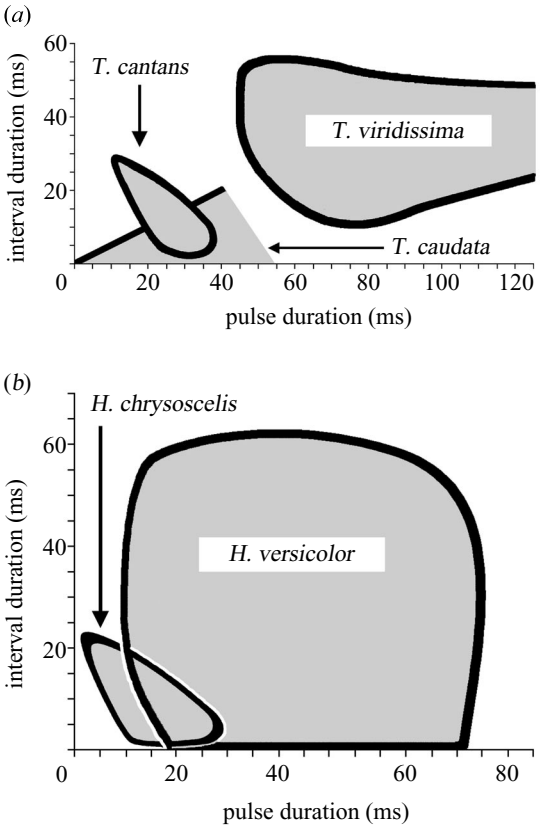

Figure 2. Schematic drawing of the phonotactic response fields dependent on pulse duration and interval duration in (*a*) the genus *Tettigonia* (Orthoptera: Tettigoniidae) and (*b*) the genus *Hyla*. The limits of the response fields of *T. caudata* and *T. viridissima* to longer pulse durations were not tested. The shapes of the fields indicate that *T. cantans* and *H. chrysoscelis* use pulse rate recognition, *T. viridissima* and *H. versicolor* evaluate absolute pulse and interval durations and *T. caudate* recognizes the conspecific call by a minimum duty cycle.

pulse rate. In both systems, call recognition does not rely on differences among species in the tuning of a single recognition mechanism, but rather exhibits qualitatively different mechanisms among species in the parameters assessed. One species in each system uses pulse rate recognition, while the sibling species evaluate either absolute pulse and interval durations, or pulse duty cycle. Thus, in both systems, changes in female call recognition during speciation did not parallel the changes in male calls, but followed an independent route to qualitatively different mechanisms.

(c) *Do current models of character evolution explain 'non-parallel coevolution'?*

Due to the focus of research on receiver preferences, no predictions about the underlying receiver mechanisms have been formulated based on the models of sender–receiver coevolution (review in Endler & Basolo 1998). Nevertheless, the evolutionary models do allow mechanistic predictions, which are briefly outlined here and compared with the findings in the *Hyla* and *Tettigonia* systems.

The classical sexual selection models predict parallel coevolution of the signal trait and receiver preference (e.g. Anderson 1994; Alexander *et al.* 1997). As female preference might shift a particular call parameter in one direction (e.g. to higher pulse rates), the preference itself should shift in a similar way. As a result, females will prefer, and males will produce calls of higher pulse rates. Thus, these models of character evolution predict primarily *quantitative* changes in traits of sender and receiver, and the call recognition mechanisms underlying call preferences should be similar among sibling species, but tuned to different parameter values.

The non-parallel changes of sender and receiver in both *Hyla* (this study) and *Tettigonia* (Schul 1998) with quantitative changes of one signal parameter (the pulse rate) but qualitative changes of the receiver mechanisms, do not conform to the predictions of classical sexual selection models of character evolution. While the patterns of male signals among the sibling species are in agreement with the evolutionary models outlined above, the qualitative changes in receiver mechanisms do not conform to their predictions. Therefore, classical sexual selection models seemingly do not explain our findings.

Receiver bias models may explain *qualitative* changes in sender and receiver (Ryan 1990). These models assume that the preference for a signal exists before the signal has evolved. The preference may arise either as an epiphenomenon of the receiver mechanisms (Enquist & Arak 1993), or from contexts other than communication (e.g. foraging or sensory traps; Proctor 1992). Once the receiver bias or hidden preference is exploited by the sender, the receiver will adapt to the new signal trait. In that process, new hidden preferences can evolve while the preference for the original trait will weaken (Enquist & Arak 1993). This process explains how qualitatively new receiver mechanisms and correlated new signal characteristics might evolve. Nevertheless, this evolutionary process should leave remains of the character change detectable, either as 'ghosts of biases past' (Ryan & Rand 1993) in the derived state and/or as pre-existing bias or hidden preference in species representing the ancestral stage of the communication system (Enquist & Arak 1993).

We could not detect any secondary maximum in the response fields of either *Hyla* species, nor did we detect any considerable responses to the calls of the sibling species, either of which would be an indication of hidden or pre-existing bias in the receiver mechanisms. The data from Schul (1998) also do not indicate the existence of hidden or pre-existing biases in the *Tettigonia* complex. There is, therefore, no evidence for an evolutionary scenario based on the receiver bias models in these taxa. These results indicate that the pattern of signals and receiver-mechanisms found in *H. chrysoscelis* and *H. versicolor* as well as in the *Tettigonia* complexes (Schul 1998) are not adequately explained by the current models of sender–receiver coevolution in communication systems. A different evolutionary mechanism seems necessary to explain the observed large-scale changes in the call recognition mechanisms of the receiver. Because of the limited number of examples currently available, any attempt to formulate a model of such a mechanism would be speculation. More comparative data are required to model an evolutionary process that could account for the non-parallel changes in senders and receivers described here.

(d) *Non-parallel coevolution: a common phenomenon?*

Few call recognition mechanisms have been studied comparatively within closely related species. This makes it difficult to judge the generality of the phenomenon of non-parallel coevolution of sender and receiver described here. Recently, however, a preliminary report of call recognition in crickets (genus *Teleogryllus*) (Hennig 2001) indicates a situation similar to the pattern that was observed in *Hyla* and *Tettigonia*. Given that this non-parallel coevolution was found in phylogenetically distant groups (treefrogs and orthopterans (katydids and crickets)), we suspect that this phenomenon might be rather common. It is possible that it went unnoticed due to the focus on communication systems in the context of sexual selection, and thus the concentration on female preferences rather than recognition mechanisms. As noted by Gould (1989, p. 121), '… one is an oddity, but two a possible generality'.

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