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Priority of precedence: receiver psychology, female preference for leading calls and sexual selection in insect choruses

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In species in which males display collectively, females may evaluate display features that arise specifically in groups in addition to basic features of signal energy. For example, in acoustic insects and anurans that chorus, males often adjust their song timing relative to neighbours, and females may pay attention to these adjustments in timing. Many laboratory studies show how males may delay the phase of their song rhythm with respect to a song stimulus such that they call just prior to the stimulus; similarly, females may choose a male whose song rhythm leads a neighbour by a brief interval. However, the importance of male phase adjustments and female attention to call order in actual choruses has remained poorly understood. We studied female choice in laboratory choruses in the bushcricket *Ephippiger diurnus*, a species with preferences for leading calls but also for longer calls and faster rhythms, features representing broadcast energy. Although chorusing males varied in all features, we found that females largely focused on call order. This overriding preference for call order may be reflected by the prevalence of male phase adjustment throughout the population, a feature that would have been subject to strong sexual selection. We found that the broadcast of leading calls within a chorus was not repeatable among males but rather shifted among the chorus participants. This observation too may reflect the strong selection imposed by female choice for call order, and it may have implications for the role of receiver psychology in the evolution of mate choice.

Thirty years of experimental study of sexual selection have revealed various patterns in receiver responses to, and preferences for, mating signals across animal species. Some of these general patterns can inform us about the potential evolution of mating signals and preferences (Bradbury & Vehrencamp, 2011). For example, one recurring finding is that female responses and preferences are directed towards intense male advertisements that transmit greater signal energy or power (Clark, 2012; Ryan, 1988). Such intensity might be expressed as higher acoustic amplitude or rhythm, elevated luminosity and duration of visual displays, or an increased concentration of pheromone (Greenfield, 2002). Because advertisement intensity can reflect the energy that a signaller expended in developing and broadcasting his message, female preferences for signal energy or power are consistent with a 'viability indicator' (good genes) mechanism of mate choice. But these preferences may also represent simple orientation towards those signals that elicit greater afferent activity in female receivers, with no expectation of any reward other than ease of localizing the signal source (cf. Endler, 1992). Alternatively, responses to intense male advertisements could indicate female choice for 'direct benefits' wherein a preferred male reliably demonstrates his potential for providing parental care, access to valuable resources (Greenfield, 1997), or health and thereby a low risk of transmitting infection during mating.

While advertisement intensity tends to be a dominant theme in receiver preferences, other studies show that signal features having no direct association with energy expended or broadcast may also figure prominently in mate choice. In many cases preferred signals bear only an especially complex form or even arbitrary features that may exploit the ways in which animals detect and discriminate stimuli, i.e. 'receiver psychology', in ways independent of absolute measures of signal energy (Miller & Bee, 2012; Wyttenbach & Farris, 2004). Moreover, some receiver preferences may be expressed only when signallers are in a tight cluster wherein individual males may be simultaneously compared in a relative fashion (Schwartz & Freeberg, 2008). Here, too, preferences are often found for signal features that are not necessarily associated with energy. Because males in many species do signal in the company of neighbouring signallers, collective evaluation and preference by females is likely to be widespread.

Collective male displays often feature specialized temporal interactions between the signals broadcast by individual males (Greenfield, 2005). These signal interactions may occur at a

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relatively crude level in which a large proportion of the local males signal during a brief interval, a collective singing bout lasting from a few seconds to several minutes, followed by an interval when relatively few signals are broadcast. This cycle would then be repeated many times during the daily activity period. Species in which males broadcast their signals with a regular rhythm present the opportunity for more precise interactions in which neighbouring males adjust the phase of their rhythm such that an overall pattern of approximate synchrony or alternation arises within a collective signalling bout (Greenfield, 2005). These temporal patterns can allow certain males to be distinguished by temporal features of their signalling that are evident only in a group context. In turn, female preferences may focus, at least in part, on these aspects of relative signal timing.

The signal interactions described above are perhaps best known in acoustic communication, notably in acoustic insects and anurans that sing in choruses (Greenfield, 1994a). In various of these species chorusing males effect precise adjustments of signal timing, generally by delaying the phase of their rhythm relative to those of neighbours (Greenfield, 1994b; Hartbauer, Kratzer, Steiner, & Römer, 2005; Nityananda & Balakrishnan, 2007). These adjustments may allow a male to call in a leading fashion, immediately prior to the onset of his neighbour's broadcast. In some orthopteran species most or all males effect these phase adjustments (Greenfield & Snedden, 2003), and the role of producing numerous 'leading' calls may seldom be fixed but rather shifts among the various males in a chorus over the course of a singing bout. None the less, some males may generate many more leading calls than others. Importantly, experiments in numerous species have shown that females are influenced by this relative timing feature and normally prefer leading calls over following ones. These preferences may be strong enough to override, to some extent, other aspects of female choice, including those for call rhythm, call length (Greenfield & Roizen, 1993) and call amplitude (Snedden & Greenfield, 1998), all of which are energy-based features. Preferences for leading signals may operate even when two signals do not overlap in time, implying that the responses could represent psychophysical 'precedence effects' (Litovsky, Colburn, Yost, & Guzman, 1999; Wallach, Newman, & Rosenzweig, 1949; Zurek, 1987) rather than simple masking of the following signal by the leading one (cf. Marshall & Gerhardt, 2010). Analogous signal timing adjustments and receiver preferences have been reported in visual (e.g. Backwell, Jennions, Passmore, & Christy, 1998; Buck & Buck, 1968) and vibrational communication (e.g. Hunt & Morton, 2001; Kotiaho, Alatalo, Mappes, & Parri, 2004), which suggest that these effects may be general features of signalling and perception that extend beyond the realm of acoustic chorusing. It is inferred that the specialized phase adjustments by which males improve their likelihood of broadcasting a leading call have evolved under the selection pressure of female choice for such calls (Greenfield, Tourtellot, & Snedden, 1997).

Whereas the responses of females to relative signal timing have been well documented in controlled laboratory tests, responses in the context of male choruses remain comparatively unexplored (e.g. Berg & Greenfield, 2005; Nityananda & Balakrishnan, 2008; Schwartz, 1993; Schwartz, Buchanan, & Gerhardt, 2001). Similarly, we know much more about the signal timing adjustments that males make in controlled playback tests than in complex choruses (e.g. Greenfield & Rand, 2000; Greenfield & Snedden, 2003; Simmons, Simmons, & Bates, 2008; Snedden, Greenfield, & Jang, 1998). However, female preferences and male signal interactions are normally expressed in choruses, and our findings in simple playback experiments may not fully inform us about these perceptual and signalling behaviours. Thus, we generally do not know the strength of leader preferences in females relative to other aspects of choice as they occur in a chorus (e.g. Höbel, 2010, 2011; Höbel & Gerhardt, 2007). Additionally, we have little information on whether certain male individuals tend to excel in broadcasting leading calls and whether such individuals, should they exist, are distinguished by other, absolute signal parameters which may reflect energy (e.g. Hartbauer et al., 2005; Nityananda & Balakrishnan, 2008; Richardson, Léna, Joly, & Lengagne, 2008). If the generation of leading calls is correlated with an energy-based signal parameter that females are known to prefer such as call rhythm or call length, are females more likely to choose a fast rhythm or lengthened calls by indirectly focusing on leading calls rather than directly on rhythm or call length? That is, these absolute, energy-based call features may be very difficult for a receiver to discern reliably in the complex acoustic environment of a chorus, whereas the incidence of leading calls could be judged more reliably and therefore might be a reasonably good proxy for signal energy. Answers to these questions could help us understand whether female preferences for signal timing features such as the incidence of leading calls are specialized adaptations as opposed to artefacts of neural function.

We addressed the above questions by studying female evaluation of chorusing males in a European bushcricket species, *Ephippiger diurnus* (Tettigoniidae: Bradyporinae), in which females prefer leading calls, and males effect phase delays of their call rhythms that can improve their likelihood of generating leading calls (Greenfield, Siegfreid, & Snedden, 2004; Greenfield et al., 1997). Females also prefer faster call rhythms or longer calls in some *E. diurnus* populations (Brunel, 2012; Ritchie, 1996). Observations and recordings made in the field show that *E. diurnus* males temporarily form small groups of two to eight individuals in which neighbours separated by 0.2–3.0 m effect mutual phase adjustments of their calling rhythms (Greenfield & Snedden, 2003; M. Goubault & M. Greenfield, personal observations August 2012). We studied female choice and male–male signal interactions in choruses established in the laboratory and focused on the relative importance of a male's incidence of leading calls, call rhythm and call length in female evaluation as well as correlations among the various male call features. Although observations of fully natural choruses in the field might be more valuable for addressing questions on adaptation in mate choice, the continuous movement of males and the relatively low rate of courtship and mating precluded this approach. On the other hand our laboratory choruses represent a considerable advance over playback tests using laboratory arenas and locomotion compensatory devices, the traditional approach to studying mate choice and signal interactions in acoustic communication.

METHODS

Acoustic Behaviour of Ephippiger diurnus

Ephippiger diurnus are large, flightless bushcrickets found in brushy habitats (garrigue) throughout southern and central France and northern Spain. The various geographical populations of *E. diurnus* differ in male song characters, notably in the number of 'syllables' per call (Duijm, 1990). Most of our study was conducted on insects from Col de Mantet, Department Pyrenees Orientales, France (42°29′ N, 2°18′ E; elevation 1700 m), a population that is distinguished by both a high density of individuals and polysyllabic calls that include a median of four, and as many as six, syllables (Fig. 1a; Brunel, 2012). Thus, females in this population would normally evaluate males chorusing with neighbours, and the complex song would present an opportunity for females to choose males based on call length. Such choice would be much less likely in the many *E. diurnus* populations in which males mostly produce a