Adaptive significance of synchronous chorusing in an acoustically signalling wolf spider

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Synchronous sexual signalling is a behavioural phenomenon that has received considerable theoretical interest, but surprisingly few empirical tests have been conducted. Here, we present a set of experiments designed to determine (i) whether the sexual signalling of the drumming wolf spider *Hygrolycosa rubrofasciata* is synchronous, and (ii) whether the synchrony may have evolved through female preference. Using controlled playback experiments, we found that males actively synchronized their drumming bouts with other males and females significantly preferred closely synchronized drumming clusters compared with loose clusters. In loose clusters, the first drumming signals attracted the most female responses, whereas in close clusters, the last drumming signals were the most heeded. We suggest that this female preference for the last drummer can maintain male synchronous signalling in *H. rubrofasciata*.

Keywords: sexual selection; adaptation; synchrony; sexual signalling

1. INTRODUCTION

Among acoustically signalling animals, one behavioural phenomenon that has attracted considerable interest is synchronous sexual signalling (Buck & Buck 1966, 1968; Lloyd 1973; Sismondo 1990; Greenfield & Roizen 1993; Backwell *et al.* 1998). So far, acoustic synchronous courtship signalling has been documented in anurans (Wells 1977; Tuttle & Ryan 1982; Grafe 1999; Greenfield & Rand 2000) and orthopterans (Walker 1969; Alexander 1975; Sismondo 1990; Greenfield & Roizen 1993; Snedden & Greenfield 1998).

The evolution of synchronous signalling has been hypothesized to arise from predator avoidance (Tuttle & Ryan 1982), help in species recognition (Lloyd 1973) or from collective increase in female attraction (Wells 1977). However, none of the above hypotheses has received much empirical support, and in most cases synchrony may be described as an epiphenomenon without adaptive significance (Greenfield 1994; Greenfield *et al.* 1997). Here, we report synchronous sexual signalling in an acoustically communicating arachnid (wolf spider *Hygrolycosa rubrofasciata*) and provide experimental evidence on female preference patterns constituting an adaptive mechanism through which the synchronous signalling may have evolved.

The courtship of *H. rubrofasciata* is somewhat unusual for spiders. Males produce clearly audible drumming by hitting their abdomen on dry fallen leaves of deciduous trees. A single drumming event consists of *ca.* 30 equally spaced pulses, with the highest amplitude in the middle of the drumming (see figure 1). The duration of a single drumming is *ca.* 1 s and the average drumming rate is one drumming per minute, but with a maximum of nine drummings per minute (Rivero *et al.* 2000). Both females and males respond to airborne sounds. However, it is likely that the actual receiving mode of the signals is substrate vibrations generated by the airborne sound. Females respond after perceiving their preferred drumming with a vibration of their body, and different characteristics of the male drumming signal have been found to be important for female choice: females prefer males with both a high drumming rate and longer and louder drumming (Kotiaho *et al.* 1996; Parri *et al.* 1997, 2002). Female preference in this system is unambiguous as female response is immediate, sometimes overlapping with the preferred drumming. In the field, males move around the habitat to search for females, stopping occasionally to engage in drumming (Kotiaho *et al.* 2000). The experiments reported here were inspired by observations that, in the field, the drumming of the neighbouring males tends to be unevenly distributed in time; sometimes most of the males seem to be drumming simultaneously—or within a few seconds of each other—followed by a pause in drumming. Based on these observations, we planned a set of controlled laboratory experiments.

2. METHODS

(a) *Study animals*

The spiders used in our study were collected in pitfall traps from a meadow in Sipoo, southern Finland (60°16′ N, 25°14′ E) between 5 May and 19 May 1995 and between 21 April and 6 May 1996. Spiders were housed individually in plastic containers at 4 °C. Maintaining spiders in a cool place ensures minimal metabolic rates and prevents them from becoming sexually active before the experiments. The bottom of each container was covered with moss (*Sphagnum* spp.), which provided humidity and a micro-habitat similar to the natural environment of the spiders. Spiders were regularly fed fruitflies (*Drosophila* sp.).

(b) *Male synchrony playback experiment*

Thirty males were tested once per day during three successive days. Each male received three treatments in random order, one treatment per day. Treatments constituted a control playback with no drumming, a playback with a drumming rate of two per minute and a playback with a rate of five drummings per minute.

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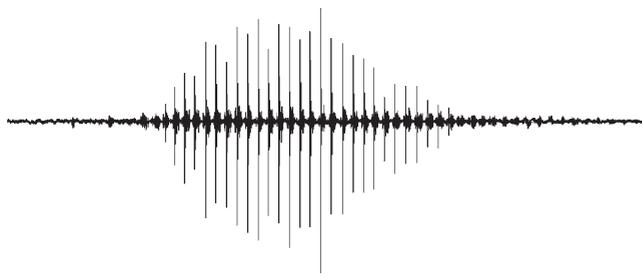
length of drumming period *ca.* 1 s.

Figure 1. An oscillogram of a drumming by a male wolf spider, *Hygrolycosa rubrofasciata*. The length of the drumming period is *ca.* 1 s.

Prior to each treatment, males were allowed to acclimatize for 10 min in the experimental arena. The drumming of each male was observed for 20 min and the timing of each drumming was recorded with an accuracy of 1 s.

To characterize the timing of the focal male's drumming relative to the playback drumming, we calculated the relative mean phase angle of the focal male's drumming (Zar 1996). Phase angles of 0° and 360° indicate complete overlap, 180° indicates complete alternation. First, we calculated the phase angle for each of the focal male's drummings and then constructed a mean phase angle for each of the focal males. Second, we tested the distribution of the focal male's drumming with a Hodges–Ajne test for circular uniformity, which does not assume sampling from any specific distribution. If the distribution was not uniform, we submitted the data to a modified Hodges–Ajne test (Batschelet test) testing for circular uniformity versus an *a priori* specified phase angle. In our case, we have an *a priori* expectation that if the distribution of drummings is not uniform, it will be clustered around the phase angle of the playback drummings. More details about the tests used can be found in Zar (1996).

(c) Female choice playback experiment

In *H. rubrofasciata*, female choice is unambiguously observable because females respond immediately after the preferred drumming with a vibration of their body that sometimes overlaps with the male drumming. We tested female preference for the timing of male drumming in a repeated-measures set-up. The set-up consisted of a looped tape containing a recording of a single drumming and two clusters of three drummings. We used a drumming from one male in each looped tape to avoid any effects of different quality in the signal itself. In one of the clusters, the drummings were separated by 1 s (close synchrony), and in the other cluster by 3 s (loose synchrony). The single drumming and the two clusters were separated by 15 s from each other. We created 20 tapes using a drumming from a different male on each tape; 20 females were tested, one with each tape. Each trial lasted for 20 min. The orders of the single drumming and the two clusters were systematically varied between the tapes. General methods for female choice playback experiments can be found in Parri *et al.* (1997, 2002).

3. RESULTS

(a) Male synchrony playback experiment

In this experiment, we determined whether synchrony exists in this system by analysing the timing of the drumming of focal males in relation to three levels of experimental playback drummings. The experimental playback

levels were: a control with no drumming (i.e. an empty tape), a playback of two drummings per minute (termed level 2) and a playback of five drummings per minute (termed level 5). To characterize the timing of the focal male's drumming in relation to the playback drumming, we calculated the relative phase angle of the focal male's drumming in each of the playback levels (Zar 1996) (see § 2). In control and level-2 playbacks, the distribution of the mean phase angles of the focal males was randomly distributed (Hodges–Ajne test: $m = 5$, $n = 16$, $p = 0.800$ and $m = 7$, $n = 25$, $p = 0.315$, respectively; figure 2a,b). However, in level-5 playback, the distribution of the mean phase angles of the focal males was significantly different from a uniform distribution (Hodges–Ajne test: $m = 4$, $n = 25$, $p = 0.013$; figure 2c). Because of the significant deviation from uniformity, we submitted the data to further analysis to test whether the mean phase angles of the focal males were concentrated around the phase angle of the playback drumming (Zar 1996). We found this to be the case (Batschelet test for circular uniformity versus an *a priori* specified angle: $C = 8$, $n = 25$, $p = 0.032$), indicating that the males were drumming synchronously.

We tested the effect of the playback level on the drumming rate of the focal males, and found a highly significant effect (repeated-measures ANOVA: $F_{2,56} = 14.69$, $p < 0.001$). Tukey *post hoc* comparisons revealed that the drumming rate of the focal males was significantly lower in the control level than in playback levels 2 or 5 (mean difference (MD) $= -0.81$, s.e. $= 0.17$, $n = 30$, $p < 0.001$ and MD $= 0.48$, s.e. $= 0.12$, $n = 29$, $p < 0.001$), but that there were no significant differences between playback levels 2 and 5 (MD $= 0.33$, s.e. $=$, $n = 0.1629$, $p = 0.053$). This result indicates that focal males increased their drumming rate in response to the drumming of other males.

(b) Female choice playback experiment

In this experiment, we tested female preference for the timing of male drumming. Female preference in *H. rubrofasciata* is easily determined since females respond to males immediately after the chosen drumming by vibrating their body. We created a looped tape containing a single male drumming and two clusters of three males drumming. In one of the clusters the drummings were separated by 1 s (close synchrony), and in the other cluster by 3 s (loose synchrony). The single drumming and the two clusters were separated by 15 s. Twenty looped tapes were created using a drumming from a different male on each. The orders of the single drumming and the two clusters were systematically varied between the looped tapes. Twenty females were tested; one with each of the looped tapes.

Overall, there was a difference in the number of female responses per drumming for the three manipulations (repeated-measures ANOVA: $F_{1.51, 28.71} = 3.80$, $p = 0.045$; to account for violation of the sphericity assumption, the degrees of freedom were Greenhouse–Geisser adjusted). Tukey *post hoc* comparisons revealed that the number of female responses per drumming for the loosely synchronous cluster was lower than that for the closely synchronous cluster or for the single drumming (MD $= -1.10$, $p = 0.002$ and MD $= -0.90$, $p = 0.042$, respectively), but there was no difference in number of female responses for the close synchrony cluster and the
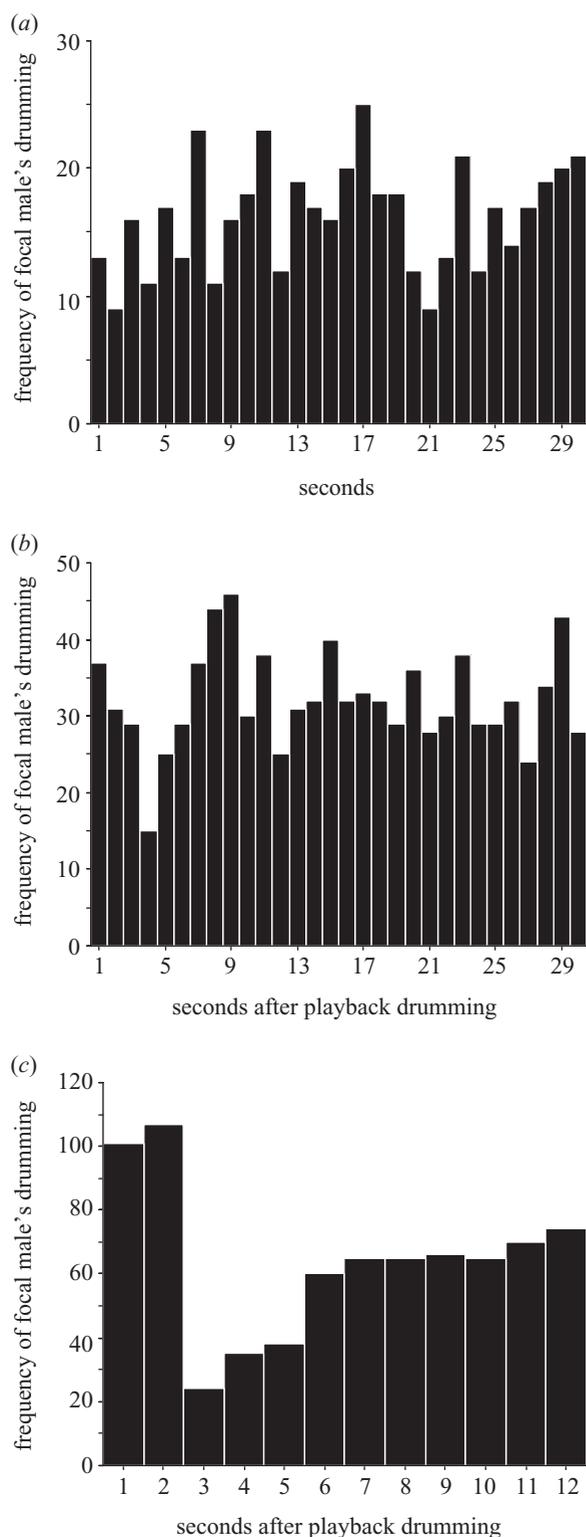
(a)

(b)

(c)

Figure 2. Histograms of the frequency of focal males' drumming in (a) a control treatment, (b) playback level 2, and (c) playback level 5. In (a), the x-axis is the time in seconds arbitrarily stacked into 30 s intervals. In (b) (two playback drummings per minute), and (c) (five playback drummings per minute), the x-axis represents time in seconds after the playback drumming. Note the different scales in both axes.

single drumming (MD = 0.20, p = 0.707). These results indicate that females prefer single males and closely synchronizing clusters of males over loosely synchronizing clusters of males. However, because closely synchronizing
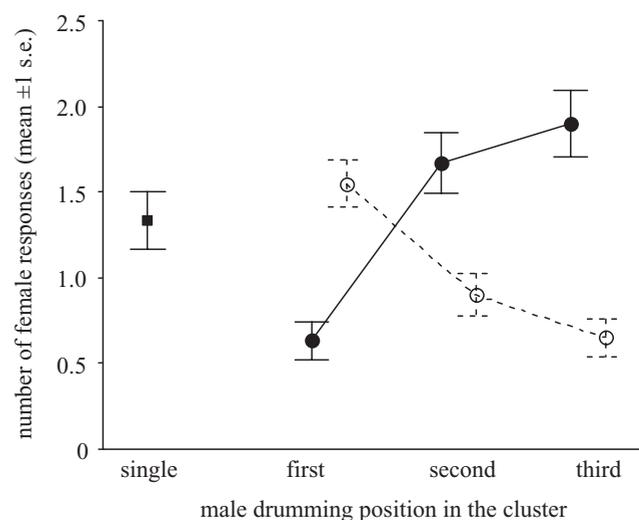
Figure 3. The number of female responses in relation to the position of the male drumming in the cluster of three synchronously drumming males. The square symbol indicates the female responses for the single drumming, open circles indicate the female responses to drummings of a loosely synchronous cluster, and the solid circles indicate the female responses to drummings of a closely synchronous cluster.

clusters did not attract more female responses per drumming than did a single drumming, there is no support for the hypothesis that synchrony in *H. rubrofasciata* has evolved as a response to a collective increase in female attraction (Wells 1977; Greenfield 1994).

When we tested for the effect of the male drumming position within a cluster (a male drums first, second or third in the cluster) and the type of synchrony in the cluster (close or loose synchrony) on number of female responses, we found a highly significant interaction effect (repeated-measures ANOVA: $F_{2,38} = 57.45$, $p < 0.001$). Figure 3 shows that the best position for males to be drumming in a synchronizing cluster of three depends on the time interval between the drummings. If the synchrony is close, then it is beneficial for a male to be the last of the cluster, i.e. to drum within 3 s after the first male's drumming. However, if the synchrony is loose, then it is beneficial for a male to be the first male of the cluster to drum (figure 3). Interestingly, this result corresponds closely to the synchronizing pattern that we observed in the first experiment. Males tend to drum within 2 s of the playback drumming and there is a clear reduction in drumming after 3 s from the playback drumming (figure 2c).

4. DISCUSSION

Synchronous acoustic chorusing has previously been documented from anurans and orthopterans, and in most instances the synchrony may be described as an epiphenomenon without adaptive significance (Greenfield 1994; Greenfield *et al.* 1997). In this study, we described synchronous chorusing from a spider *H. rubrofasciata*. Results from two experiments suggest that males are sexually selected to synchronize their signals. Females prefer the single male and a cluster of three closely synchronizing males over a cluster of three loosely synchronizing males. This creates positive directional sexual selection for males that are able to drum first without other males drumming

after them, and for males that are able to drum instantly after another male. Conversely, there is also negative sexual selection against males that drum first but are instantly followed by the drumming of another male, but also against males that drum a few seconds too late after the first male's drumming.

In our first experiment the synchrony was not observed with playback level 2, but arose only with playback level 5. When the general drumming rate is as low as two times per minute, it may be more beneficial for the male to be drumming independently than waiting for the opportunity to synchronize with another male. However, with a general drumming rate of five times per minute, the importance of timing of the drumming increases substantially. It is still beneficial to drum alone if one is able to, but it is also beneficial to be in close synchrony. However, as it is costly to be in loose synchrony, the timing of the drumming becomes important and it is likely that close synchrony will arise.

We predict that synchronous chorusing can evolve according to a set of game-theoretical decision rules: because pay-offs for drumming directly after another male are higher than drumming following a short pause, males will adopt a decision rule to drum in close synchrony. Furthermore, because the pay-offs for following another male in close synchrony are higher than drumming first, males will be selected to drum after another male has drummed. Nevertheless, although drumming first has, on average, a lower pay-off than drumming second, it has higher pay-off than not drumming at all, and this maintains drumming in this system.

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