*Zoosymposia* 24: 022–043 (2023)
https://www.mapress.com/j/zs


**Article**

ISSN 1178-9905 (print edition)
**ZOOSYMPOSIA**
ISSN 1178-9913 (online edition)

https://doi.org/10.11646/zoosymposia.24.1.5
http://zoobank.org/urn:lsid:zoobank.org:pub:AD32CA6F-6A0F-453E-B3B8-0A065F97C308

# Stonefly drumming behavior descriptions of three *Soliperla* Ricker, 1952 species (Plecoptera: Peltoperlidae)

JOHN B. SANDBERG
*CDFW Aquatic Bioassessment Lab & CSUC Enterprises, 233 Holt Hall, 940 West First Street, California State University, Chico, CA 95929-0555, U.S.A.*
*jsandberg@csuchico.edu; https://orcid.org/0000-0001-9231-2914*

## Abstract

One new drumming call signal description and two updated call descriptions of three *Soliperla* Ricker, 1952 species in the stonefly family Peltoperlidae are presented. It was determined after recording and analysis that these signals differed from the previous descriptions, warranting a revision. Percussive signal interval patterns for the three species are described for the first time. The previous monophasic call signal pattern descriptions of *Soliperla quadrispinula* (Jewett, 1954) and *S. thyra* (Needham & Smith, 1916) are updated to the repeated monophasic pattern. The male call and response of *S. sierra* Stark, 1983 and the response signal of *S. quadrispinula* are described for the first time. The call descriptions of the three California species consist of one to six monophasic signals with inconsistent inter-call intervals. Sequenced monophasic female answers did not follow all repeated male calls. Male monophasic responses occasionally followed female answers in sequenced 3-way exchanges.

**Key words**: Stonefly vibrational communication, mate finding behavior

## Introduction

The roachfly genus *Soliperla* Ricker (Plecoptera: Peltoperlidae) consists of eight United States species distributed in California, Idaho, Montana, Nevada, Oregon and Washington (DeWalt *et al.* 2022), and one species from Sichuan, China (Huo, Du & Yuan 2017). Stonefly drumming is a mate finding behavior that involves polygamous males searching for stationary monogamous females within the riparian ecotone. The males produce call signals while searching, usually by tapping the postero-ventral abdomen upon resonant surfaces (percussive signals). Calls, female answers and a second male response signal are produced by tapping, rubbing, and tremulation methods. Signal pattern complexity ranges from simple monophasic to tribeat, diphasic, combination, grouped, monophasic and grouped, and rub (considered both a method and a pattern).

I consider that most lone stonefly monophasic call descriptions are preliminary and not complete until a duet with the female has been included. The previous three California *Soliperla* descriptions included only one species with both male and female drumming descriptions but lacked the interval pattern descriptions required for a complete description (Stewart & Zeigler 1984; Abbott & Stewart 1997). This (in-part) provided cause to update the drumming descriptions of the three California *Soliperla* species discussed in this paper.

The drumming signals of five Nearctic *Soliperla* species have been described (Table 1). Male call signal pattern complexity in the genus ranges from simple-monophasic to intermediate-diphasic signals (Sandberg et al 2015). However, not all drumming characters, e.g., interbeat interval patterns, intraphase interval patterns and signal durations were completely described. Instead, descriptions reported only a single mean composed of all interbeat intervals from an entire multi-beat signal. This is not optimal.

 *Submitted: 15 Oct. 2022; Accepted by R. Edward DeWalt: 1 May 2023; published: 31 Jul. 2023*

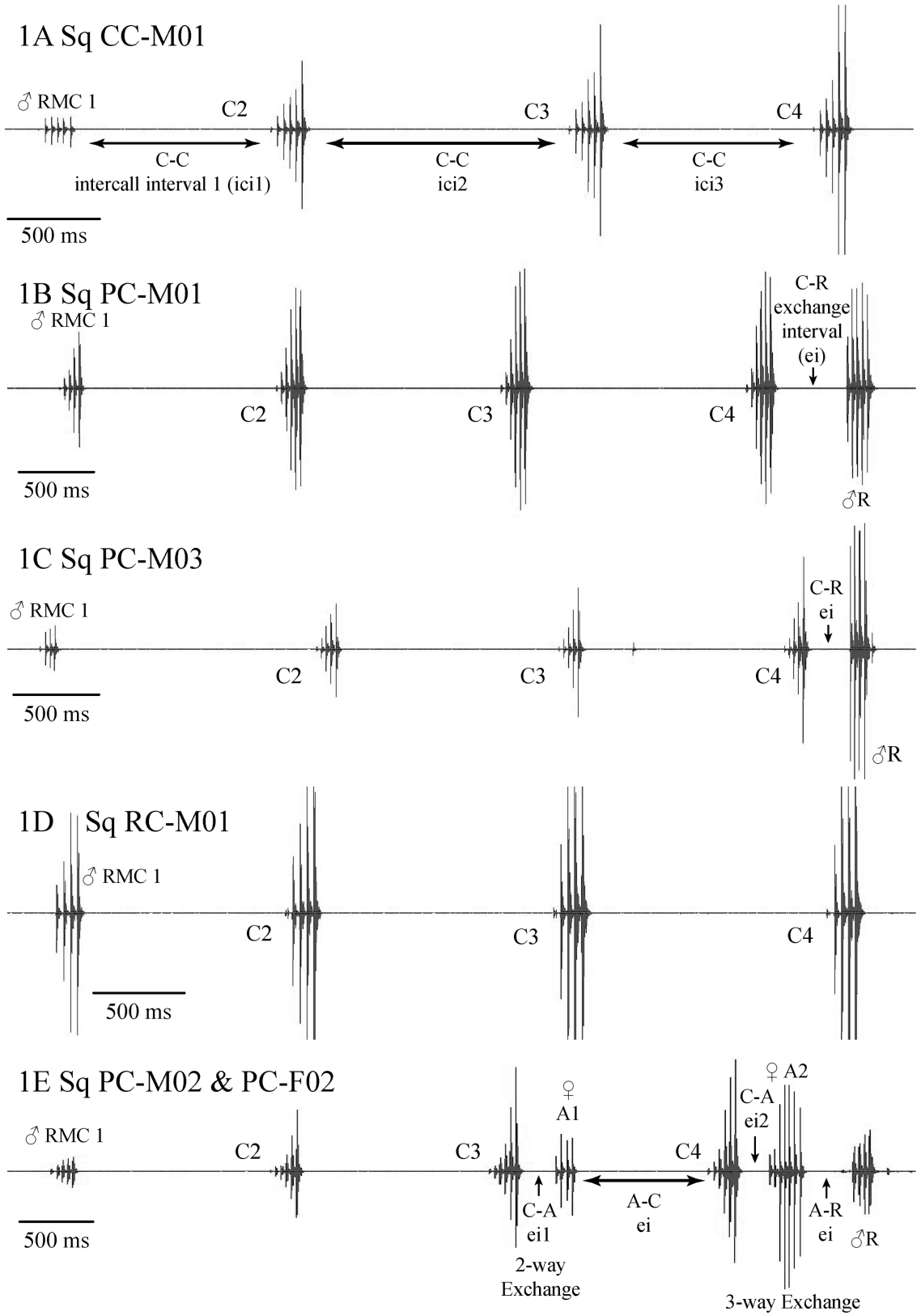


**FIGURE 1.** *Soliperla quadrispinula* drumming oscillographs. 1A. Clear Creek M01, four (C1–C4) repeated monophasic calls (RMC) and three call-call (C-C) intercall intervals. 1B. Puter Creek M01, four repeated monophasic calls, one sequenced response (R) with one call-response (C-R) exchange interval (ei). 1C. Puter Creek M03, four repeated monophasic calls, one sequenced response (R). 1D. Roaring Creek M01, four repeated monophasic calls. 1E. Putter Creek M02-F02, four repeated monophasic calls, two sequenced answers (A) and one response (R). Two call-answer (C-A), one answer-call (A-C) and one answer-response (A-R) exchange intervals.

**TABLE 1.** Previously published stonefly drumming descriptions. Call (C), answer (A) and response (R) signal characters of five Nearctic *Soliperla* species 1984–2006. *Interval pattern estimated from the reported interval standard deviation.

| Species, Gender, Description Author, Location & State | T ºC (Age) | Call[1], Answer[2] & Response[3] Signal Patterns | Estimated Interval Pattern | ♂C-♀A-♂R Exchange Pattern | Mean # Beats/ Call, Answer, Response or Phase (P) | Mean (range) Interbeat & Intraphase Interval (ms) | Mean Interphase Interval (ms) | Mean Signal Duration (ms) |
|---|---|---|---|---|---|---|---|---|
| 1. *S. campanula* ♀ (Sandberg & Stewart 2006) Kink Cr OR | | | | | | | | |
| | ?TºC (3d) | Monophasic[1] | Even | n/a | 6.2±2.7 | 25.4±2.5 (22.4-28.4) | n/a | 133.3±73.6 |
| 2. *S. fenderi* ♂♀ (Stewart & Zeigler 1984) St. Andrews & Puyallup Cr seeps WA | | | | | | | | |
| | 20-22 (?d) | Diphasic[1] Monophasic[2] Monophasic[3] | P1: ↓Varied-Beat P2: Even | Sequenced 3way | P1: 3.2±1.7 P2: 7.6±1.5 A: 7.6±2.7 R: 2.1±0.5 | P1 306±221 P2 29±3 A: 30±3 R: 33±5 | 504.0±213 | ? |
| 3. *S. quadrispinula* ♂ (Stewart & Zeigler 1984) Grassy Cr CA | | | | | | | | |
| | 22 (?d) | Monophasic[1] | Even | n/a | 4 (n=1) | 37±0.6 | n/a | ? |
| *S. quadrispinula* ♀ (Stewart & Zeigler 1984) Lake Cr OR | | | | | | | | |
| | 22 (?d) | Monophasic[1] | Even | n/a | 6.3±0.6 | 34±2 (32-36) | n/a | ? |
| 4. *S. sierra* ♀ (Stewart & Zeigler 1984) Big Springs CA | | | | | | | | |
| | 23 (?d) | Monophasic[1] | Even | n/a | 6.4±0.8 | 33±2 | n/a | ? |
| 5. *S. thyra* ♂♀ (Stewart & Zeigler 1984) Unnamed Cr CA | | | | | | | | |
| | 23 (?d) | Monophasic[1] Monophasic[2] Monophasic[3] | Even | Sequenced 2-3way | C: 6±0.6 A: 6.2±0.6 R: 4 | C: 19±1 A: 23±3 R: 22±0 | n/a | ? |
| 6. *S. thyra* ♂ (Abbot & Stewart 1997) N Cosumnes R seep CA | | | | | | | | |
| | 22-24 (?d) | Monophasic[1] | Even | n/a | 7.1±0.9 | 26.1±0.9 | n/a | ? |

? Indicates character was not reported.

## Material and methods

Seventeen wild adults, including two reared virgin males and one virgin female were recorded from the following locations (Table 2). The specimens are preserved in 80% ethanol and stored in the author's personal collection. The specimens recorded are presented below.

### *Soliperla quadrispinula* (Jewett, 1954)

USA, California, Trinity Co., Clear Creek, Hwy 36, 4.2 km west of Forest Glen Campground, 40.37411 N, 123.36347 W, J.B. Sandberg, 23 MAY 2020.

USA, California, Humboldt Co., Puter Creek, at trail 0.64 km south of Mad River Fish Hatchery, 40.84934 N, 123.99246 W, J.J. Lee, J.B. Sandberg, 28 MAY 2020.

USA, California, Shasta Co., Roaring Creek, Big Bend Rd. near Wengler, 40.919026 N, 121.915298 W, J.B. Sandberg, 09 MAY 2020.

**TABLE 2.** Specimen data for three *Soliperla* species and 18 new repeated monophasic call descriptions from six additional California streams, 2018 and 2020. Repeated monophasic calls (RMC) contained 1–6 monophasic signals (MS). *Soliperla thyra* males StSCM03, StSCM04 and female StSCF01 had known ages indicated by an asterisk. All other specimen ages were days after collection.

| Species & Location | Specimen ID & Date Collected or Reared* Male | Female | Date Recorded | Age (d) ♂ | ♀ | Temperature ºC | Number of RMC/MS (Duets) | Total # RMC/MS |
|---|---|---|---|---|---|---|---|---|
| *Soliperla quadrispinula* | | | | | | | | |
| 1. Clear Cr. | 1. CC-M01 5/23/2020 | | 5/25 | 2 | - | 22.7 | 15/38 | 79/264 |
| 2. Puter Cr. | 2. PC-M01 5/28/2020 | | 5/29-30 | 1-2 | - | 22.7 | 20/50 | |
| | 5. PC-M02 5/28/2020 | PC-F02 5/28 | 5/31 | 3 | 3 | 22.7 | 23/102 (29) | |
| | 3. PC-M03 5/28/2020 | | 5/31 | 3 | - | 22.7 | 11/39 | |
| 3. Roaring Cr. | 4. RC-M01 5/9/2020 | | 5/10 | 1 | - | 21.1 | 10/35 | |
| *Soliperla sierra* | | | | | | | | |
| 4. French Cr. | 6. FC-M01 5/8/2020 | | 5/10 | 2 | - | 21.1 | 23/105 | 86/362 |
| | 7. FC-M02 5/8/2020 | | 5/11 | 3 | - | 21.1 | 10/53 | |
| | 13. FC-M02 5/8/2020 | FC-F01 5/8 | 5/11 | 3 | 3 | 21.1 | 10/51 (28) | |
| | 8. FC-M03 5/8/2020 | | 5/12 | 4 | - | 21.1 | 10/45 | |
| | 9. FC-M05 5/8/2020 | | 5/12 | 4 | - | 21.1 | 5/22 | |
| | 10. FC-M07 5/8/2020 | | 5/13 | 5 | - | 21.1 | 10/28 | |
| | 11. FC-M08 5/8/2020 | | 5/13 | 5 | - | 21.1 | 10/34 | |
| 5. Rattlesnake Cr. tributary | 12. RCt-M02 6/18/2018 | | 6/25/2018 | 7 | - | 23.8 | 8/24 | |
| *Soliperla thyra* | | | | | | | | |
| 6. Salt Cr. | 14. SC-M01 5/16/2020 | | 5/17 | 1 | - | 21.6 | 10/44 | 43/171 |
| | 15. SC-M02 5/16/2020 | | 5/19 | 3 | - | 21.6 | 11/35 | |
| | 16. SC-M02 5/16/2020 | | 5/21 | 5 | - | 21.6 | 7/14 | |
| | 17. SC-M03 5/16/2020 | SC-F015/20* | 5/21 | 5 | 1* | 21.6 | 15/68 (28) | |
| | 18. SC-M04 5/22/2020* | SC-F015/20* | 5/23 | 1* | 3* | 21.6 | 5/10 (9) | |
| **Total number of repeated calls/monophasic signals and (duets) analyzed** | | | | | | | **213/797 (94)** | **213/797** |

### *Soliperla sierra* Stark, 1983

USA, California, Plumas Co., French Creek, Water Tank on Caribou Rd., 6.1 km south of Butt Valley Reservoir, 40.08635 N, 121.15490 W, J.B. Sandberg, 8 MAY 2020.

USA, California, Tehama Co., Rattlesnake Creek unnamed tributary, FR 27N05 6.1 km east of Hwy 32, 40.16996 N, 121.52199 W, A.B. Richards, J.B. Sandberg, 18 JUNE 2018.

### *Soliperla thyra* (Needham & Smith, 1916)

USA, California, Glen Co., Salt Creek, Sanhedrin Rd., 2.8 km south of Alder Springs, 39.637988 N, 122.736319 W, D.P. Pickard, J.B. Sandberg, 16 MAY 2020 (M04 & F01 reared).

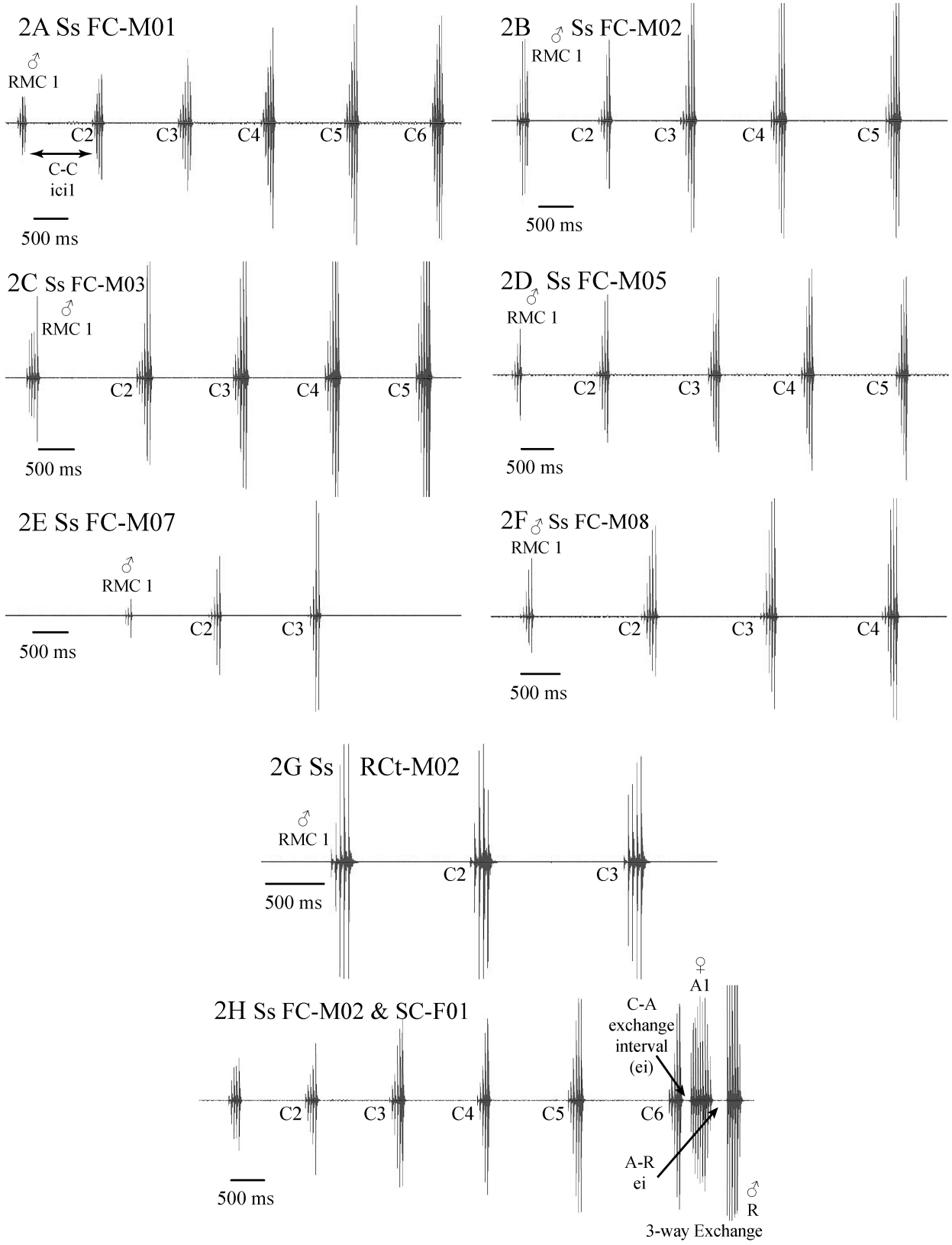


**FIGURE 2.** *Soliperla sierra* drumming oscillographs. 2A. French Creek M01, six (C1–C6) repeated monophasic calls (RMC) and five call-call (C-C) intercall intervals. 2B. French Creek M02, five repeated monophasic calls. 2C. French Creek M03, five repeated monophasic calls. 2D. French Creek M05, five repeated monophasic calls. 2E. French Creek M07, three repeated monophasic calls. 2F. French Creek M08, four repeated monophasic calls. 2G. Rattlesnake Cr Trib M02, three repeated monophasic calls. 2H. French Cr M02-F01, six repeated monophasic calls, one sequenced answer (A) and response (R). One call-answer (C-A) and one answer-response (A-R) exchange intervals.

Stonefly collecting, rearing, drumming signal recording, and digital audio signal analysis follow Sandberg *et al.* (2015). Mean general drumming call characters are reported for individual males of the three species including signal count, beat count and duration. Detailed characters including mean interval patterns, duet (or exchange) intervals, and response interval patterns are provided. The mean interbeat interval differences (ID) were calculated following Sandberg *et al.* (2015) and indicated if interval patterns were even (charted pattern nearly horizontal) or uneven (charted pattern increasing or decreasing). However, the ID could have been calculated for each signal if "both" signals with even and varied beat interval patterns were present. Mean interval patterns were charted using line and marker graphs utilizing two y-axes; the left for short interbeat intervals, and the right for longer exchange intervals. The mean ID was used to estimate the lacking previously published interval patterns.

## Results

A total of 213 repeated monophasic calls and call-answer exchanges from 16 males and three females were recorded May 10–30, 2020, and 25 June 2018 (Table 2). A total of 797 monophasic signals were analyzed. The repeated calls of these three species were not analyzed as they would be for grouped call signals. Ambient drumming recording temperature ranged from 21.1–23.8 ºC (Table 2). The actual age of most adults was unknown, consequently, the relative age after collection ranged from 1–7 days. Only three adults were reared from Salt Creek with known ages that ranged from 1–3 days. Mean character data presented in text are followed by standard deviation.

*Soliperla quadrispinula* Clear Creek Male 01. Fifteen repeated monophasic calls (RMC) containing a total of 38 monophasic signals (range 2–4 per RMC) were recorded from this 2-day old male at 22.7 ºC (Tables 2–3). Recording occurred between 07:47–14:05 on May 25, 2020. The number of call beats per monophasic signal ranged 4–6, and the mean RMC duration was 2482.18 ± 1237.13 ms (Fig. 1A and Table 3).

The mean monophasic call signal interval pattern ranged 35.22–37.09 ms over five (i1–i5) interbeat intervals, and mean duration was 169.95 ± 21.38 ms (Fig. 4 and Table 4). Interval patterns are described as approximately even (nearly horizontal), increasing, decreasing, or combinations of increasing and decreasing as expressed in charts graphing the individual mean interval patterns. Moderately high RMC and monophasic signal duration standard deviation was due to the range in number of monophasic signals per RMC and beats per monophasic signal respectively. Male call-call (or intercall) exchange intervals (C-C) varied greatly 1338.03 ± 181.90 ms (Table 4). This result was similar for the other species and specimens in the current study.

This male's (CC-M01) relatively even (less variable) mean monophasic call interbeat interval pattern compared intermediately (middle) among the other conspecific males (Fig. 4 and Table 4). All repeated monophasic calls and atypical responses were summarized into mean interval patterns in Table 4. Repeated monophasic calls would not have been summarized into a single signal if they belonged to the grouped call pattern. Mean interval difference (max minus min mean interval) for intervals one-five (i1–i5) was less than 10 ms (ID: 37.09–35.22 = 1.87). Interestingly, but not uncommon, this male produced response signals without female answer signals present.

*Soliperla quadrispinula*—Puter Creek Male 01. Twenty RMC's containing 50 monophasic signals (range 1–4 per RMC) were recorded from this 1–2-day old male at 22.7 ºC (Tables 2–3). Recording occurred between 23:00 May 29 and 07:00 May 30, 2020. The number of call beats per monophasic signal ranged 2–5, and the mean repeated RMC duration was 2887.77 ± 1335.00 ms (Fig. 1B and Table 3).

The mean monophasic call signal interval pattern ranged 30.36–33.41 ms, and mean duration was 138.53 ± 23.08 ms (Fig. 4 and Table 4). Male C-C exchange intervals varied greatly 1568.26 ± 187.28 ms. Five repeated calls without a female present concluded with atypical response signals that would typically follow female answers in 3 way exchanges (Fig. 1B). The number of beats/response ranged from 4–5 (Table 3), and mean response duration was 153.75 ± 11.42 ms (Table 4). The atypical mean call-response (C-R) exchange interval was 590.64 ± 100.02 ms.

This male's (PC-M01) mean monophasic call interbeat interval pattern compared intermediately among the other males (Fig. 4 and Table 4). The pattern had slightly shorter interbeat intervals than male CC-M01 and RC-M01. Mean interval difference for call intervals i1–i5 was less than 10 ms (ID: 33.41–30.36 = 3.05) and the response ID was 2.54.

**TABLE 3.** *Soliperla quadrispinula* (Sq), *S. sierra* (Ss) and *S. thyra* (St) monophasic signal (MS and monophasic response (MR) drumming characters. Count and duration data for 14 male repeated monophasic call (RMC) descriptions from Clear Creek (CC), Puter Creek (PC), Roaring Creek (RC), French Creek (FC), Rattlesnake Creek tributary (RCt) and Salt Creek (SC). St SC-M02 recorded twice on 5/19/2020 and 5/21/2020.

| | Number of MS/ RMC | Number of Call Beats/ MS | Number of Beats/ MR | RMC Duration (ms) | | Number of MS/ RMC | Number of Call Beats/ MS | Number of Beats/ MR | RMC Duration (ms) |
|---|---|---|---|---|---|---|---|---|---|
| **Sq CC-M01** (N=15 RMC's w/ 38 monophasic signals) | | | | | **Ss FC-M05** (N=5 RMC's w/ 22 monophasic signals) | | | | |
| AVG | 2.53 | 5.68 | n/a | 2482.18 | AVG | 4.40 | 4.82 | n/a | 5509.46 |
| MAX | 4 | 6 | | 4647.00 | MAX | 5 | 6 | | 6659.80 |
| MIN | 2 | 4 | | 1434.79 | MIN | 4 | 3 | | 4699.53 |
| STD | 0.83 | 0.57 | | 1237.13 | STD | 0.55 | 0.59 | | 985.65 |
| N | 15 | 38 | | 15 | N | 5 | 22 | | 5 |
| **Sq PC-M01** (N=20 RMC's w/ 50 monophasic signals) | | | | | **Ss FC-M07** (N=10 RMC's w/ 28 monophasic signals) | | | | |
| AVG | 2.50 | 4.44 | 4.80 | 2887.77 | AVG | 2.80 | 4.30 | n/a | 2855.97 |
| MAX | 4 | 5 | 5 | 5493.61 | MAX | 3 | 5 | | 3351.82 |
| MIN | 1 | 2 | 4 | 756.93 | MIN | 2 | 3 | | 2930.32 |
| STD | 0.79 | 0.69 | 0.45 | 1335.00 | STD | 0.42 | 0.75 | | 590.95 |
| N | 20 | 55 | 5 | 20 | N | 10 | 28 | | 10 |
| **Sq PC-M03** (N=11 RMC's w/ 39 monophasic signals) | | | | | **Ss FC-M08** (N=10 RMC's w/ 34 monophasic signals) | | | | |
| AVG | 3.55 | 5.50 | 4.00 | 3729.65 | AVG | 3.40 | 5.56 | n/a | 3660.86 |
| MAX | 4 | 6 | 4 | 4960.57 | MAX | 4 | 6 | | 5003.58 |
| MIN | 3 | 4 | 4 | 2778.93 | MIN | 3 | 5 | | 2793.97 |
| STD | 0.52 | 0.64 | | 834.48 | STD | 0.52 | 0.50 | | 916.31 |
| N | 11 | 40 | 1 | 11 | N | 10 | 34 | | 10 |
| **Sq RC-M01** (N=10 RMC's w/ 35 monophasic signals) | | | | | **Ss RCt-M02** (N=8 RMC's w/ 24 monophasic signals) | | | | |
| AVG | 3.50 | 5.00 | n/a | 4076.33 | AVG | 3.00 | 4.63 | n/a | 2425.59 |
| MAX | 4 | 6 | | 5049.54 | MAX | 4 | 6 | | 3629.60 |
| MIN | 3 | 4 | | 3123.93 | MIN | 2 | 2 | | 1357.29 |
| STD | 0.53 | 0.49 | | 793.42 | STD | 0.53 | 0.88 | | 628.14 |
| N | 10 | 35 | | 10 | N | 8 | 24 | | 8 |
| **Ss FC-M01** (N=23 RMC's w/ 105 monophasic signals) | | | | | **St SC-M01** (N=10 RMC's w/ 44 monophasic signals) | | | | |
| AVG | 4.57 | 4.99 | n/a | 4951.32 | AVG | 4.40 | 6.91 | n/a | 6807.77 |
| MAX | 6 | 6 | | 6640.95 | MAX | 6 | 8 | | 9781.00 |
| MIN | 4 | 4 | | 3702.30 | MIN | 3 | 5 | | 4009.39 |
| STD | 0.51 | 0.65 | | 856.35 | STD | 0.84 | 0.60 | | 1754.32 |
| N | 23 | 105 | | 23 | N | 10 | 44 | | 10 |
| **Ss FC-M02** (N=10 RMC's w/ 53 monophasic signals) | | | | | **St SC-M02** (5/19) (N=11 RMC's w/ 35 mono. signals) | | | | |
| AVG | 5.30 | 5.45 | n/a | 5789.90 | AVG | 3.18 | 8.06 | n/a | 4641.14 |
| MAX | 6 | 6 | | 6893.93 | MAX | 5 | 9 | | 8605.20 |
| MIN | 4 | 4 | | 3934.87 | MIN | 3 | 5 | | 3540.33 |
| STD | 0.67 | 0.61 | | 943.07 | STD | 0.60 | 0.87 | | 1365.01 |
| N | 10 | 53 | | 10 | N | 11 | 35 | | 11 |
| **Ss FC-M03** (N=10 RMC's w/ 45 monophasic signals) | | | | | **St SC-M02** (5/21) (N=7 RMC's w/ 14 mono. signals) | | | | |
| AVG | 4.50 | 5.42 | n/a | 5133.88 | AVG | 2.00 | 8.29 | n/a | 3267.42 |
| MAX | 5 | 6 | | 5928.08 | MAX | 2 | 9 | | 3922.43 |
| MIN | 3 | 4 | | 3029.58 | MIN | 2 | 6 | | 2967.99 |
| STD | 0.71 | 0.72 | | 924.52 | STD | n/a | 0.83 | | 426.08 |
| N | 10 | 45 | | 10 | N | 7 | 14 | | 7 |

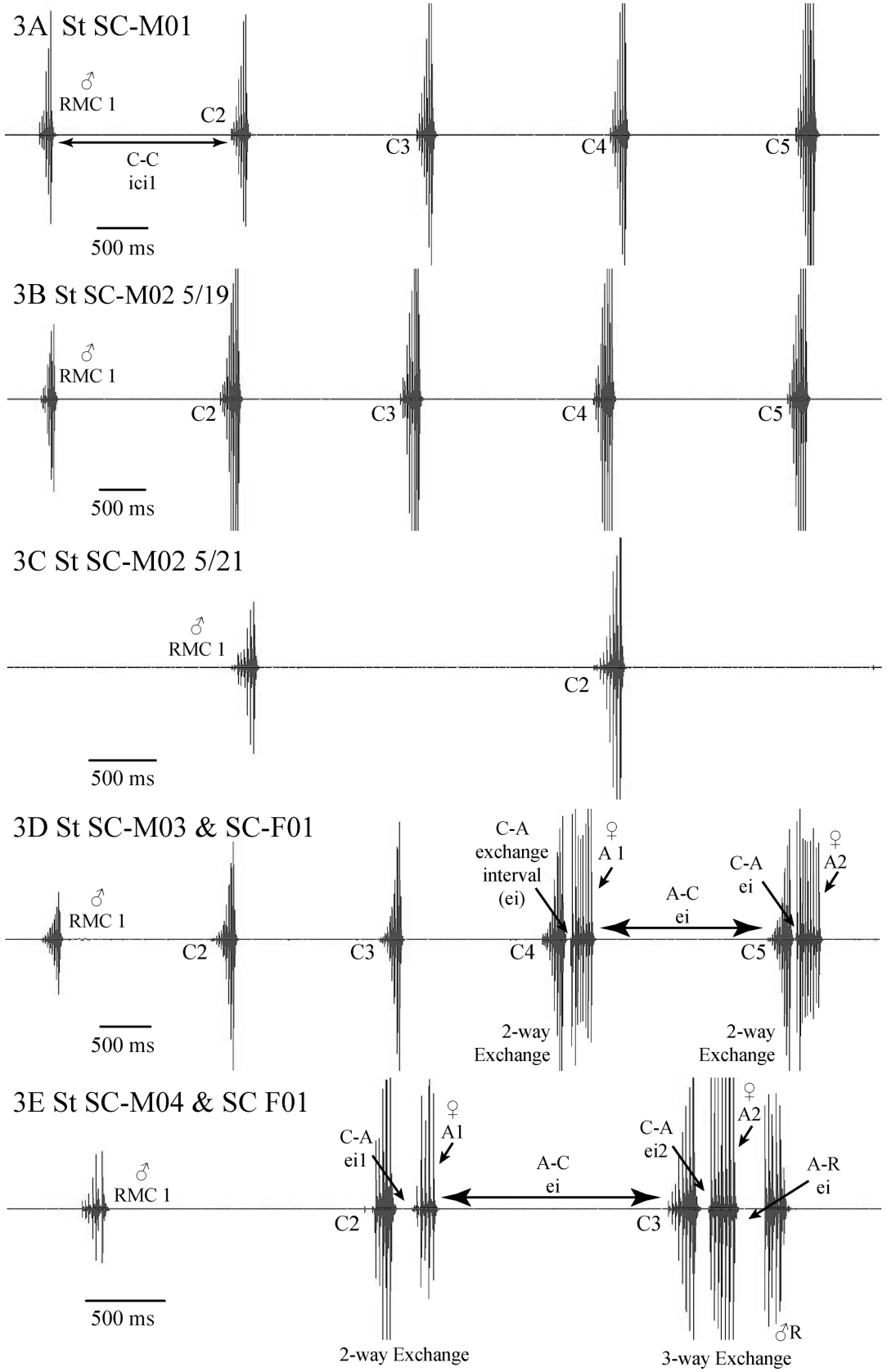


**FIGURE 3.** *Soliperla thyra* drumming oscillographs. 3A. Salt Creek M0, 1 five (C1–C5) repeated monophasic calls (RMC) and four call-call (C-C) intercall intervals. 3B. Salt Creek M02 0519, five repeated monophasic calls. 3C. Salt Creek M02 0520, two repeated monophasic calls. 3D. Salt Creek M03–F01, five repeated monophasic calls, two sequenced answers (A). Two call-answer (C-A) and one answer-call (A-C) exchange intervals. 3E. Salt Creek M04–F01, three repeated monophasic calls, two sequenced answers and one response (R). Two call-answer, one answer-call and one answer-response (A-R) exchange intervals.

**TABLE 4.** *Soliperla quadrispinula* (Sq) monophasic signal interbeat interval (IBI) patterns (intervals i1–i5) from Clear Creek (CC), Puter Creek (PC) and Roaring Creek (RC). All repeated monophasic calls (RMC) were condensed into one monophasic call signal per male. Number of monophasic signals/RMC ranged from 1–4 and number of beats per call ranged from 2–6. Male call-response (C-R) exchange intervals and sequenced monophasic response signals occurred infrequently by lone males. Mean call and response interval differences (ID = maximum–minimum) indicated by underlining.

| | Monophasic Signal IBI Pattern (ms) | | | | | | Intercall & Exchange Intervals (ms) | | Monophasic Response IBI Pattern (ms) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sq CC-M01** (ID=1.87) | | | | | | | | | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | Dur | C-C | C-R | i1 | i2 | i3 | i4 | i5 | Dur |
| AVG | 37.09 | 35.98 | 35.22 | 36.62 | 36.60 | 169.95 | 1338.03 | | | | | | | |
| MAX | 41.52 | 40.23 | 41.56 | 41.36 | 43.67 | 195.99 | 1678.93 | | | | | | | |
| MIN | 32.83 | 31.11 | 30.48 | 31.90 | 30.68 | 107.25 | 964.63 | | | | | | | |
| STD | 2.27 | 2.14 | 2.63 | 2.28 | 2.83 | 21.38 | 181.90 | | | | | | | |
| N | 38 | 38 | 38 | 36 | 28 | 38 | 23 | | | | | | | |
| **Sq PC-M01** (ID=3.05) | | | | | | | | | ID=2.54 | | | | | |
| | i1 | i2 | i3 | i4 | i5 | Dur | C-C | C-R | i1 | i2 | i3 | i4 | i5 | Dur |
| AVG | 33.41 | 31.52 | 30.36 | 30.87 | 31.97 | 138.53 | 1568.26 | 590.64 | 31.09 | 30.92 | 31.88 | 33.09 | 33.46 | 153.75 |
| MAX | 38.73 | 34.29 | 33.36 | 34.69 | 42.52 | 167.17 | 2246.53 | 752.99 | 32.86 | 32.52 | 35.37 | 34.54 | 37.23 | 165.60 |
| MIN | 25.96 | 26.85 | 28.64 | 29.46 | 30.18 | 55.48 | 1339.64 | 509.57 | 29.27 | 29.59 | 29.48 | 30.77 | 31.45 | 135.29 |
| STD | 2.14 | 1.51 | 1.15 | 1.14 | 2.34 | 23.08 | 187.28 | 100.02 | 1.36 | 1.18 | 2.31 | 1.65 | 2.57 | 11.42 |
| N | 50 | 50 | 49 | 46 | 26 | 49 | 30 | 5 | 5 | 5 | 5 | 5 | 4 | 5 |
| **Sq PC-M03** (ID=2.55) | | | | | | | | | ID=4.97 | | | | | |
| | i1 | i2 | i3 | i4 | i5 | Dur | C-C | C-R | i1 | i2 | i3 | i4 | i5 | Dur |
| AVG | 30.99 | 28.44 | 28.88 | 28.93 | 29.09 | 132.91 | 1266.91 | 281.84 | 26.21 | 30.07 | 31.18 | | | 87.46 |
| MAX | 35.44 | 30.50 | 30.05 | 30.88 | 30.07 | 151.22 | 1636.78 | 281.84 | 26.21 | 30.07 | 31.18 | | | 87.46 |
| MIN | 27.55 | 25.71 | 27.41 | 27.55 | 28.19 | 87.97 | 1067.87 | 281.84 | 26.21 | 30.07 | 31.18 | | | 87.46 |
| STD | 1.90 | 0.87 | 0.62 | 0.80 | 0.56 | 18.09 | 136.57 | n/a | n/a | n/a | n/a | | | n/a |
| N | 39 | 39 | 39 | 37 | 23 | 39 | 28 | 1 | 1 | 1 | 1 | | | 1 |
| **Sq RC-M01** (ID=2.19) | | | | | | | | | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | Dur | C-C | C-R | i1 | i2 | i3 | i4 | i5 | Dur |
| AVG | 41.89 | 39.70 | 39.89 | 40.97 | 42.99 | 160.70 | 1402.78 | | | | | | | |
| MAX | 47.89 | 45.76 | 46.58 | 46.71 | 45.01 | 207.55 | 1900.23 | | | | | | | |
| MIN | 30.95 | 36.37 | 36.67 | 36.37 | 41.39 | 118.39 | 1189.00 | | | | | | | |
| STD | 3.21 | 2.20 | 2.43 | 2.46 | 1.54 | 19.62 | 156.49 | | | | | | | |
| N | 35 | 35 | 35 | 31 | 4 | 35 | 25 | | | | | | | |

*Soliperla quadrispinula*—Puter Creek Male 03. Eleven RMC's having 39 monophasic signals (range 3–4 per call) were recorded from this 3-day old male at 22.7ºC (Tables 2 & 3). Recording occurred between 15:10–16:13 May 31, 2020. The number of call beats per monophasic signal ranged from 4–6, and the mean RMC duration was 3729.65 ± 834.48 ms (Fig. 1C and Table 3).

The mean monophasic call signal interval pattern ranged 28.44–30.99 ms, and mean duration was 132.91 ± 18.09 (Fig. 4 and Table 4). Male C-C exchange intervals varied greatly 1266.91 ± 136.57 ms. One atypical, repeated call concluded with a response signal (Fig. 1C). There were four beats/response (Table 3). The atypical mean C-R exchange interval was 281.84 ms and the response duration was 87.46 ms (Table 4).

This male's (PC-M03) mean monophasic call interbeat interval pattern was the shortest amongst the other male interval patterns (Fig. 4 and Table 4). Mean interval difference for call intervals i1–i5 was less than 10 ms (ID: 30.99–28.44 = 2.55) and response interval difference was 4.97.

*Soliperla quadrispinula*—Roaring Creek Male 01. Ten RMC's that had 35 monophasic signals (range 3–4 per call) were recorded from this 1-day old male at 21.1ºC (Tables 2 & 3). Recording occurred between 08:53–16:19 May 10, 2020. The number of call beats per monophasic signal ranged from 4–6, and the mean RMC duration was 4076.33 ± 793.42 (Fig. 1D and Table 3).

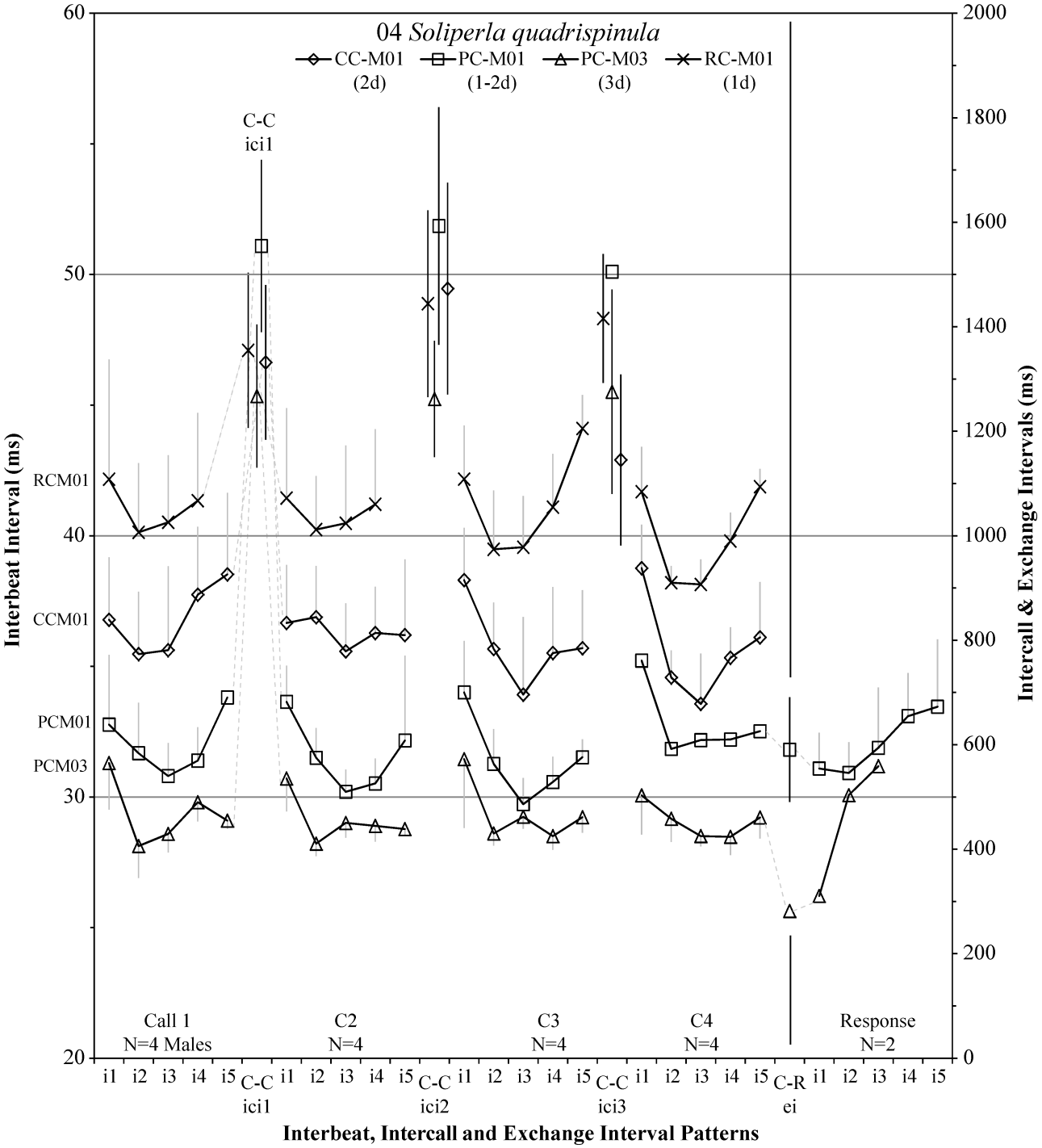


**FIGURE 4.** *Soliperla quadrispinula* repeated monophasic call and response interbeat interval patterns from Clear Creek (N=1 male), Puter Creek (N=2 males) and Roaring Creek (N=1 male). Mean interbeat intervals (i1–i5), mean call-call intercall intervals (C-C ici1-ici5) and mean atypical call-response exchange intervals (C-R) for 56 RMC's contained 1–4 monophasic signals. Standard deviation indicated by vertical bars.

The mean monophasic call signal interval pattern ranged 39.70–41.89 ms and mean call duration was 160.70 ± 19.62 ms (Fig. 4 and Table 4). Male C-C exchange intervals varied greatly 1402.78 ± 156.49 ms. This male's (RC-M01) mean monophasic call interbeat interval pattern was the longest (slowest) amongst the other call interval patterns (Fig. 4 and Table 4). Mean interval difference for intervals i1–i5 was less than 10 ms (ID: 41.89−39.70 = 2.19).

*Soliperla quadrispinula*—Puter Creek M02-F02. RMC's included 10 without female answers and thirteen with 2-way and 3-way exchanges (Fig. 1E). Some of the 13 RMC exchanges included more than one female answer (Table 2). The RMC's were long and variable due to the range in the numbers of call, answer, and response signals. Puter Creek Male-02 had 23 repeated monophasic calls composed of 102 monophasic signals and ranged 1–6 per RMC (Tables 2 & 7). Female-02 answered 13 RMC's with 29 sequenced monophasic signals and Male-02 completed five RMC's with sequenced monophasic response signals (Table 7). The pair was recorded three days after collection at 22.7 ºC, between 08:20–10:45 May 31, 2020 (Table 2). The number of call beats per monophasic signals ranged 5–6 and the mean call and duet (C&D) duration for 23 RMC's (10 lone calls, 13 duets) was 5864.00 ± 2360.61 ms (Table 7).

The mean call signal duration was 159.33 ± 18.65 ms (Table 7) and the mean call interval pattern was approximately even with a range of 33.08−36.45 ms (Table 8). Mean male C-C exchange interval was 1423.55 ± 157.06 ms (Fig. 7 and Table 7). The number of answers per RMC ranged from 1–4, beats per answer ranged 2–10, and mean answer duration was 183.06 ± 63.43 ms (Table 7). Mean call-answer (C-A) exchanges were approximately consistent at 211.77 ± 32.54 ms (Fig. 7). The number of response beats per signal ranged 4–8, and mean response duration was 164.13 ± 58.65 ms (Table 7). Mean answer-response exchange intervals (A-R) were consistent at 334.25 ± 32.80 ms (Fig. 7). The mean answer-call (A-C) exchanges, like call-call exchanges, were less consistent at 997.09 ± 205.89 ms. These exchanges would have had smaller standard deviations if the RMC's and answers were grouped signal patterns, with consistent intragroup and intergroup intervals.

This pair's (PC M02-F02) mean monophasic call, answer, and response interbeat interval patterns were relatively even (Fig. 7 and Table 8). Mean call interval difference for intervals i1–i6 was less than 10 ms (ID = 3.37). Mean answer interval difference for intervals i1–i9 was less than 10 ms (ID: 38.21−30.98 = 7.23) and mean response interval difference for intervals i1–i7 was less than 10 (ID: 40.32−34.79 = 5.53). The male response signals followed female answers A1, A2, and A4, but were placed at the end of the chart for simplicity (Fig. 7).

*Soliperla sierra*—French Creek M01. A total of 23 RMC's containing a 105 monophasic signals (range 4–6 per RMC) were recorded from this 2-day old male at 21.1 ºC (Tables 2–3). Recording occurred between 08:53–16:19 on May 10, 2020. The number of call beats per monophasic signal ranged 4–6, and mean RMC duration was 4951.32 ± 856.35 ms (Fig. 2A and Table 3).

The mean monophasic call signal interval pattern was approximately even over intervals i1–i5 and ranged 34.24–36.54 ms, and mean duration was 142.18 ± 23.93 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1159.11 ± 145.93 ms. This male's (FC-M01) relatively even mean monophasic interbeat interval pattern had the shortest initial intervals among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i5 was less than 10 ms (ID: 36.54–34.24 = 2.30).

*Soliperla sierra*—French Creek M02. Ten RMC's containing 53 monophasic signals (range 4–6 per RMC) were recorded from this 3-day old male at 21.1ºC (Tables 2–3). Recording occurred between 10:11–10:43 May 11, 2020. The number of call beats per monophasic signal ranged 4–6, and mean RMC duration was 5789.90 ± 943.07 ms (Fig. 2B and Table 3).

The mean interbeat interval pattern for monophasic call signals was approximately even over intervals i1–i5 (range 38.83–39.83 ms), and mean duration was 175.53 ± 23.83 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1130.58 ± 109.17 ms. This male's (FC-M02) interbeat interval pattern compared intermediately among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i5 was less than 10 ms (ID = 1.00).

*Soliperla sierra*—French Creek M03. Ten RMC's containing 45 monophasic signals (range 3–5 per RMC) were recorded from this 4-day old male at 21.1 ºC (Tables 2 & 3). Recording occurred between 09:36–13:11 May 12, 2020. The number of call beats per monophasic signal ranged 4–6, and the mean RMC duration was 5133.88 ± 924.52 ms (Fig. 2C and Table 3).

The mean monophasic call interbeat interval pattern was approximately even over intervals i1–i5 (range 38.08–39.29 ms), and mean duration was 168.79 ± 26.29 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1249.81 ± 134.45 ms. This male's (FC-M03) interbeat interval pattern compared intermediately among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i5 was less than 10 ms (ID = 2.45).

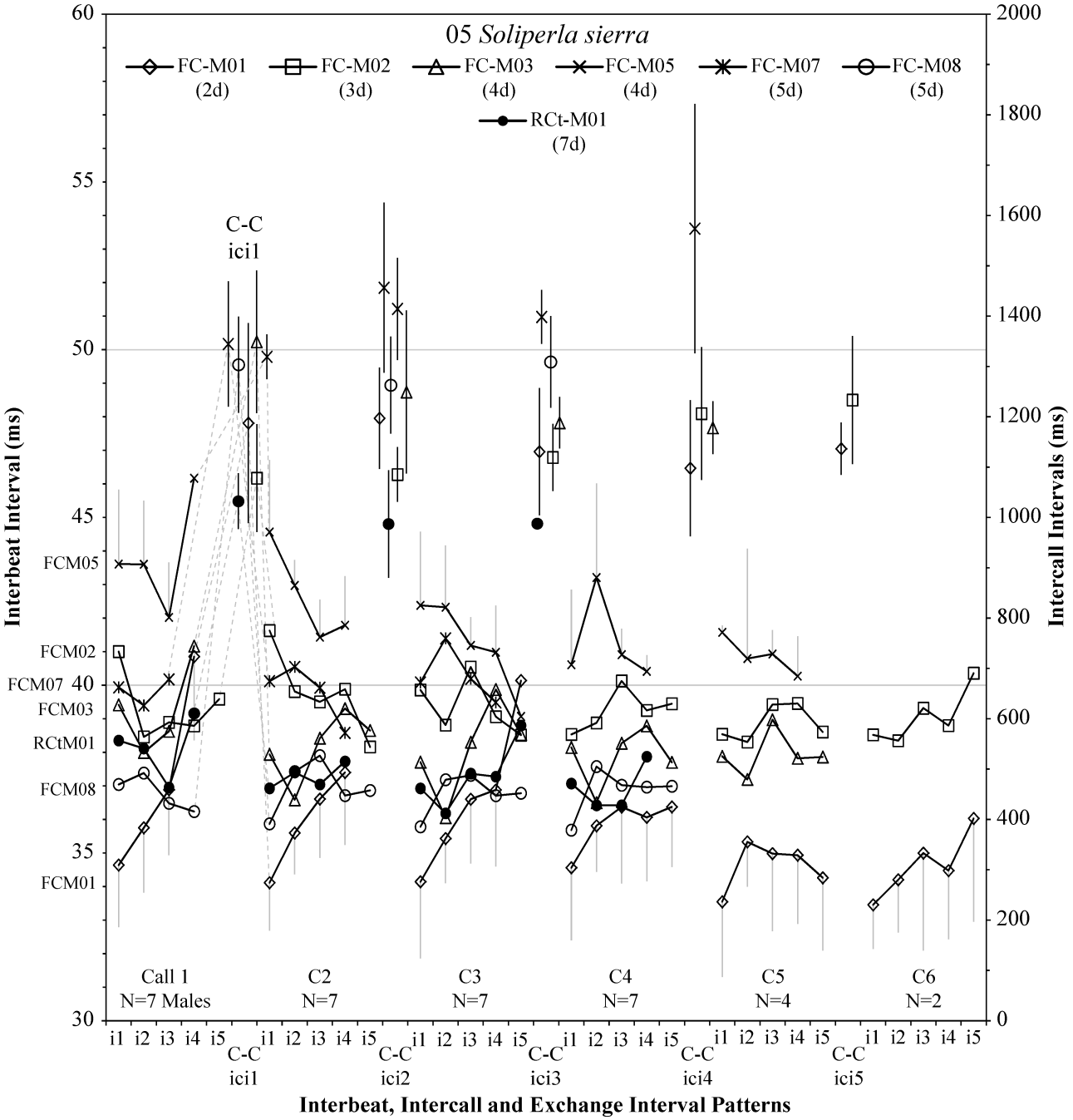


**FIGURE 5.** *Soliperla sierra* repeated monophasic call interbeat interval patterns from French Creek (N=6 males) and Rattlesnake Creek unnamed tributary (N=1 male). Mean interbeat intervals (i1–i5) and mean call-call intercall intervals (C-C ici1–ici5) for 76 RMC's contained 2–6 monophasic signals. Some interbeat interval standard deviation not charted (vertical bars).

*Soliperla sierra*—French Creek M05. Five RMC's containing 22 monophasic signals (range 4–5 per RMC) were recorded from this 4-day old male at 21.1ºC (Tables 2–3). Recording occurred between 22:16–22:29 May 12, 2020. The number of call beats per monophasic signal ranged 3–6, and the mean RMC duration was 5509.46 ± 985.65 ms (Fig. 2D and Table 3).

The mean interbeat interval pattern for monophasic call signals was approximately even over intervals i1–i5 (range 39.07–42.83 ms), and the mean duration was 160.47 ± 22.83 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1412.76 ± 137.23 ms. This male's (FC-M05) interbeat interval pattern was the longest among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i5 was less than 10 ms (ID = 3.76).

**TABLE 5.** *Soliperla sierra* (Ss) monophasic signal interbeat interval (IBI) patterns (intervals i1–i5) from French Creek (FC) and Rattlesnake Creek tributary (RCt). All repeated monophasic calls (RMC) were condensed into one monophasic call signal per male. Number of monophasic signals per RMC ranged from 2–6 and number of beats per call ranged from 2–6. Male call-response exchange intervals and sequenced monophasic response signals were not observed. Mean call interval differences (ID = maximum –minimum) indicated by underlining.

| | Monophasic Signal IBI Pattern (ms) | | | | | | | Intercall Interval (ms) |
|---|---|---|---|---|---|---|---|---|
| **Ss FC-M01** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-5 |
| AVG | 34.24 | 35.57 | 36.37 | 36.54 | 35.55 | 142.18 | 2.30 | 1159.11 |
| MAX | 39.14 | 39.86 | 40.59 | 43.47 | 40.14 | 188.53 | | 1637.87 |
| MIN | 29.52 | 32.27 | 32.13 | 32.56 | 30.52 | 100.22 | | 846.46 |
| STD | 1.98 | 1.47 | 2.09 | 2.39 | 2.41 | 23.93 | | 145.93 |
| N | 108 | 108 | 108 | 85 | 22 | 108 | | 85 |
| **Ss FC-M02** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-5 |
| AVG | 39.83 | 38.83 | 39.69 | 39.26 | 38.88 | 175.53 | 1.00 | 1130.58 |
| MAX | 44.56 | 41.13 | 42.99 | 41.90 | 40.61 | 202.11 | | 1532.31 |
| MIN | 36.03 | 36.05 | 37.71 | 35.58 | 34.13 | 116.98 | | 938.32 |
| STD | 1.99 | 1.19 | 1.10 | 1.07 | 1.36 | 23.83 | | 109.17 |
| N | 52 | 52 | 52 | 49 | 27 | 52 | | 43 |
| **Ss FC-M03** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-4 |
| AVG | 38.25 | 36.84 | 38.48 | 39.29 | 38.08 | 168.79 | 2.45 | 1249.81 |
| MAX | 44.04 | 41.75 | 40.88 | 42.27 | 39.43 | 196.89 | | 1654.90 |
| MIN | 34.24 | 34.42 | 36.19 | 37.07 | 36.21 | 110.48 | | 972.93 |
| STD | 2.13 | 1.48 | 1.05 | 1.26 | 0.81 | 26.29 | | 134.45 |
| N | 45 | 45 | 45 | 39 | 25 | 45 | | 35 |
| **Ss FC-M05** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-4 |
| AVG | 42.68 | 42.83 | 41.31 | 41.26 | 39.07 | 160.47 | 3.76 | 1412.76 |
| MAX | 46.12 | 47.98 | 43.70 | 46.17 | 39.07 | 201.39 | | 1748.98 |
| MIN | 37.57 | 38.48 | 39.77 | 39.43 | 39.07 | 89.63 | | 1267.76 |
| STD | 2.43 | 2.02 | 1.05 | 1.72 | | 22.83 | | 137.23 |
| N | 22 | 22 | 21 | 18 | 1 | 22 | | 17 |
| **Ss FC-M07** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-2 |
| AVG | 40.04 | 40.38 | 40.08 | 39.03 | | 135.72 | 1.35 | 1375.53 |
| MAX | 44.15 | 42.74 | 44.81 | 40.54 | | 165.34 | | 1560.09 |
| MIN | 34.24 | 37.39 | 37.53 | 36.30 | | 77.21 | | 1169.34 |
| STD | 1.80 | 1.55 | 1.56 | 1.15 | | 28.72 | | 117.21 |
| N | 28 | 28 | 25 | 14 | | 28 | | 18 |
| **Ss FC-M08** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-3 |
| AVG | 36.17 | 37.36 | 37.21 | 36.60 | 36.85 | 167.92 | 1.19 | 1287.47 |
| MAX | 38.98 | 40.20 | 38.57 | 37.46 | 37.73 | 185.72 | | 1462.11 |
| MIN | 33.51 | 35.46 | 35.26 | 34.97 | 36.28 | 144.47 | | 1138.07 |
| STD | 1.11 | 1.05 | 0.83 | 0.54 | 0.39 | 18.59 | | 93.46 |
| N | 34 | 34 | 34 | 34 | 19 | 34 | | 24 |
| **Ss RCt-M02** | i1 | i2 | i3 | i4 | i5 | Dur | ID | C-C 1-3 |
| AVG | 37.41 | 37.20 | 37.10 | 37.72 | 38.80 | 135.43 | 3.29 | 1009.65 |
| MAX | 41.93 | 43.79 | 38.66 | 40.54 | 38.80 | 182.00 | | 1205.85 |
| MIN | 31.86 | 34.35 | 35.26 | 36.15 | 38.80 | 37.76 | | 895.40 |
| STD | 2.10 | 2.17 | 0.91 | 1.19 | | 31.70 | | 80.91 |
| N | 24 | 23 | 21 | 18 | 1 | 24 | | 16 |

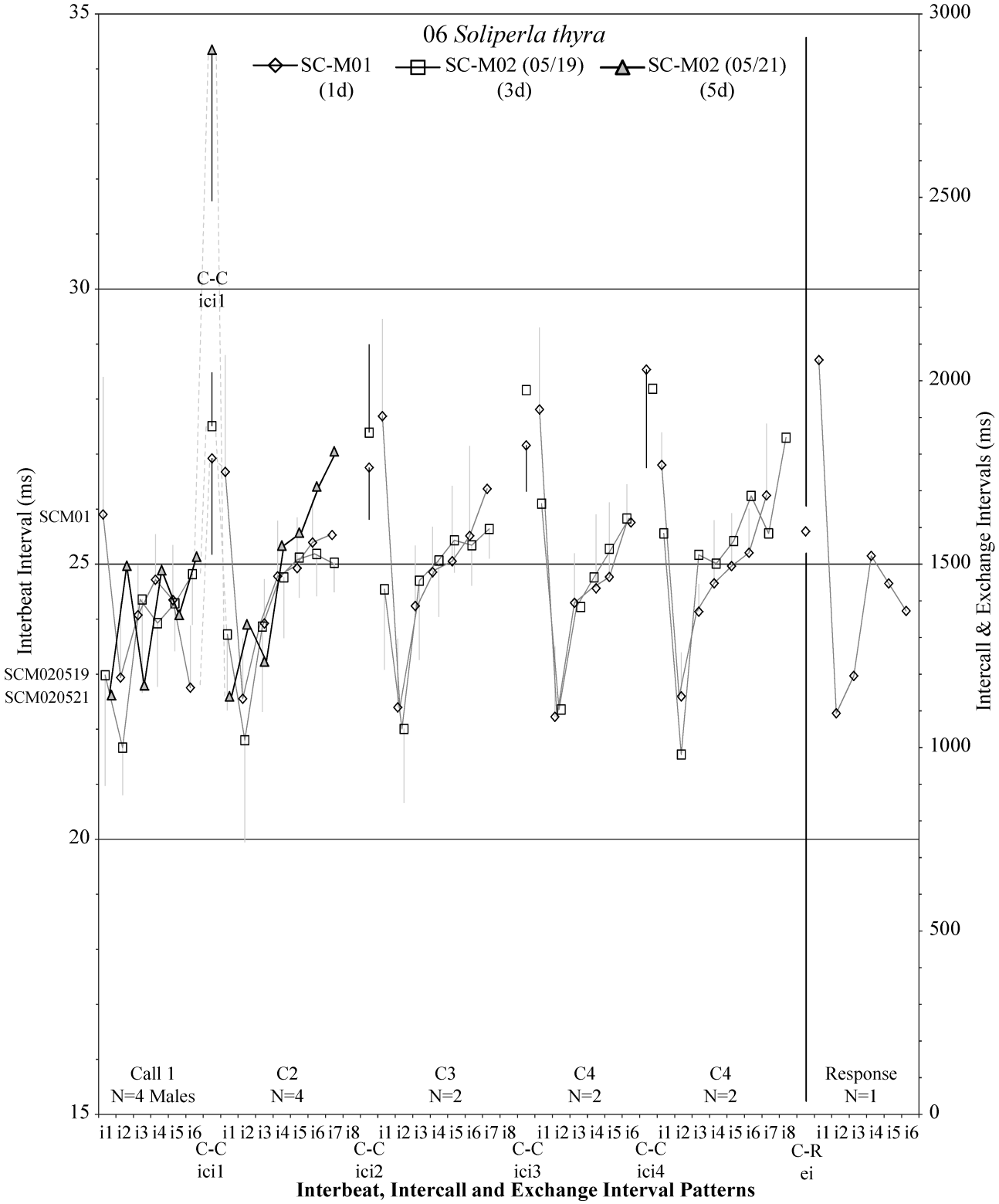


**FIGURE 6.** *Soliperla thyra* repeated monophasic call interbeat interval patterns from Salt Creek (N=2 males, M02 on two different dates). Mean interbeat intervals (i1–i8), call-call intercall intervals (C-C ici1-ici5) and call-response exchange interval for 28 RMC's contained 2–6 monophasic signals. Standard deviation (vertical bars).

**TABLE 6.** *Soliperla thyra* (St) monophasic call interbeat interval (IBI) patterns (intervals i1–i8) from Salt Creek (SC). Number of repeated monophasic calls ranged from 2–6 and number of beats per call ranged from 5–9. Male call-response (C-R) exchange intervals and sequenced monophasic response signals were not observed. Mean call interval differences (ID = maximum –minimum) indicated by underlining.

| | Monophasic Call IBI Pattern (ms) | | | | | | | | | | Intercall Interval (ms) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **St SC-M01** | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | Dur | ID | C-C 1-5 |
| AVG | 27.02 | 22.54 | 24.10 | 24.74 | 24.82 | 25.18 | 26.10 | | 146.22 | 4.48 | 1813.06 |
| MAX | 31.86 | 24.72 | 26.35 | 26.35 | 27.66 | 27.82 | 27.17 | | 180.49 | | 2376.73 |
| MIN | 21.77 | 19.77 | 22.02 | 22.65 | 22.79 | 21.54 | 25.33 | | 99.18 | | 1505.03 |
| STD | 1.99 | 1.17 | 0.88 | 0.97 | 1.12 | 1.36 | 0.84 | | 15.76 | | 207.12 |
| N | 44 | 44 | 44 | 44 | 42 | 38 | 4 | | 44 | | 34 |
| **St SC-M02 (05/19)** | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | Dur | | C-C 1-4 |
| AVG | 23.87 | 21.83 | 24.33 | 24.59 | 24.98 | 25.18 | 25.41 | 26.03 | 171.86 | 4.20 | 1876.57 |
| MAX | 26.35 | 24.90 | 27.17 | 26.17 | 26.49 | 26.30 | 28.07 | 27.30 | 203.39 | | 2370.23 |
| MIN | 20.14 | 19.18 | 21.00 | 21.56 | 22.13 | 23.22 | 23.88 | 24.20 | 87.10 | | 1513.36 |
| STD | 1.74 | 1.34 | 1.52 | 1.13 | 0.84 | 0.82 | 0.79 | 0.80 | 25.81 | | 188.21 |
| N | 35 | 35 | 35 | 35 | 34 | 34 | 28 | 11 | 35 | | 24 |
| **St SC-M02 (05/21)** | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | Dur | | C-C 1 |
| AVG | 22.61 | 24.44 | 23.02 | 25.12 | 24.83 | 25.82 | 26.64 | 27.54 | 182.49 | 4.93 | 2902.43 |
| MAX | 27.35 | 26.37 | 23.85 | 26.55 | 27.60 | 27.26 | 28.96 | 28.34 | 205.07 | | 3528.37 |
| MIN | 19.80 | 21.20 | 21.43 | 23.27 | 22.97 | 24.33 | 25.08 | 26.28 | 121.41 | | 2601.66 |
| STD | 2.16 | 1.44 | 0.68 | 0.89 | 1.37 | 0.83 | 0.94 | 0.76 | 22.99 | | 412.63 |
| N | 14 | 14 | 14 | 14 | 14 | 13 | 13 | 7 | 14 | | 7 |

*Soliperla sierra*—French Creek M07. Ten RMC's containing 28 monophasic signals (range 2–3 per RMC) were recorded from this 5-day old male at 21.1ºC (Tables 2–3). Recording occurred between 08:54–13:25 May 13, 2020. The number of call beats per monophasic signal ranged 3–5, and the mean RMC duration was 2855.97 ± 590.95 ms (Fig. 2E and Table 3).

The mean monophasic call interbeat interval pattern was approximately even over intervals i1–i4 (range 39.03–40.38 ms), and mean duration was 135.72 ± 28.72 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1375.53 ± 117.21 ms. This male's (FC-M07) interbeat interval pattern compared intermediately among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i4 was less than 10 ms (ID = 1.35).

*Soliperla sierra*—French Creek M08. Ten RMC's containing 34 monophasic signals (range 3–4 per RMC) were recorded from this 5-day old male at 21.1ºC (Tables 2–3). Recording occurred between 08:54–10:35 May 13, 2020. The number of call beats per monophasic signal ranged 5–6, and the mean RMC duration was 3660.86 ± 916.31 ms (Fig. 2F and Table 3).

The mean call interbeat interval pattern was approximately even over intervals i1–i5 (range 36.17–37.36 ms), and mean duration was 167.92 ± 18.59 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1287.47 ± 93.46 ms. This male's (FC-M08) interbeat interval pattern compared intermediately among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i5 was less than 10 ms (ID = 1.19).

*Soliperla sierra*—Rattlesnake Creek tributary M02. Eight RMC's containing 24 monophasic signals (range 2–4 per RMC) were recorded from this 7-day old male at 23.8ºC (Tables 2–3). Recording occurred at 06:25 May 25, 2020. The number of beats per monophasic signal ranged 2–6, and the mean RMC duration was 2425.59 ± 628.14 ms (Fig. 2G and Table 3).

The mean monophasic interbeat interval pattern was approximately even over intervals i1–i5 (range 37.10–38.80 ms), and the mean monophasic call signal duration was 135.43 ± 31.70 ms (Fig. 5 and Table 5). Male C-C exchange intervals varied greatly 1009.65 ± 80.91 ms. This male's (RCt-M02) interbeat interval pattern compared intermediately among the other conspecific male interval patterns (Fig. 5 and Table 5). Mean interval difference for intervals i1–i5 was less than 10 ms (ID = 3.29).

*Soliperla sierra*—French Creek M02-F01. Repeated monophasic 2–3 way intersexual exchanges were long and variable due to the range in the numbers of call, answer, and response signals (Fig. 8). French Creek Male-02 had ten RMC's composed of 51 monophasic signals with a range 2–8 per RMC (Tables 2 and 7). Female-01 answered 10 RMC's with 28 sequenced monophasic signals (Table 7). Male-02 completed one RMC with a sequenced monophasic response signal (Table 7). The pair was recorded three days after collection at 21.1ºC, between 12:49–13:08 May 11, 2020 (Table 2). The number call beats per monophasic signal ranged 4–6, and mean C&D duration for 10 RMC's and 28 duets was 5887.03 ± 2205.40 ms (Fig. 2H and Table 7).

The mean call signal duration was 170.91 ± 24.02 ms (Table 7) and the mean call interval pattern was approximately even with a range of 36.93–38.89 ms (Fig. 8 and Table 8). Mean male C-C exchange interval was 1115.30 ± 75.76 ms (Fig. 8 and Table 7). The number of answers per RMC ranged from 1–5, beats per answer ranged 3–9, and mean answer duration was 204.46 ± 53.01 ms (Fig. 8 and Table 7). Mean C-A exchanges were approximately consistent at 163.08 ± 23.24 ms. The number of beats per response signal was 6 (N=1), and one response duration was 185.86 ms (Table 7). The A-R exchange was 254.31 ms. The mean A-C exchanges, like call-call exchanges, were less consistent at 806.50 ± 94.41 ms.

This pair's (FC M02-F01) mean call and response interbeat interval patterns were approximately even and the female answer interval pattern less even (Fig. 8 and Table 8). Mean call interval difference for intervals i1–i5 was less than 10 (ID = 1.96). Mean answer interval difference for intervals i1–i8 was greater than 10 (ID: 48.48–35.98 = 12.5) and mean response interval difference for intervals i1–i5 was less than 10 ms (ID: 40.16–32.34 = 7.82). The female answer had a monophasic signal pattern and a varied beat interval pattern.

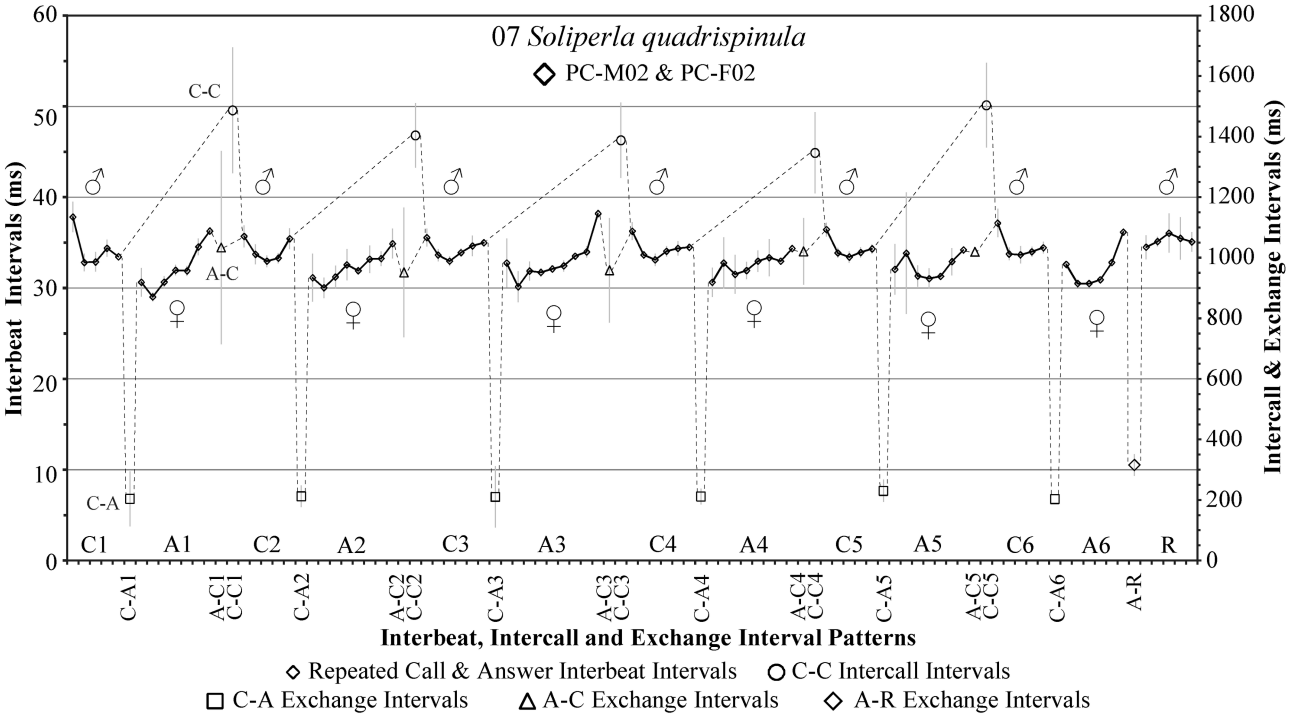


**FIGURE 7.** *Soliperla quadrispinula* duets from Puter Creek (1 male & 1 female). Repeated monophasic 2-way and 3-way (call-answer-response) interbeat, intercall and exchange interval patterns. Mean interbeat intervals (solid lines) of calls (C) and answers (A) for 13 repeated monophasic intersexual exchanges (duets) contained 1–6 calls, 1–4 answers and four responses. Mean signal exchanges included call-answer (C-A 1–6), answer-call (A-C 1–5), call-call (C-C 1–4) and four three-way call-answer-responses (A-R). Interbeat intervals (i1–i9) not labeled under x-axis and interval standard deviation indicated by vertical bars.

*Soliperla thyra*—Salt Creek M01. Ten RMC's containing 44 monophasic signals (range 3–6 per RMC) were recorded from this 1-day old male at 21.6 ºC (Tables 2–3). Recording occurred between 10:10–17:00 May 17, 2020. The number of beats per monophasic signal ranged 5–8, and the mean RMC duration was 6807.77 ± 1754.32 ms (Fig. 3A and Table 3).

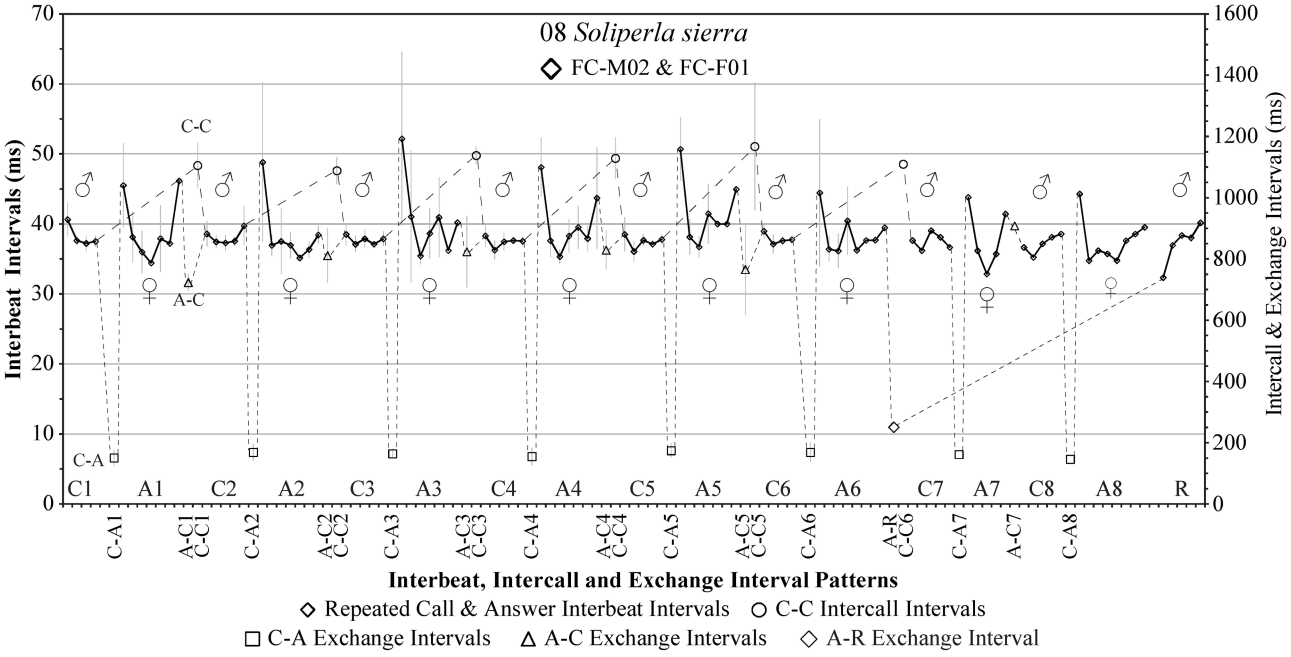


**FIGURE 8.** *Soliperla sierra* duets from French Creek (1 male & 1 female). Repeated monophasic 2-way and 3-way (call-answer-response) interbeat, intercall and exchange interval patterns. Mean interbeat intervals (solid lines) of calls (C) and answers (A) for 10 repeated monophasic exchanges contained 2–8 calls, 1–5 answers and one response. Mean signal exchanges included call-answer (C-A 1–8), answer-call (A-C 1–7), call-call (C-C 1–6) and one 3-way call-answer-response (A-R). Interbeat intervals (i1–i8) not labeled under x-axis and interval standard deviation indicated by vertical bars.

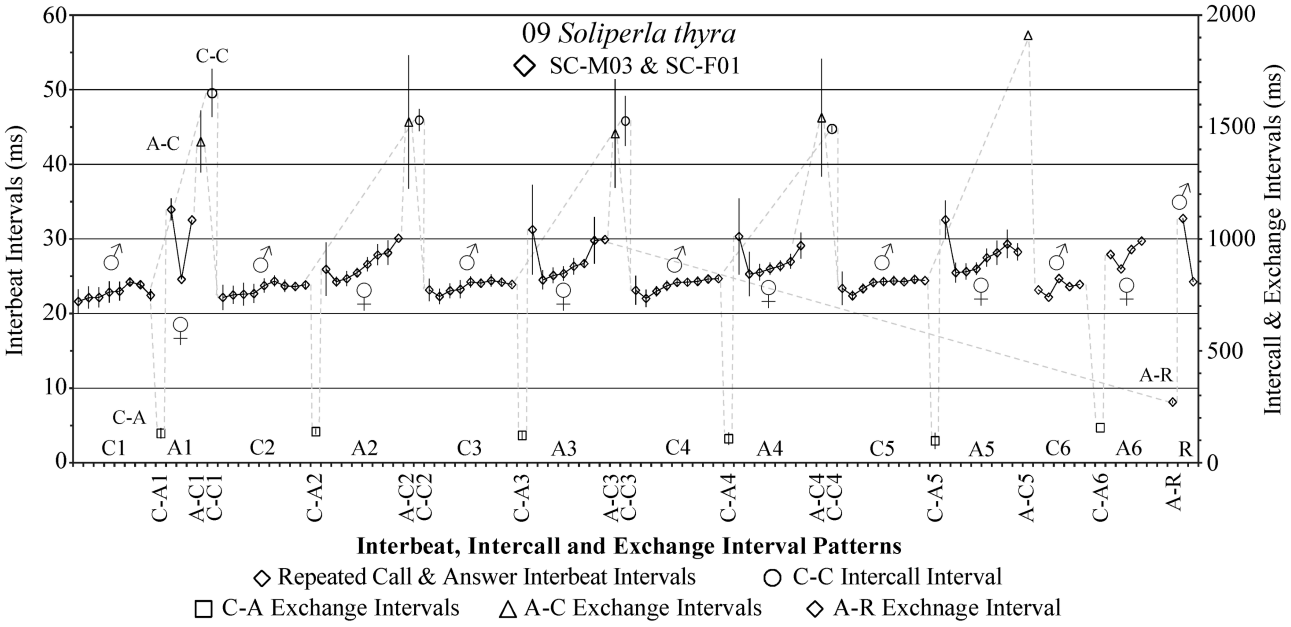


**FIGURE 9.** *Soliperla thyra* duets from Salt Creek (1 male & 1 female). Repeated monophasic 2-way and 3-way (call-answer-response) interbeat, intercall and exchange interval patterns. Mean interbeat intervals (solid lines) of calls (C) and answers (A) for 15 repeated monophasic exchanges contained 4–6 calls, 2–4 answers and one response. Mean signal exchanges included call-answer (C-A 1–6), answer-call (A-C 1–5), call-call (C-C 1–4) and one 3-way call-answer-response (A-R). Interbeat intervals (i1–i9) not labeled under x-axis and interval standard deviation indicated by vertical bars.

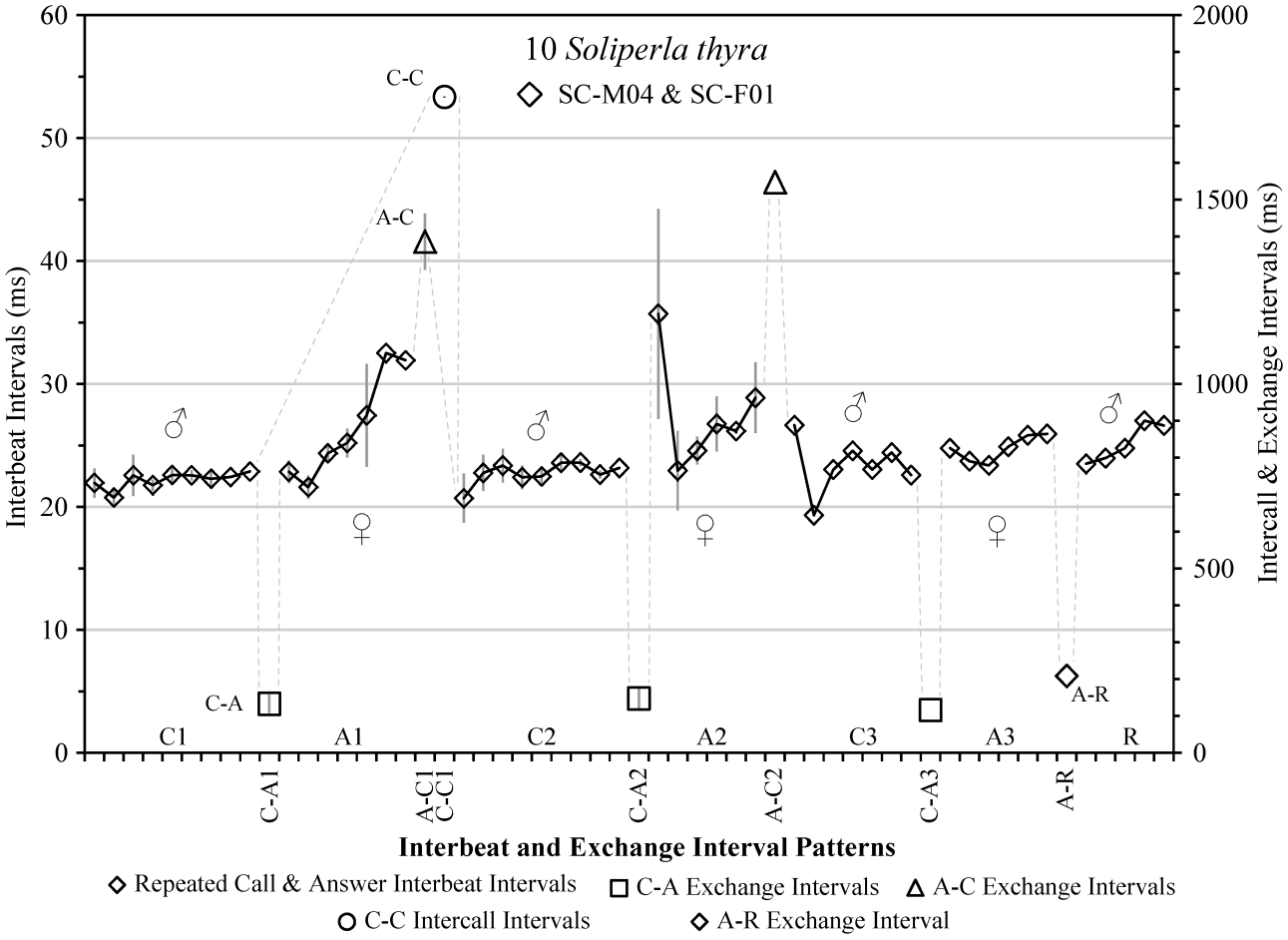


**FIGURE 10.** *Soliperla thyra* duets from Salt Creek (1 male & 1 female). Repeated monophasic 2-way and 3-way (call-answer-response) interbeat, intercall and exchange interval patterns. Mean interbeat intervals (solid lines) of calls (C) and answers (A) for 5 repeated monophasic exchanges contained 1–3 calls, 2–3 answers and one response. Mean signal exchanges included call-answer (C-A 1–3), answer-call (A-C 1–2), call-call (C-C 1) and one 3-way call-answer-response (A-R). Interbeat intervals (i1–i9) not labeled under x-axis and interval standard deviation indicated by vertical bars.

The mean call interbeat interval pattern was approximately even over intervals i1–i7 (range 22.54–27.02 ms), and mean call duration was 146.22 ± 15.76 ms (Fig. 6 and Table 6). Male C-C exchange intervals varied greatly 1813.06 ± 207.12 ms. This male's (SC-M01) approximately even mean interbeat interval pattern compared intermediately among the other conspecific males (Fig. 6 and Table 6). Mean interval difference for intervals i1–i8 was less than 10 ms (ID = 4.48).

*Soliperla thyra*—Salt Creek M02 (recorded 05/19/2020). Eleven RMC's containing 35 monophasic signals (range 3–5 per RMS) were recorded from this 3-day old male at 21.6ºC (Tables 2–3). Recording occurred at 12:53–21:17 May 19, 2020. The number of beats per monophasic signal ranged 5–9, and the mean RMC duration was 4641.14 ± 1365.01 ms (Fig. 3B and Table 3).

The mean interbeat interval pattern for calls was approximately even over intervals i1–i8 (range 21.83–26.03 ms), and mean signal duration was 171.86 ± 25.81 ms (Fig. 6 and Table 6). Male C-C exchange intervals varied greatly 1876.57 ± 188.21 ms. This male's (SC-M02 0519) mean interbeat interval pattern differed from Male-01 with slightly shorter second intervals (i2) (Fig. 6 and Table 6). Mean interval difference for intervals i1–i8 was less than 10 ms (ID: = 4.20).

**TABLE 7.** Exchange (duet) characters of male repeated monophasic calls (RMC) sequenced female answer and male response signals. *Soliperla quadrispinula* Putter Cr. (Sq PC M02-F02), *S. sierra* French Cr. (Ss FC M02-F01) and *S. thyra* Salt Cr (St SC M03-F01 & SC-M04-F01). Number of monophasic signals/RMC (#MS/RMC), number of beats/monophasic signal (#B/MS), monophasic signal duration (MS Dur), call-call intercall interval (C-C), call-answer interval (C-A), number of answers/RMC (#A/RMC), number of beats/answer (#B/A), answer duration (A Dur), answer-call interval (A-C), answer-response interval (A-R), number of beats/response (#B/R), response duration (R Dur) and call-duet duration (C&D Dur).

| | Male Calls | | | Intercall & Exchange Intervals | | Female Answers | | | Exchange Intervals | | Male Responses | RMC & Duet | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sq PC-M02 & PC-F02** | | | | | | | | | | | | | |
| | #MS/ RMC | #B/ MS | MS Dur (ms) | C-C (ms) | C-A (ms) | #A/ RMC | #B/ A | A Dur (ms) | A-C (ms) | A-R (ms) | #B/ R | R Dur (ms) | C&D Dur (ms) |
| AVG | 4.43 | 5.62 | 159.33 | 1423.55 | 211.77 | 2.23 | 6.59 | 183.06 | 997.09 | 334.25 | 5.6 | 164.13 | 5864.00 |
| MAX | 6 | 6 | 207 | 1790.45 | 272.52 | 4 | 10 | 297 | 1371.38 | 362.31 | 8 | 248 | 8794.76 |
| MIN | 1 | 5 | 133 | 1154.42 | 138.91 | 1 | 2 | 31 | 677.64 | 284.04 | 4 | 106 | 1079.57 |
| STD | 1.56 | 0.49 | 18.65 | 157.06 | 32.54 | 1.17 | 1.88 | 63.43 | 205.89 | 32.80 | 1.67 | 58.65 | 2360.61 |
| N | 23 | 102 | 102 | 62 | 29 | 13 | 29 | 29 | 17 | 5 | 5 | 5 | 23 |
| **Ss FC-M02 & FC-F01** | | | | | | | | | | | | | |
| | #MS/ RMC | #B/ MS | MS Dur (ms) | C-C (ms) | C-A (ms) | #A/ RMC | #B/ A | A Dur (ms) | A-C (ms) | A-R (ms) | #B/ R | R Dur (ms) | C&D Dur (ms) |
| AVG | 5.1 | 5.53 | 170.91 | 1115.30 | 163.08 | 3.10 | 6.10 | 204.46 | 806.50 | 254.31 | 6.0 | 185.86 | 5887.03 |
| MAX | 8 | 6 | 196.21 | 1314.17 | 209.09 | 5 | 9 | 301.45 | 1010.93 | 254.31 | 6 | 185.86 | 10095.24 |
| MIN | 2 | 4 | 112.40 | 989.16 | 114.51 | 1 | 3 | 128.78 | 660.48 | 254.31 | 6 | 185.86 | 1658.75 |
| STD | 2.16 | 0.64 | 24.02 | 75.76 | 23.24 | 1.20 | 1.64 | 53.01 | 94.41 | n/a | n/a | n/a | 2205.40 |
| N | 10 | 51 | 51 | 19 | 31 | 10 | 28 | 28 | 22 | 1 | 1 | 1 | 10 |
| **St SC-M03 & SC-F01** | | | | | | | | | | | | | |
| | #MS/ RMC | #B/ MS | MS Dur (ms) | C-C (ms) | C-A (ms) | #A/ RMC | #B/ A | A Dur (ms) | A-C (ms) | A-R (ms) | #B/ R | R Dur (ms) | C&D Dur (ms) |
| AVG | 4.53 | 8.79 | 182.47 | 1570.42 | 118.97 | 2.70 | 7.41 | 174.38 | 1524.51 | 271.45 | 3.0 | 57.00 | 6879.79 |
| MAX | 6 | 10 | 218.07 | 1849.77 | 156.95 | 4 | 9 | 234.19 | 1909.50 | 271.45 | 3 | 57.00 | 11304.91 |
| MIN | 4 | 6 | 117.85 | 1407.50 | 59.46 | 2 | 2 | 34.97 | 1184.47 | 271.45 | 3 | 57.00 | 5139.38 |
| STD | 0.64 | 1.02 | 24.48 | 109.78 | 28.24 | 0.82 | 1.95 | 50.94 | 253.04 | n/a | n/a | n/a | 1553.66 |
| N | 15 | 68 | 68 | 35 | 28 | 10 | 27 | 27 | 18 | 1 | 1 | 1 | 15 |
| **St SC-M04 & SC-F01** | | | | | | | | | | | | | |
| | #MS/ RMC | #B/ MS | MS Dur (ms) | C-C (ms) | C-A (ms) | #A/ RMC | #B/ A | A Dur (ms) | A-C (ms) | A-R (ms) | #B/ R | R Dur (ms) | C&D Dur (ms) |
| AVG | 2.00 | 7.80 | 154.76 | 1778.57 | 137.54 | 2.25 | 6.33 | 138.76 | 1426.19 | 55.73 | 6.0 | 125.89 | 2370.40 |
| MAX | 3 | 10 | 202.26 | n/a | 180.59 | 3 | 8 | 184.05 | 1547.23 | 208.50 | 6 | 125.89 | 4618.18 |
| MIN | 1 | 6 | 110.26 | n/a | 100.59 | 2 | 5 | 117.05 | 1297.53 | 23.51 | 6 | 125.89 | 393.99 |
| STD | 0.71 | 1.32 | 32.72 | n/a | 25.38 | 0.50 | 1.00 | 22.41 | 102.04 | 74.85 | n/a | n/a | 1500.29 |
| N | 5 | 10 | 10 | 1 | 9 | 4 | 9 | 9 | 4 | 6 | 1 | 1 | 5 |

*Soliperla thyra*—Salt Creek M02 (recorded 05/21/2020). Seven RMC's containing 14 monophasic signals (N = 2 per RMC) were recorded from this 5-day old male at 21.6ºC (Tables 2–3). Recording occurred at 09:02–09:40 May 21, 2020. The older Salt Creek male always called with two monophasic signals per RMC, the number of beats per call signal ranged 6–9, and the mean RMC duration was 3267.42 ± 426.08 ms (Fig. 3C and Table 3).

The mean interbeat interval pattern for call signals was approximately even over intervals i1–i8 (range 22.61–27.54 ms), and the mean call duration was 182.49 ± 22.99 ms (Fig. 6 and Table 6). Male C-C exchange intervals varied greatly 1813.06 ± 207.12 ms. This male's (SC-M02 0521) interbeat interval pattern differed slightly because it had fewer numbers of calls per signal and longer C-C exchange intervals (Fig. 6 and Table 6). Mean interval difference for intervals i1–i7 was less than 10 ms (ID: = 4.93).

**TABLE 8.** Monophasic interbeat interval patterns of calls, answers and responses (2–3-way sequenced exchanges). *Soliperla quadrispinula* Puter Cr (Sq PC-M02 & PC-F01), *S. sierra* French Cr (Ss FC-M02 & FC-F01) and *S. thyra* Salt Cr (St SC-M03 & SC-F01 and SC-M04 & SC-F01). Interval differences (ID) indicated by underlining.

| Monophasic Call, Answer and Response Interbeat Interval Patterns (ms) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Sq PC-M02 & PC-F02** (ID=3.37) | | | | Calls | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 |
| AVG | 36.45 | 33.51 | 33.08 | 33.92 | 34.57 | 34.82 | | | |
| MAX | 40.54 | 37.72 | 35.10 | 36.79 | 37.55 | 35.28 | | | |
| MIN | 32.95 | 30.86 | 30.41 | 32.18 | 31.49 | 34.49 | | | |
| STD | 1.48 | 0.88 | 0.78 | 0.74 | 0.92 | 0.41 | | | |
| N | 102 | 102 | 102 | 102 | 63 | 3 | | | |
| **Ss FC-M02 & FC-F01** (ID=1.96) | | | | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 |
| AVG | 38.89 | 36.93 | 37.53 | 37.45 | 37.90 | | | | |
| MAX | 46.96 | 39.09 | 40.50 | 38.75 | 42.86 | | | | |
| MIN | 33.95 | 33.88 | 35.49 | 36.46 | 36.62 | | | | |
| STD | 2.01 | 1.23 | 1.09 | 0.59 | 1.19 | | | | |
| N | 51 | 51 | 51 | 47 | 31 | | | | |
| **St SC-M03 & SC-F01** (ID=1.98) | | | | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 |
| AVG | 22.61 | 22.25 | 22.78 | 23.23 | 23.83 | 24.23 | 24.09 | 24.07 | 24.02 |
| MAX | 27.53 | 24.92 | 26.69 | 25.76 | 25.37 | 25.76 | 25.92 | 25.56 | 24.94 |
| MIN | 18.84 | 19.14 | 20.57 | 20.98 | 20.59 | 22.99 | 22.18 | 21.61 | 23.02 |
| STD | 1.82 | 1.16 | 1.19 | 1.21 | 0.99 | 0.61 | 0.75 | 0.86 | 0.54 |
| N | 68 | 68 | 68 | 68 | 68 | 66 | 60 | 47 | 18 |
| **St SC-M04 & SC-F01** (ID=0.88) | | | | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 |
| AVG | 21.92 | 21.42 | 22.93 | 22.30 | 22.60 | 23.19 | 22.78 | 22.56 | 23.03 |
| MAX | 26.64 | 24.33 | 25.33 | 24.56 | 23.40 | 24.42 | 23.81 | 22.86 | 23.17 |
| MIN | 18.37 | 19.32 | 20.88 | 21.18 | 21.50 | 22.18 | 21.61 | 22.40 | 22.88 |
| STD | 2.26 | 1.57 | 1.43 | 1.07 | 0.59 | 0.83 | 0.76 | 0.26 | 0.21 |
| N | 10 | 10 | 10 | 10 | 10 | 8 | 6 | 3 | 2 |

| **Sq PC-M02 & PC-F01** (ID=7.23) | | | | | | | | | | (ID=5.53) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Answers | | | | | | | | | Responses | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 | i1 | i2 | i3 | i4 | i5 | i6 | i7 |
| AVG | 31.28 | 30.98 | 31.27 | 31.97 | 32.16 | 33.40 | 33.63 | 34.43 | 38.21 | 34.79 | 35.26 | 35.76 | 36.01 | 35.34 | 37.26 | 40.32 |
| MAX | 36.83 | 41.41 | 36.05 | 36.26 | 34.92 | 36.17 | 36.28 | 36.60 | 38.21 | 35.96 | 35.83 | 38.64 | 37.12 | 35.85 | 37.26 | 40.32 |
| MIN | 28.28 | 28.02 | 29.12 | 30.25 | 31.07 | 31.61 | 32.54 | 33.33 | 38.21 | 33.33 | 34.58 | 34.01 | 33.83 | 34.33 | 37.26 | 40.32 |
| STD | 2.17 | 2.93 | 1.37 | 1.15 | 0.81 | 1.52 | 1.05 | 1.11 | | 1.32 | 0.57 | 1.98 | 1.89 | 0.87 | | |
| N | 29 | 28 | 28 | 24 | 22 | 16 | 11 | 7 | 1 | 5 | 5 | 5 | 3 | 3 | 1 | 1 |
| | **Ss FC-M02 & FC-F01** (ID=12.5) | | | | | | | | | ID=7.82 | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 | i1 | i2 | i3 | i4 | i5 | i6 | i7 |
| AVG | 48.48 | 38.10 | 35.98 | 38.45 | 38.63 | 37.47 | 41.31 | 39.49 | | 32.34 | 36.96 | 38.37 | 38.03 | 40.16 | | |
| MAX | 73.70 | 59.91 | 44.51 | 47.48 | 47.28 | 40.02 | 48.82 | 39.52 | | 32.34 | 36.96 | 38.37 | 38.03 | 40.16 | | |
| MIN | 32.34 | 34.10 | 32.86 | 34.33 | 34.54 | 35.49 | 37.53 | 39.46 | | 32.34 | 36.96 | 38.37 | 38.03 | 40.16 | | |
| STD | 8.22 | 4.78 | 2.32 | 3.48 | 3.69 | 1.41 | 4.19 | 0.04 | | | | | | | | |
| N | 28 | 28 | 27 | 25 | 15 | 9 | 9 | 2 | | 1 | 1 | 1 | 1 | 1 | | |
| | **St SC-M03 & SC-F01** (ID=5.27) | | | | | | | | | ID=8.84 | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 | i1 | i2 | i3 | i4 | i5 | i6 | i7 |
| AVG | 30.26 | 24.99 | 25.70 | 25.92 | 26.64 | 27.37 | 29.11 | 29.51 | | 32.74 | 24.26 | | | | | |
| MAX | 38.28 | 31.95 | 32.54 | 29.73 | 29.59 | 30.98 | 34.04 | 32.63 | | 32.74 | 24.26 | | | | | |
| MIN | 21.04 | 22.65 | 23.31 | 24.20 | 25.33 | 25.67 | 26.53 | 27.39 | | 32.74 | 24.26 | | | | | |
| STD | 4.76 | 1.94 | 1.87 | 1.14 | 1.00 | 1.25 | 1.98 | 1.80 | | | | | | | | |
| N | 27 | 25 | 25 | 24 | 23 | 23 | 19 | 7 | | 1 | 1 | | | | | |
| | **St SC-M04 & SC-F01** (ID=9.50) | | | | | | | | | ID=3.50 | | | | | | |
| | i1 | i2 | i3 | i4 | i5 | i6 | i7 | i8 | i9 | i1 | i2 | i3 | i4 | i5 | i6 | i7 |
| AVG | 28.78 | 22.43 | 24.35 | 25.86 | 26.85 | 29.06 | 31.93 | 28.78 | 22.43 | 23.51 | 23.97 | 24.78 | 27.01 | 26.62 | | |
| MAX | 45.24 | 26.17 | 25.94 | 29.23 | 33.61 | 32.52 | 31.93 | 45.24 | 26.17 | 23.51 | 23.97 | 24.78 | 27.01 | 26.62 | | |
| MIN | 21.93 | 20.11 | 23.20 | 24.22 | 24.49 | 25.94 | 31.93 | 21.93 | 20.11 | 23.51 | 23.97 | 24.78 | 27.01 | 26.62 | | |
| STD | 8.44 | 2.22 | 0.92 | 1.76 | 3.05 | 3.16 | | 8.44 | 2.22 | | | | | | | |
| N | 9 | 9 | 9 | 9 | 7 | 4 | 1 | 9 | 9 | 1 | 1 | 1 | 1 | 1 | | |

*Soliperla thyra*—Salt Creek M03-F01. Repeated monophasic 2–3-way intersexual exchanges were long and variable due to the range in the numbers of call, answer and response signals (Fig. 9). Salt Creek Male-03 had fifteen RMC's composed of 68 monophasic signals with a range 4–6 per RMC (Tables 2 and 7). Female-01 answered 10 RMC's with 27 sequenced monophasic signals (Table 7). Male-03 completed only one RMC with a sequenced monophasic response signal (Table 7). The pair was recorded five and one days respectively after collection at 21.6ºC, between

09:51–11:07, on May 22, 2020 (Fig. 3D and Tables 2 & 9). The numbers of call beats per monophasic signal ranged 6–10, and mean C&D duration for 15 RMC's and 27 duets was 6879.79 ± 1553.66 ms. (Fig. 3D and Table 7).

The mean call signal duration was 182.47 ± 24.48 ms (Table 7) and the mean call interbeat interval pattern was approximately even with a range of 22.25–24.23 ms (Table 8). Mean male C-C exchange interval was 1570.42 ± 109.78 ms (Table 7). The numbers of answers per RMC ranged 2–4, beats per answer 2–9, and mean answer duration was 174.38 ± 50.94 ms (Table 7). Mean C-A exchanges were approximately consistent at 118.97 ± 28.24 ms. The number of response beats per signal was 3 (N=1), and the response duration was 57.00 ms (Table 7). The A-R exchange was 271.45 ms. The less-consistent mean A-C exchanges were 1524.51 ± 253.04 ms.

This pair's (SC M03-F01) mean monophasic call, answer, and response interbeat interval patterns were approximately even (Fig. 9 and Table 8). Mean call interval difference for intervals i1–i8 was less than 10 (ID = 1.98). Mean answer interval difference for intervals i1–i8 was less than 10 ms (ID = 5.27) and mean response interval difference for intervals i1–i2 was less than 10 (ID = 8.84).

*Soliperla thyra*—Salt Creek M04-F01. Repeated monophasic 2–3-way intersexual exchanges were short and variable due to the range in the numbers of call, answer, and response signals (Fig. 10). Salt Creek Male-04 had five RMC's composed of 10 monophasic signals with a range 1–3 per RMC (Tables 2 and 7). Female-01 answered four RMC's with nine sequenced monophasic signals (Table 7). Male-04 completed one RMC with a sequenced monophasic response signal (Table 7). The reared male and female were recorded one and three days after laboratory emergence respectively at 21.6ºC, between 01:19–01:25, on May 23, 2020 (Fig. 3E, and Tables 2 & 8). The number of call beats per monophasic signal ranged 6–10, and mean C&D duration for five repeated calls and 9 duets was 2370.40 ± 1500.29 ms. (Fig. 3E and Table 7).

The mean call signal duration was 154.76 ± 32.72 ms (Table 7) and the mean call interbeat interval pattern was approximately even with a range of 21.42–23.30 ms (Table 8). The one male C-C exchange interval was 1778.57 ms (Table 7). The numbers of answers per RMC ranged 2–3, beats per answer 5–8, and mean answer duration was 138.76 ± 22.41 ms (Table 7). Mean C-A exchanges were approximately consistent at 137.54 ± 25.38 ms. The number of response beats per signal was 6 (N=1), and the response duration was 125.89 ms (Table 7). Mean A-R exchanges were less consistent at 55.73 ± 74.58 ms. The less-consistent mean A-C exchanges were 1426.19 ± 102.04 ms.

This pair's (SC M04-F01) mean monophasic call, answer and response interbeat interval patterns were approximately even, (Fig. 10 and Table 8). Mean call interval difference for intervals i1–i9 was less than 10 (ID = 0.88). Mean answer interval difference for intervals i1–19 was less than 10 (ID = 9.50) and mean response interval difference for intervals i1–i5 was less than 10 ms (ID = 3.50).

## Discussion

The drumming descriptions for three California *Soliperla* species have been updated. These updated descriptions include previously missing call, answer and response interval patterns. The results are preliminary because only two individuals were reared with known ages.

Males usually called with repeated monophasic signal patterns, updated from previous monophasic signal pattern descriptions (Table 1). This repeated signal pattern was confirmed by male C-C exchange intervals that varied greatly (Tables 4–6), and provided evidence that repeated calls did not conform to the grouped call signal definition (Sandberg *et al.* 2015). The female answers and male response always had monophasic signal patterns and sequenced intersexual exchanges. Male-Female exchanges (2 and 3-way duets) were long and variable including multiple repeated calls, answers and sometimes an exchange-ending response.

The mean number of beats per call and mean interbeat interval patterns of *Soliperla quadrispinula* and *S. sierra* overlapped (Tables 3–5); however the interval patterns differed slightly (Figs. 4–5). Stonefly species with similar drumming behavior are thought to be separated by phenology or distribution. In California, only *S. quadrispinula* and *S. thyra* have been collected in suspected sympatry from the main stem and a smaller tributary of Willow Creek, Humboldt County (Stark *et al.* 2017). *Soliperla thyra* calls had more mean beats/signal and shorter mean interbeat interval patterns.

Repeated monophasic call patterns have been previously reported for three additional Nearctic genera including seven species (Maketon & Stewart 1984a, Stewart *et al.* 1988, Sandberg & Stewart 2006, Sandberg 2011a).

Because it is suspected that the repeated monophasic drumming signal pattern is more prevalent than reported, new monophasic descriptions should include the female answer and interval pattern.

## Acknowledgments

I thank Jon J. Lee, JL Consulting, Eureka CA, for help collecting *S. quadrispinula* in Humboldt County. Brady Richards, ABL-Chico CA, aided in collecting *S. sierra* in Tehama County. I appreciate the assistance of the editors and reviewers for making corrections to the manuscript.

## References

Abbott, J.C. & Stewart, K.W. (1997) Drumming of three *Mesocapnia* species (Capniidae) and Soliperla thyra (Peltoperlidae) from California, USA. *In*: Landolt, P. & Satori, M. (Eds.), *Ephemeroptera & Plecoptera, Biology-Ecology-Systematics*, *Proceedings of the Eighth International Conference on Ephemeroptera and the Twelfth International Symposium on Plecoptera, Lausanne, Switzerland*. Mauron + Tinguely & Lachat SA., Fribourg, Switzerland, pp. 88–92.

DeWalt, R.E., Maehr, M.D., Hopkins, H., Neu-Becker, U. & Stueber, G. (2022) *Plecoptera Species File Online*. Version 5.0/5.0. [http://plecoptera.speciesfile.org/]

Huo, Q.B., Du, Y.Z. & Yuan, D. (2017) First record of the genus *Soliperla* (Plecoptera: Peltoperlidae) from China with description of a new species. *Zootaxa*, 4362 (4), 589–600.
https://doi.org/10.11646/zootaxa.4362.4.8

Jewett, S.W. (1954) New stoneflies from California and Oregon. *Pan-Pacific Entomologist,* 30 (3), 167–180. [https://www.biodiversitylibrary.org/item/254684#page/201/mode/1up]

Maketon, M. & Stewart, K.W. (1984) Drumming behavior in four North American Perlodidae (Plecoptera) species. *Annals of the Entomological Society of America*, 77 (5), 621–626. [https://academic.oup.com/aesa/article-abstract/77/5/621/27765?redirectedFrom=fulltext]
https://doi.org/10.1093/aesa/77.5.621

Needham, J.G. & Smith, L.W. (1916) The stoneflies of the genus *Peltoperla*. *Canadian Entomologist,* 48 (3), 80–88. [https://www.biodiversitylibrary.org/page/28153660#page/96/mode/1up]

Ricker, W.E. (1952) Systematic studies in Plecoptera. *Indiana University Publications Science Series,* 18, 1–200. [http://www.nativefishlab.net/library/textpdf/16861.pdf]

Sandberg, J.B. (2011a) Vibrational communication of *Isoperla* Banks from California and Oregon (Plecoptera: Perlodidae). *Illiesia*, 7 (1), 1–23. [http://illiesia.speciesfile.org/html/2011.html]

Sandberg, J.B. & Stewart, K.W. (2006) Continued studies of vibrational communication (drumming) of North American Plecoptera. *Illiesia*, 2 (1), 1–14. [http://illiesia.speciesfile.org/html/2006.html]

Sandberg, J.B., Serpa, L.E. & Drake, E.F. (2015) The drumming signals of three winter stonefly species (Capniidae, Leuctridae: Plecoptera); with discussion resolving two common interval patterns. *Illiesia*, 11 (6), 51–74. [http://illiesia.speciesfile.org/html/2015.html]

Stark, B.P. (1983) A review of the genus *Soliperla* (Plecoptera: Peltoperlidae). *Great Basin Naturalist,* 43 (1), 30–44.

Stark, B.P., Sandberg, J.B. & Lee, J.J. (2017) California *Soliperla* Ricker, 1952 (Plecoptera: Peltoperlidae) distribution and taxonomic character. *Illiesia*, 13 (7), 82–93. [http://illiesia.speciesfile.org/html/2017.html]

Stewart, K.W. & Sandberg, J.B. (2006) Vibrational communication and mate searching behavior in stoneflies. *In*: Drosopoulos, S. & Claridge, M. (Eds.), *Insect Sounds and Communication: Physiology, Behavior, Ecology and Evolution*. CRC Press, Boca Raton, London, pp. 179–186. [https://www.taylorfrancis.com/chapters/mono/10.1201/9781420039337-17/vibratory-communication-mate-searching-behaviour-stone%EF%AC%82ies-sakis-drosopoulos-michael-claridge]
https://doi.org/10.1201/9781420039337-17

Stewart, K.W. & Zeigler, D.D. (1984) Drumming behavior of twelve North American stonefly (Plecoptera) species: first descriptions in Peltoperlidae, Taeniopterygidae and Chloroperlidae. *Aquatic Insects*, 6 (1), 49–61. [https://www.tandfonline.com/doi/abs/10.1080/01650428409361162]
https://doi.org/10.1080/01650428409361162

Stewart, K.W., Szczytko, S.W. & Maketon, M. (1988) Drumming as a behavioral line of evidence for delineating species in the genera *Isoperla*, *Pteronarcys* and *Taeniopteryx* (Plecoptera). *Annals of the Entomological Society of America*, 81 (4), 689–699. [https://academic.oup.com/aesa/article-abstract/81/4/689/17697?redirectedFrom=fulltext]
https://doi.org/10.1093/aesa/81.4.689