

TEMPERATURE RESPONSES AND HABITAT SHARING IN TWO SYMPATRIC SPECIES OF OKANAGANA (HOMOPTERA: CICADOIDEA)

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ABSTRACT.—*Okanagana striatipes* and *O. utahensis* are species synchronous in location of activity and utilization of host plants. They possess similar acoustic behavior. Analysis of calling songs shows that calls overlap in frequency but differ in temporal pattern. Based on characteristics of the cicada auditory system and the species recognition mechanism, the potential for acoustic interference exists. Both species are ectothermic behavioral thermoregulators. Measurements of thermal preference and body temperature during singing show that although thermal preferences are similar, *O. utahensis* sings at a significantly higher body temperature. Differences in body temperature required to coordinate singing in the 2 species provide a partial temporal separation of acoustic signaling. We suggest the physiological mechanisms that permit synchronous utilization of a habitat by the 2 species are the production of calling songs of different temporal patterns and the presence of different thermal requirements, which may permit and/or facilitate temporal separation of the acoustic environment during the day.

Key words: *Okanagana striatipes*, *Okanagana utahensis*, temperature, thermal adaptation, communication, song, cicadas.

Okanagana striatipes (Haldeman) and *Okanagana utahensis* Davis share sagebrush fields of the western United States. *Okanagana utahensis* is described as resembling *O. striatipes* but is slightly larger and darker in color (Davis 1919). The 2 species are active in adult form during June and July (Davis 1919). Both *O. striatipes* (Davis 1930) and *O. utahensis* (Davis 1919) have been associated with sagebrush (*Artemisia* spp.). Although the cicadas may sing from other plant species, a species of sagebrush is always present in the habitat and appears to be the host plant for both species. Cryptic coloration makes the cicadas very difficult to see when perched on sagebrush (Davis 1932).

Acoustic behavior of the 2 species is also similar. Both species, for example, are solitary animals when calling. Frequency ranges of the calling songs appear to overlap. *Okanagana striatipes* produces a calling song of medium pitch and average duration (Beamer and Beamer 1930, Davis 1930), whereas the song of *O. utahensis* is a long, shrill cry (Davis 1919) or a continuous song (Davis 1921).

Most male cicadas produce acoustic signals to attract females. Acoustic interference between

species inhabiting the same environment has been shown in insects (Perdeck 1958, Ulagaraj and Walker 1973, Morris and Fullard 1983, Latimer and Broughton 1984, Bailey and Morris 1986, Greenfield 1988, Römer et al. 1989, Schatral 1990), frogs (Schwartz and Wells 1983, Schwartz 1993), and birds (Cody and Brown 1969, Ficken et al. 1974, Popp et al. 1985). Cicada calls also have been shown to cause acoustic interference in frogs (Paez et al. 1993). It has been suggested that temporal separation (Wolda 1993, Gogala and Riede 1995, Riede 1995, Riede 1997) or frequency separation (Gogala and Riede 1995, Riede 1996) occurs in cicada communities to decrease acoustic interference.

The important song parameter in cicada long-distance communication has been shown to be call frequency (Doolan and Young 1989) or call intensity (Daws et al. 1997). Because the songs of *O. utahensis* and *O. striatipes* appear to overlap in frequency and the calls are of similar intensity (Sanborn and Phillips 1995), the potential for acoustic interference exists between these cicadas sharing the same habitat.

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Although the songs of *O. striatipes* and *O. utahensis* appear to differ in their temporal patterns, the potential for acoustic interference between the species still exists due to characteristics of the cicada auditory system and the species recognition process. The auditory system of cicadas usually shows a peak sensitivity at the frequency of the species calling song but is sensitive to a wide range of frequencies (Katsuki and Suga 1958, 1960, Hagiwara and Ogura 1960, Katsuki 1960, Enger et al. 1969, Popov 1969, 1981, Simmons et al. 1971, Young and Hill 1977, Schildberger et al. 1986, Huber et al. 1990; but see Popov et al. 1985, Popov and Sergeeva 1987, Fonseca 1993 for exceptions). In fact, Huber et al. (1990) showed that the auditory system in *Magiccicada cassinii* (Fisher) is more sensitive to the call of *M. septendecim* (L.) than the auditory system of *M. septendecim*. Physical properties of the sound-production system prevent *O. striatipes* and *O. utahensis* from altering the frequency of their calling songs to prevent acoustic interference. Since one species is probably capable of hearing the other quite well, temporal patterns of the song must act to separate the species.

Popov and Shuvalov (1974) described cicada auditory receptors as a specialized system in the analysis of amplitude-modulation patterns. However, these receptors respond to a wide range of temporal patterns; they are not an integral part of the conspecific signal recognizer (Huber 1983). Pringle (1954, 1956) suggested the frequency of a cicada song acts as an information carrier, while the species-specific information is carried in temporal patterns of the song (Hagiwara and Ogura 1960, Moore 1961, Frings and Frings 1977, Huber 1984, Joermann and Schneider 1987). Since auditory receptors respond to a wide variety of signals, auditory neural pathways must be responsible for filtering out species-specific calls.

The primary response to a conspecific song is based on the spectral content of the song (Huber et al. 1979). Nerve fibers respond to natural calling and courtship sounds with a specificity dependent on carrier frequency, rhythm, and transient content of the presented sound (Huber et al. 1980). Cicada auditory nerves respond synchronously to the temporal pattern of a conspecific song while the response to allospecific calls is not clearly

related to song activity (Pringle 1954, Katsuki and Suga 1960, Schildberger et al. 1986, Huber et al. 1980, 1990). Cicada auditory receptors are sensitive to intensity changes (Hagiwara and Ogura 1960, Katsuki 1960, Katsuki and Suga 1960) and are especially sensitive to transient stimuli found in calling songs (Huber et al. 1979, 1980). Amplitude modulations within the call elicit groups of spikes in the auditory nerve (Huber et al. 1980). Interneurons are responsible for filtering the auditory input to the brain, and apparently these interneurons react only to conspecific calls (Huber et al. 1980, Huber 1984).

Okanagana striatipes and *O. utahensis* are synchronous in time of activity during the year, location of activity, utilization of host plants, and possession of similar acoustic behavior. These similarities expose the 2 species to interspecific competition for physical and acoustic resources within their environment. We try to determine with this study whether there are differences in acoustic signals produced by the species and the possible role of thermal requirements for singing in the 2 species that may act as physiological mechanisms to permit synchronous sympatry.

MATERIALS AND METHODS

Animals

The species *Okanagana striatipes* and *O. utahensis* were studied in Cortez, Montezuma County, Colorado, USA. Animals were randomly sampled for data collection in the field and for specimen collection for laboratory experimentation. Experiments were performed in early July, approximately in the middle of the emergence period for each species, during 1982, 1983, 1984, 1986, 1988, and 1989. The species were active in an almost pure flat of Great Basin sagebrush (*Artemisia tridentata*). We placed the animals captured for laboratory experimentation in a cardboard carton on ice with a plant specimen and a wet paper towel to prevent dehydration. Live weights were measured with a Cent-O-Gram triple beam balance sensitive to ± 5 mg.

Song Analysis

We recorded calling songs of both species on 1/4 inch audio tape using a Uher 4000 Report Monitor portable tape deck and an Electro-Voice RE 55 dynamic microphone.

Songs were recorded at a tape speed of 19 cm · sec⁻¹. Recordings were analyzed with Mac-Speech Lab II (GW Instruments, Somerville, MA) and a Macintosh computer. Recordings were digitized at a sampling rate of 40 kHz, and a narrow band FFT was used to determine peak frequency. Figures 1–4 were generated with a Kay Elemetrics Corporation Digital Sona-graph 7800 using an intermediate bandwidth analysis filter and a Sona-graph Printer 7900.

Temperature Responses

In the laboratory we recorded insect body temperatures at the minimum temperature for controlled flight, maximum voluntary tolerance or shade-seeking temperature, and temperature of heat torpor. Minimum flight and heat torpor temperatures represent body temperature limits of full activity since cicadas with body temperatures beyond this range are torpid. Maximum voluntary tolerance temperature represents a thermoregulatory point (Heath 1970). Procedures we used to determine thermal responses were the same as those used in previous cicada studies (Heath 1967, Heath and Wilkin 1970).

Temperatures were measured with a Physitemp Model BAT-12 digital thermocouple thermometer and a type MT 29/1 29 gauge hypodermic microprobe copper/constantan thermocouple that had been calibrated to a National Institute of Standards and Technology mercury thermometer. Body temperatures were measured by inserting the probe midway into the dorsal mesothorax. When an animal was oriented for insertion of the probe, we handled it by grasping the wingtips between the thumb and forefinger. This procedure prevented conductive heat transfer between the insect and the experimenter. All body temperatures were recorded within 5 seconds of the insect performing the activity of interest.

To determine the minimum flight temperature, we repeatedly tossed a pre-cooled animal vertically 1–2 m. As the animal warmed, it began attempts at flight. Initially, it produced small wing movements with the wings folded against the body. As body temperature increased, the wings were extended and normal flight movements of the wings began. The animals sometimes glided as they warmed before they could fly efficiently. When an animal made

a controlled flight or landing, we recorded body temperature.

Maximum voluntary tolerance was determined by placing a pre-cooled animal on a vertical surface and warming the insect with a heat lamp. The heat lamp was placed 45–50 cm from the vertical surface, and the insect was placed in the center of the beam emanating from the lamp. Animals basked in the heat produced by the heat lamp until their body temperature reached the maximum voluntary tolerance temperature. When body temperature corresponding to maximum voluntary tolerance was reached, the animals walked or flew out of the central portion of the heat lamp. When an animal began to move, we measured body temperature.

Temperature of heat torpor was determined by placing an animal in a cardboard container and heating the insect with a heat lamp. The container prevented the specimen's escape during heating. Body temperature of the insect was measured when motor control ceased due to increase in body temperature. Heat torpor temperature is not a lethal temperature, and animals recover after their body temperature has decreased to the temperature range normally experienced.

Field Temperatures

We recorded body temperatures of singing animals in the field. Animals were captured in an insect net, which contracted around the animal to prevent movement. The temperature probe was inserted through the net into the dorsal mesothorax of the animal to measure body temperature. This procedure prevented conductive heat transfer between the experimenter and the animal that could have altered insect body temperature. All body temperature measurements were made within 5 seconds of capture. Species identification of each specimen was made after measuring body temperature.

Thermoregulation in ectothermic cicadas can be modeled as a coupled on-off regulator (Heath et al. 1971a). When body temperature is below a certain set point, the animal remains exposed to solar radiation. Whenever the body temperature exceeds this set point, the cicada retreats to shade. The degree of radiant heating is altered by changing activity location. The insect can obtain a similar result by changing body orientation with respect to the sun.

We collected behavioral data on body orientation at the same time that body temperatures were recorded in the field to determine if the cicadas behaviorally thermoregulate. Orientation of the animals with respect to the sun can be interpreted as an indication of "preferred" thermal state. Animals with their bodies positively oriented to the sun are positioned to maximize radiant heat gain and can be thought of as attempting to elevate body temperature. Negatively oriented animals have minimized heat gain from solar radiation and may be viewed as trying to maintain or decrease body temperature. An animal that is oriented with the side of the body toward the sun may be thought of as being near its "preferred" body temperature. Side-orientation permits the animal to increase or decrease body temperature slowly, depending upon the rate of radiant heat input and the rate of heat loss to the environment.

Information on calling activity was obtained by determining which species were singing at different times of the day. Species determination was made through animals captured for body temperature measurements and from calls being produced by uncaptured animals.

All statistics are reported as mean \pm 1 standard error.

RESULTS

The species involved in the present study are medium-sized cicadas. Live weight determined for *O. striatipes* (386.76 ± 10.510 mg, $n = 17$) is significantly smaller ($t = -7.905$, $df = 52$, $P < 0.0001$) than measured weight of *O. utahensis* (582.70 ± 16.025 mg, $n = 37$).

The calling song of *O. striatipes* is a continuous train of constant-amplitude sound pulses (Fig. 1C). The song begins as a train of syllables of varying duration and interburst intervals (Fig. 1A). Syllables begin to fuse together (Fig. 1B) until sound pulses become a continuous train, producing the calling song. Frequency spread of the song is approximately 7 kHz to 12 kHz. Peak sound energy in the power spectrum is 9.74 ± 0.345 kHz ($n = 7$, range 8.56–10.27 kHz). Expansion of the time wave (Fig. 2) shows sound pulses are produced at a rate of approximately 247 ± 42 pulses \cdot sec⁻¹ ($n = 7$, range 181.6–321.9).

The calling song of *O. utahensis* is composed of a train of syllables (Fig. 3). Each syllable

(Fig. 4) is composed of about 26 individual sound pulses (26.1 ± 0.34 , $n = 21$, range 23–29). The syllables are 87.0 ± 1.6 msec in duration ($n = 21$, range 75.6–107.2) and separated by 6.3 ± 0.62 msec ($n = 20$, range 3.6–12.57). The pulse repetition rate is 300.96 ± 17.81 sec⁻¹ within each syllable ($n = 21$, range 251.9–325.8). Sound energy of the call is distributed between 6 kHz and 11 kHz. There is an increase in intensity and a change in the emphasized frequency midway through the syllable. Peak energy is at 8.85 kHz (8.85 ± 0.07 kHz, $n = 21$, range 8.20–9.36) near the beginning of a syllable and 9.13 kHz (9.13 ± 0.07 kHz, $n = 21$, range 8.36–9.64) when the intensity increases midway through a syllable. Sound energy is concentrated in a more narrow frequency range or is more sharply tuned during the earlier portion of the call.

Table 1 summarizes temperature responses of *O. striatipes* and *O. utahensis*. Minimum flight temperatures are approximately equal ($t = -0.0888$, $df = 52$, $P = 0.4986$). Mean maximum voluntary tolerance and heat torpor temperatures are not significantly different ($t = -0.7983$, $df = 54$, $P = 0.2142$ and $t = -0.8137$, $df = 52$, $P = 0.2098$, respectively).

Figure 5 compares the number of each species singing in a given body temperature range. Mean body temperatures of singing animals for each species are significantly different ($t = -7.0385$, $df = 56$, $P < 0.00001$), with *O. utahensis* singing at higher body temperatures than *O. striatipes*. Body temperatures of singing animals range from 33.5°C to 37.8°C in *O. striatipes* and from 34.9°C to 40.2°C in *O. utahensis*.

The relationship between maximum voluntary tolerance temperatures and mean singing temperatures is different for each species (Table 2). *Okanagana striatipes* sings at a body temperature approximately equal to and not significantly different from ($t = -0.6773$, $df = 34$, $P = 0.2514$) the maximum voluntary tolerance temperature of the species. However, *O. utahensis* sings at a body temperature significantly greater than the maximum voluntary tolerance temperature determined for the species ($t = -5.3755$, $df = 72$, $P < 0.0001$).

Both *O. striatipes* and *O. utahensis* are ectothermic behavioral thermoregulators. Solar radiation is used to elevate body temperature for activity. Shuttling movements between sunny and shaded perches and changes in

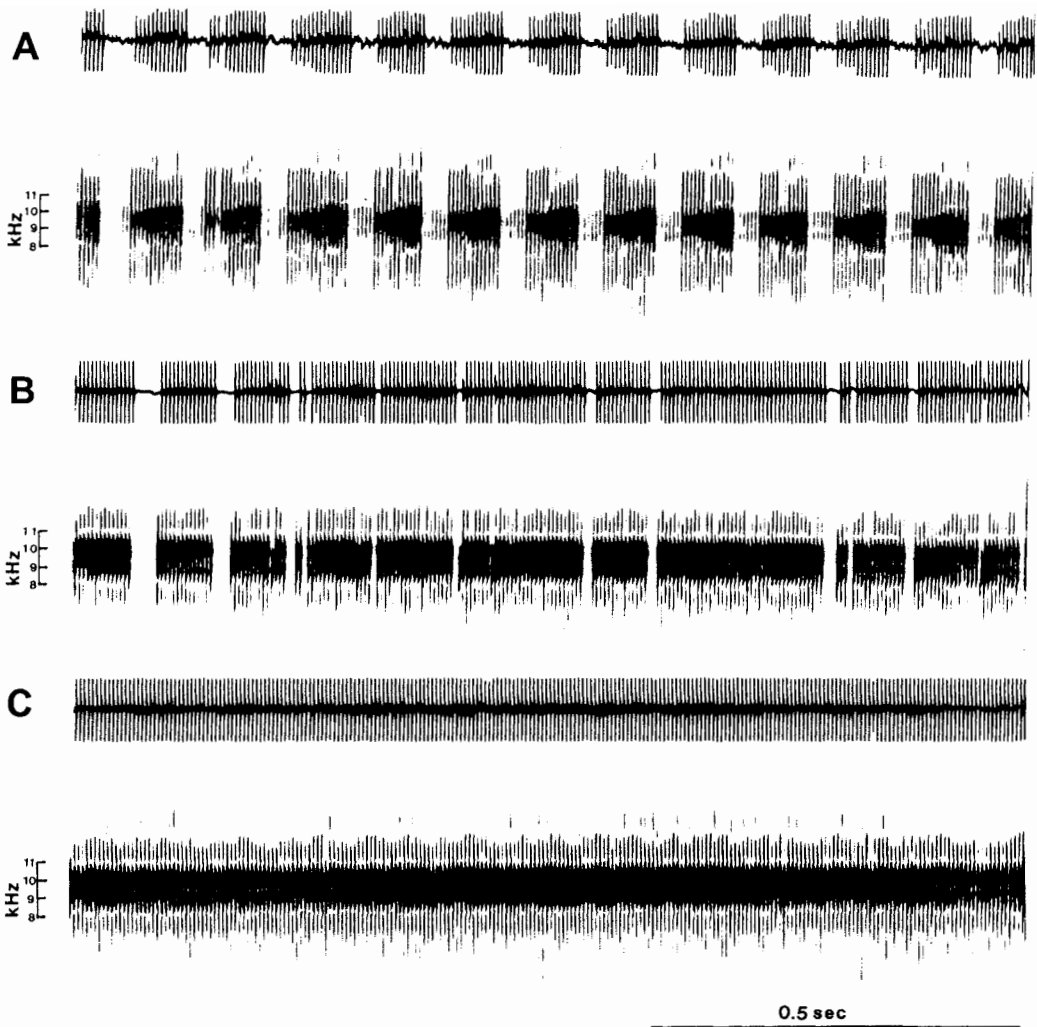


Fig. 1. *Okanagana striatipes* calling song. Upper trace in each pair is the time wave and lower trace is the sona-gram. Frequency spread of the song is approximately 7 kHz to 12 kHz. The song begins as a train of syllables varying in duration and interburst interval (A). Syllables become longer and begin to fuse together (B) until the sound pulses produce the continuous calling song (C).

body orientation are then used by both species to regulate body temperature during activity. *O. striatipes* at lower body temperatures (33–34°C) illustrated in Figure 5 were positively oriented to the sun. Animals with highest body temperatures (36–37°C) were negatively oriented or side-oriented. Animals in the central body temperature range (34–36°C) were positively oriented, side-oriented, or negatively oriented. Most (7 of 9) *O. striatipes* with body temperatures below the recorded mean singing

temperature (35.87°C) for the species were positively oriented. Animals with body temperatures greater than the mean were found in all possible states of orientation. These data suggest the animals were actively regulating body temperature around the mean temperature recorded.

Okanagana utahensis showed a similar pattern of orientation with respect to the sun. Animals with lower body temperatures (34–37°C) were positively oriented while animals

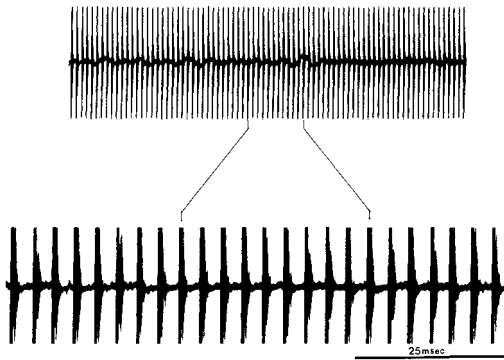


Fig. 2. Expanded time wave of the *Okanagana striatipes* calling song. Sound pulses are produced at a rate of about 182 sec⁻¹ during the full song.

at the upper end of the distribution (39–41°C) showed negative or side-orientation. The difference between the species is that *O. utahensis* remains positively oriented at a temperature range (36–37°C) when *O. striatipes* has positioned itself to decrease radiant heat gain. Although both species are behavioral thermo-regulators, *O. utahensis* regulates body temperature at a higher temperature than *O. striatipes*.

Acoustic activity of the 2 species differs throughout the day, producing a partial temporal separation of acoustic activity that is dependent on species-specific thermal preferences. Both species show an initial burst of activity in the morning when ambient conditions are sufficient to elevate body temperature to the species-specific level required for singing. *Okanagana striatipes* begins to sing before *O. utahensis*. The lower body temperature required for singing gives *O. striatipes* a period of about 20–30 minutes in the morning when it is the only cicada species calling. When ambient conditions are sufficient to elevate body temperature in *O. utahensis*, this species begins to sing as well. Singing in *O. striatipes* begins to decline as *O. utahensis* proceeds through its initial peak of acoustic signaling, which lasts 2.5 to 3 hours. As ambient temperature (T_a) continues to rise during the afternoon, *O. utahensis* continues sporadic signaling while activity in *O. striatipes* decreases. *Okanagana striatipes* then resumes activity to a greater degree as T_a falls in the late afternoon while activity in *O. utahensis* is suppressed by falling body temperature.

Although these generalizations of the calling activity in the 2 species hold true, activity patterns can be altered by ambient conditions. Singing activity in both species is inhibited by extremely high ambient temperatures. Similarly, on a mostly cloudy day, *O. striatipes* sang to a greater degree than normal, and *O. utahensis* sang to a lesser degree than normal in the early afternoon. Clouds not only prevented T_a from rising to a level that would passively raise body temperature high enough for singing, but also prevented *O. utahensis* from using radiant heat to elevate body temperature. On the other hand, *O. striatipes* was able to elevate body temperature a sufficient amount and continued calling while activity was suppressed in *O. utahensis* due to the ambient conditions.

DISCUSSION

Thermal requirements of *O. striatipes* and *O. utahensis* represent a possible mechanism to decrease the potential for acoustic interference. Laboratory temperature responses of the 2 species are approximately equal (Table 1). This would be expected in 2 animals sharing a habitat because they are exposed to the same environmental conditions. However, the mean body temperature of singing *O. utahensis* is significantly greater than the mean body temperature of singing *O. striatipes* (Table 2). It appears *O. utahensis* “prefers” or requires a higher body temperature to coordinate singing activity.

Crawford and Dadone (1979) suggested that temperature sets limits on the ability of cicadas to coordinate motor control of singing. The rate of action for potential firing in the timbal nerve is temperature dependent (Wakabayashi and Hagiwara 1953, Wakabayashi and Ikeda 1961). Raising thoracic temperature during activity in *Cystosoma saundersii* causes the song cycle period to change (Josephson and Young 1979), and the change in body temperature in *Tibicen winnemanna* (Davis) during endothermic warming is responsible for changes in acoustic activity of that species (Sanborn 1997). These data suggest the ability of the cicada nervous system to coordinate calling songs is temperature dependent.

Cicadas perform complex activities, such as singing, over a small temperature range. The temperature range may represent the maximum range over which the cicada can adjust

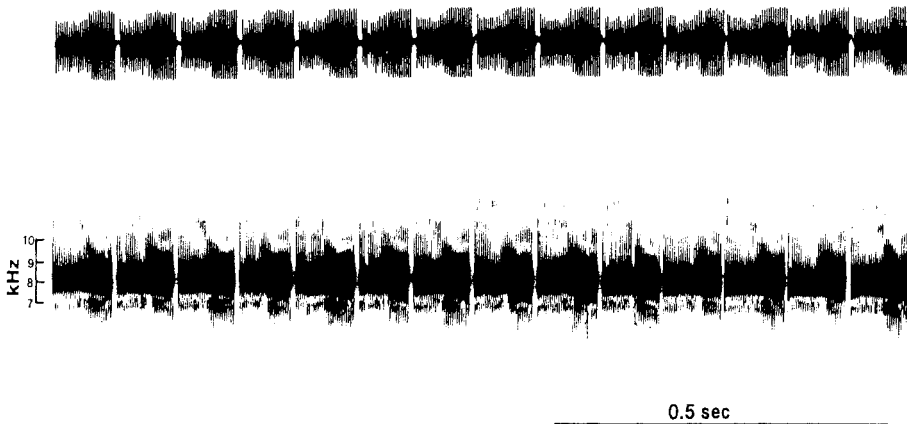


Fig. 3. *Okanagana utahensis* calling song. The song is composed of a train of syllables with sound energy between 6 kHz and 11 kHz.

its rate of activity to compensate for the direct effect of temperature on metabolic processes (Heath et al. 1971b). The body temperature range of singing ectothermic cicadas has been reported as 25.0–31.8°C in *Magicicada cassinii* (Heath 1967), 32.2–41.5°C in *Tibicen chloromerus* (Walker) (Sanborn 2000), 35.0–40.8°C in *Diceroprocta olympusa* (Walker) (Sanborn and Maté 2000), 33.5–43.0°C in *Cacama valvata* (Uhler) (Heath et al. 1972), 38.0–41.9°C in *Okanagodes gracilis* Davis (Sanborn et al. 1992), and 39.0–41.8°C in *Okanagana hesperia* (Uhler) (Heath 1972). Body temperatures of singing *O. striatipes* were measured between 33.5°C and 37.8°C. Body temperatures of calling *O. utahensis* ranged from 34.9°C to 40.9°C, both within the range of body temperatures reported for other cicadas to coordinate singing activity. The range is also similar to the body temperature range of singing in endothermic cicada species (Sanborn et al. 1995a, 1995b, Sanborn 2000).

Comparison of the data in the singing temperature histogram (Fig. 5) suggests the species select different body temperature ranges when singing. Orientation of the species with respect to the sun also suggests different thermal preferences. *Okanagana striatipes* begins thermoregulatory behaviors to decrease body temperature while at the same body temperatures *O. utahensis* continues to maximize radiant heat gain. Comparison of maximum voluntary tolerance temperatures and mean singing tem-

peratures of each species illustrates a difference in thermal activity of the species. *Okanagana striatipes* sings at a body temperature approximately equal to the maximum voluntary tolerance temperature of the species, while *O. utahensis* sings at a body temperature significantly greater than the maximum voluntary tolerance temperature determined for the species. Although maximum voluntary tolerance temperatures are approximately equal between species, *O. utahensis* selects a higher body temperature range for activity. Singing at body temperatures greater than the maximum voluntary tolerance temperature has also been described in the cicada *Diceroprocta apache* (Davis) (Heath and Wilkin 1970).

Singing at temperatures above an upper thermoregulatory point suggests *O. utahensis* requires an elevated body temperature for the singing mechanism to function properly. *Okanagana utahensis* may require a higher body temperature due to the song parameters of the species. Amplitude modulations within syllables, production of syllables themselves, and/or greater pulse repetition rate of the *O. utahensis* song may require a higher body temperature for coordination than that required by *O. striatipes* to coordinate a continuous, unmodulated song. *Okanagana utahensis* produces sound pulses at a rate of approximately 300 sec⁻¹ compared to 250 sec⁻¹ in *O. striatipes*. Since timbal muscle contraction kinetics are temperature dependent (Josephson and Young

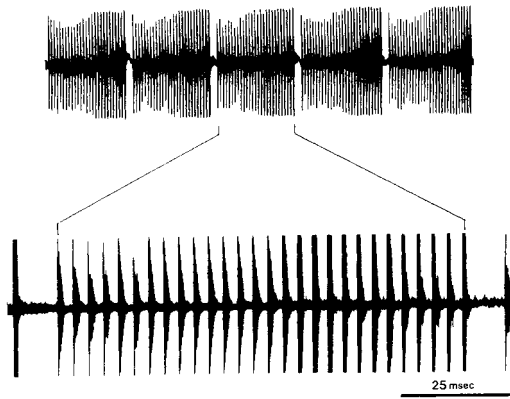


Fig. 4. Expanded time wave of the *Okanagana utahensis* calling song. Syllables are composed of approximately 26 individual sound pulses produced at the rate of 300 sec^{-1} . Syllables are about 87 msec in duration and separated by 6.3 msec. Intensity increases and dominant frequency changes midway through the syllable produced by lateral abdominal movements.

1979, 1985, Josephson 1981, Young and Josephson 1983, Sanborn 2001), the greater pulse repetition rate may require a higher timbal muscle temperature for the timbal to contract at the frequency necessary to produce the calling song.

Temperature requirements affect daily activity cycles of the 2 species. It is through this temporal separation of species activity that differences in singing body temperature become important. The lower body temperature of singing *O. striatipes* permits the species to sing in the morning and late afternoon when *O. utahensis* is potentially unable to raise body temperature to the range necessary for acoustic activity. Similarly, the higher body temperature required by singing *O. utahensis* permits acoustic activity during the heat of the day when *O. striatipes* is forced to retreat to shaded sites. Thus, thermal requirements act to separate reproductive activity temporally and to reduce or eliminate acoustic interference between the species. Thermal separation of activity has been described in ants (Cros et al. 1997), beetles (Colombini et al. 1994, Fallaci et al. 1997), and flies (Gaugler and Schutz 1989, Schutz and Gaugler 1992) that share a habitat.

Cicadas have developed several behavioral and physiological methods to minimize acoustic

interference, competition for environmental resources, and interspecific interactions. Cicadas using similar songs for communication or similar host plants can avoid interspecific competition through geographic separation (Pringle 1954, Fleming 1971), microhabitat segregation (Schedl 1986, Riede 1997), temporal separation of calling times (Hayashi 1975a, Wolda 1993, Gogala and Riede 1995, Riede 1995, 1997) or time of year the species are active (Young 1981a, 1981b), or maximizing communicatory differences (Fleming 1971, Walker 1974).

Okanagana striatipes and *O. utahensis*, however, are similar morphological species using the same host plant; they are active in the same place at the same time of year; males of both species are solitary animals when calling; they produce mating calls that overlap in frequency; and both are diurnally active. They are species that contradict the general patterns used by cicadas to avoid interspecific competition, and yet they are able to share an environment while using the same resources, both physical and acoustic.

The songs of cicadas act as an isolating mechanism between species (Alexander 1957, Alexander and Moore 1958, Moore and Alexander 1958, DuMortier 1963, Haskell 1974, Bennet-Clark 1975, Fleming 1975, 1984). When related sympatric species share an environment, selection should minimize signal differences within a species and maximize differences between species (Alexander 1967, Walker 1974, Young 1981a). In general, sympatric species differ markedly in calling song structure and/or frequency (Pringle 1954, Alexander 1956, 1957, 1967, Moore and Alexander 1958, Alexander and Moore 1962, DuMortier 1963, Fleming 1971, 1984, Walker 1974, Young 1981a). However, *O. striatipes* and *O. utahensis* possess similar songs and acoustic behavior.

The overlap of calling song frequency in *O. striatipes* and *O. utahensis* is probably due to the similar size of the animals. The frequency of a cicada's song is determined by the natural period of timbal vibration, which is then modified by several body parts (Pringle 1954, Moore and Sawyer 1966, Popov 1975, Popov et al. 1985, Huber et al. 1990, Bennet-Clark and Young 1992, Fonseca 1996, Bennet-Clark 1997, 1999) and scaled to body size (Daniel et al. 1993, Bennet-Clark and Young 1994). Because the 2 cicadas are physically similar in size,

TABLE 1. Temperature responses ($^{\circ}\text{C}$) of *Okanagana striatipes* and *Okanagana utahensis* from Cortez, Colorado.

Behavior	<i>O. striatipes</i> (mean \pm $s_{\bar{x}}$)	<i>O. utahensis</i> (mean \pm $s_{\bar{x}}$)
Minimum flight temperature	20.66 (\pm 0.348) $n = 17$	20.71 (\pm 0.313) $n = 37$
Maximum voluntary tolerance temperature	35.46 (\pm 0.571) $n = 17$	36.03 (\pm 0.404) $n = 37$
Heat torpor temperature	45.52 (\pm 0.605) $n = 17$	46.08 (\pm 0.375) $n = 37$

All interactions $P > 0.2$.

timbal size is probably similar in the species and call frequencies also should be similar. The slightly larger size, together with a slightly larger timbal, of *O. utahensis* is probably responsible for the lower emphasized frequency of the call.

Calling song temporal patterns have been suggested as a means of separating many sympatric species of cicadas. Four species of *Maoricicada* are thought to remain isolated by the pulse-repetition frequency of their calling songs (Fleming 1971). Jiang (1985) suggested that the number of sound pulses, pulse length, and repetition frequency of amplitude-modulated pulse trains separate *Acutivalva choui* Yao, *Aola bindusara* (Distant), and *Lingualva sinensis* Chou and Yao. All 3 species inhabit the same location, sing only from 0630 to 0645 hours, and produce calls of similar frequency. The sympatric sibling species *Platypleura maytenophila* Villet and *P. hirtipennis* (Germar) (Villet 1987) overlap in calling song frequency but differ in temporal pattern (Villet 1988). Nakao and Kanmiya (1988) showed that there are significant differences in the songs produced by the cicada *Meimuna kuroiwae* Matsumura over its entire range. *Meimuna kuroiwae* is a synonymized species of what were originally 7 independent species (Hayashi 1975b) and should probably be classified as separate species based on their calling songs.

Temporal patterns of the songs of the 2 species we studied are markedly different. *Okanagana striatipes* produces a continuous train of constant-amplitude sound pulses (Fig. 1). The song of *O. utahensis* is a train of syllables that exhibit an amplitude-modulation pattern within each syllable (Fig. 3). Temporal patterns of the songs probably facilitate segregation of the 2 species during interspecific interactions.

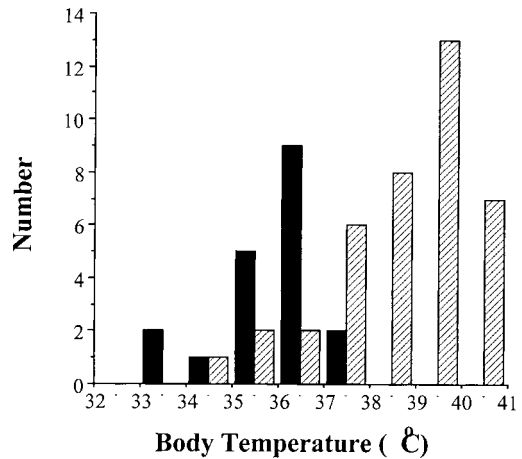


Fig. 5. Distribution of body temperatures of singing *Okanagana striatipes* (solid bars) and *O. utahensis* (striped bars). Mean body temperature of singing *O. striatipes* is $35.87 \pm 0.257^{\circ}\text{C}$ (mean \pm $s_{\bar{x}}$, $n = 19$). Mean body temperature of singing *O. utahensis* is $38.62 \pm 0.242^{\circ}\text{C}$ ($n = 39$). Mean singing temperatures are significantly different ($t = -7.0385$, $df = 56$, $P << 0.0001$).

Abdominal movements also may produce the amplitude modulation seen in *O. utahensis* syllables. The cicada abdomen acts as a resonating structure, increasing the volume of the sound produced (Pringle 1954, Moore and Sawyer 1966, Young 1972, Simmons and Young 1978, Bennet-Clark 1999). When the abdomen is tuned to the natural period of timbal vibration, the intensity of the song increases (Pringle 1954). The observed increase in intensity may also be facilitated by changes in abdominal position. By altering the gap between the opercula and the tympana, the tension placed on the timbals, tympana, and folded membrane is changed, causing an increase in sound

TABLE 2. Comparison of maximum voluntary tolerance temperatures ($^{\circ}\text{C}$) and field singing temperatures ($^{\circ}\text{C}$) of *Okanagana striatipes* and *Okanagana utahensis*.

Species	Maximum voluntary tolerance temperature (mean \pm $s_{\bar{x}}$)	Singing temperature (mean \pm $s_{\bar{x}}$)
<i>Okanagana striatipes</i>	35.46 (\pm 0.571) $n = 17$	35.87 (\pm 0.257) ^b $n = 19$
<i>Okanagana utahensis</i>	36.03 (\pm 0.404) ^a $n = 37$	38.62 (\pm 0.242) ^{ab} $n = 39$

^{a,b} $p < 0.001$.

intensity (Pringle 1954, Weber et al. 1987, Villet 1988, Young 1990). Another possibility for the increased intensity could be increased activity in the timbal tensor muscle during the syllable (Hennig et al. 1994). Altering the size of the opercula-tympanal distance may also produce change in the emphasized frequency within *O. utahensis* syllables as described in many species of cicadas (Allard 1946, Young 1972, Joermann and Schneider 1987, Sanborn 1997).

Although cicada auditory receptors react to allospecific calls, the response of the auditory neurons to different portions of the calls could help to separate *O. striatipes* and *O. utahensis*. Amplitude modulation, intensity changes, and syllables of the *O. utahensis* calling song represent stimuli to which the cicada auditory system has already been shown to be sensitive (Hagiwara and Ogura 1960, Katsuki 1960, Katsuki and Suga 1960, Huber et al. 1979, 1980). Production of syllables by *O. striatipes* prior to production of the calling song may negate any benefit *O. utahensis* has in possessing a song constructed of syllables.

Temporal patterns of the full calling songs may be sufficient in isolating *O. striatipes* and *O. utahensis*, but the overlap in frequency could cause acoustic interference between the 2 species. Walker (1986) collected 2 species of cicadas attracted to synthetic cricket calls. Doolan and Young (1989) showed that the call frequency of *Cystosoma saundersii* Westwood is important in eliciting steering behavior in tethered females. The correct temporal pattern of the species song is necessary for the females to exhibit courtship behavior. If *O. striatipes* and *O. utahensis* possess a similar 2-step recognition process, simultaneous calling could cause females to waste time and energy in interspecific interactions. In addition, females flying to males of the wrong species could be exposing themselves to predation. Flying *C. saundersii*

females fall victim to bird predation when flying to a calling male (Doolan and MacNally 1981). Different thermal requirements of each species decrease the chance of acoustic interference between these closely related species of *Okanagana*.

We therefore suggest that *O. striatipes* and *O. utahensis* are able to share the same environment by (1) producing calling songs of different temporal patterns and (2) utilizing different thermal requirements that permit and/or facilitate temporal separation of the day.

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