

Long-range Acoustical Signals, Phonotaxis, and Risk in the Sexual Pair-Forming Behaviors of *Okanagana canadensis* and *O. rimosa* (Hemiptera: Cicadidae)

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ABSTRACT The sexual behaviors of *Okanagana canadensis* (Provancher) and *O. rimosa* (Say) are described. In northern Michigan, *O. canadensis* is typically found in coniferous vegetation, such as cedars; whereas *O. rimosa* frequent deciduous vegetation. In both species, males call from stationary perches, and females approach them. Females have no specialized receptivity signals, but both males and females engage in bouts of wing flicking that may be alternative, low-risk signaling. Mating is brief and involves no elaborate courtship. The *Okanagana* mating system, characterized by male advertisement and female searching, is contrasted with that of *Magicicada* spp., the periodical cicadas of North America, and discussed in the context of relative risks of signaling and searching behaviors.

KEY WORDS Cicadidae, communication, *Okanagana*, signal evolution, sexual pair formation

SEXUAL PAIR-FORMATION IN singing insects (Orthoptera and Hemiptera that employ airborne long-range acoustical signals) can be classified on the basis of male and female movements during pairing. At one extreme, found in phaneropterine katydids (Spooner 1968, Heller 1990, Heller and von Helversen 1993), acridid grasshoppers (von Helversen and von Helversen 1983, Ewing 1989), and some cicadas (Lane 1995, Gwynne 1987, Cooley and Marshall 2001) males signal using discontinuous call phrases while searching for responding females (male signal/search strategy; Alexander 1968). At the other extreme, found in crickets (Alexander 1968), some katydids (Greenfield 1990, Ewing 1989), and some cicadas (Myers 1929, Alexander 1968), males make continuous, long-range acoustical advertisements from stationary perches, and females approach them (male advertisement/female phonotaxis; Ewing 1989, Bailey 1991, Alexander et al. 1997).

The adoption by either sex of a leading role in signaling or searching is influenced by the risk involved in each. Advertisement signals reveal the location of the signaler to predators, while searching involves travel-related risk exposure (Burk 1982). A classic example of a generalist predator locating an acoustically signaling male is Walker's (1964) description of a cat stalking a cricket. Even pheromonal signals, which are unlikely to be exploited by generalist predators (Alexander et al. 1997, Zuk and Kolluru 1998, Haynes and Yeorgan 1999), are risky in the presence of specialist predators (Dunkelblum et al. 2000).

However, travel to a signaling mate may also be risky; while searching for females, male tick-tock cicadas are more likely to be captured by spiders (Gwynne 1987). Aggressively mimicking predators broadcast false navigational information and thereby increase the risk of travel relative to the risk of signaling; examples include female *Photuris* fireflies that mimic the female sexual signals of other firefly species, luring males into predation (Lloyd 1975), and bolas spiders (*Mastophora* spp.) that emit a mimic pheromone to attract male noctuids (*Spodoptera* spp., Eberhard 1977). For any given species, risks influence which sex signals and which sex searches. In general, the sexes divide the roles of signaling and searching, and females adopt the least risky of them (an ultimate outcome of asymmetrical parental investment patterns; Parker et al. 1972, Trivers 1972, Alexander and Borgia 1979, Parker 1983, Hammerstein and Parker 1987, Alexander et al. 1997).

Apparent exceptions to this generalization involve cases where males both signal and search, such as in some orthopterans and cicadas (Alexander 1968, Spooner 1968, von Helversen and von Helversen 1983, Gwynne 1987, Heller 1990, Heller and von Helversen 1993, Lane 1995, Cooley and Marshall 2001). In these cases, not only do males signal and search, but females signal responsively to male calls, a pattern that could result from males and females splitting the tasks of long- and short- range signaling or from reduced or absent risks associated with signaling or searching.

Other exceptions to the division of risk involve signal channels that are not readily available to generalist predators. Green lacewings (Wells and Henry 1992, Henry 1994), leafhoppers and planthoppers (Claridge 1985, Hunt and Nault 1991, Hunt et al. 1992), cave-dwelling cixiids (Hoch and Howarth 1993), and

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primitive cicadas of the genus *Tettigarcta* (Claridge et al. 1999) all employ vibrational signals. Vibrational signals may involve only comparatively minor risk exposure because of their low intensity, limited broadcast range, and difficulty of detection. In many of these species, the sexes do not divide the roles of signaling and searching.

This study presents details of sexual behaviors, especially those of females, in North American *Okanagana canadensis* Provancher, and *O. rimosa* (Say). The sexual behaviors of *Okanagana* appear superficially similar to those of other male advertise/female approach cicada species, such as some *Tibicen* (Alexander 1960, Alexander and Moore 1962, J.R.C., unpublished data), and *Diceroprocta* (Alexander and Moore 1962). Cicadas are some of the most recognizable spring and summer insects in North America, and their habits vary from solitary singing individuals, such as the "Dog Day" cicadas (North American *Tibicen*) to gregariousness, as in the periodical cicadas (*Magicalcica*). Information about the habits of particular species provide the foundation for understanding the influence of risks on sex-specific roles of searching or signaling and how risk has contributed to shaping the evolution of cicada mating systems.

Materials and Methods

General Methods. Cicadas were observed either free-flying in the field, in a large (3 by 3 by 2.5-m) screen tent placed over living vegetation (a "flight cage"), or in small cages made by folding a piece of white nylon tulle or gray fiberglass window screen ≈ 1 by 2 m over living vegetation (A "bag cage"). When not being observed or videotaped, cicadas were segregated by sex and stored in bag cages. Copulation durations of three *O. canadensis* and four *O. rimosa* mating pairs were measured over the course of this study by observing cicadas continuously during courtship and mating, recording (1) the time at which the male first engaged his genitalia and (2) the time at which he separated completely. All observations and tape recordings were made when air temperatures were between 20 and 25°C.

Okanagana canadensis. I watched a total of 30 focal male *O. canadensis* for over 15 total hours near the interchange of U.S. Highway 2 and Interstate 75, Mackinac County, MI, on 16, 24, 25 July and 1 August 1996, 27 July 1997, and on 20 June 1998. The primary location for observations of *O. canadensis* was an overgrown field bounded by U.S. 2 (eastbound), an entrance ramp to Interstate 75 (southbound), and Bridge View Road. Vegetation in this field consisted primarily of cherry (*Prunus* spp.) and small northern white cedars (*Thuja occidentalis* L.). For some observations, I placed cicadas in bag cages enclosing small cedar seedlings. In 1996–2000, I also drove slowly along M-48 and M-134 in the eastern part of the Upper Peninsula, noting the perch locations of 643 individual calling male *O. canadensis* over the course of the study.

Four male and six female *Okanagana canadensis* were captured in the vicinity of I-75 and U.S. 2 on

25–28 July 1997. On 29 July, they were transported to a "flight cage" placed over an elm sapling (<10 cm diameter at breast height [dbh]) on a farm in Freedom Township, Washtenaw County, MI. During this process, the cicadas were deprived of fresh vegetation for a maximum of 6 h. On 30 July, the cicadas were placed in the cage, and any obscuring vegetation was trimmed. The cicadas were observed continuously for a total of 5 h over 20–31 July from a truck parked within 4 m of the base of the sapling on its sunny side. Use of the vehicle as an observation blind reduced the likelihood that the presence of an observer would startle the cicadas. All sexual interactions were videotaped, which required the observer to be out of the truck, but the position of the truck prevented the observer from being silhouetted against the horizon, and the cicadas appeared undisturbed.

Okanagana rimosa. *O. rimosa* was observed only in 1998, when it emerged in locally high densities (≈ 50 emergence holes per square meter). The primary collecting site for this species was an open, sandy field dominated by bigtooth aspen (*Populus grandidentata* Michaux) and blackberries (*Rubus alleghaniensis* Porter) near the University of Michigan Biological Station Streams Laboratory. Most observations were conducted in a "flight cage" erected over a small quaking aspen (*Populus tremuloides*). *O. rimosa* seemed undisturbed by the presence of a human observer, so no observation blind was necessary.

Results

Okanagana canadensis. Males typically call one per tree. For example, in one sample of 25 males, 21 were alone in their tree, and the four remaining males occurred in two pairs. In northern Michigan, male *O. canadensis* tend to perch within three m of the ground (20/20 males in one sample were within 3 m of the ground), sometimes at ground level, on the main trunks of small trees, usually northern white cedar (*Thuja occidentalis* L.) or occasionally Scots pine (*Pinus sylvestris* L.). Males call with wings slightly open, and abdomen extended, sometimes facing down, or, if on a side branch, toward the main trunk. Male calls are broad-frequency, slightly metallic lisps of variable duration (Fig. 1). In 1997, 22 male *O. canadensis* calling bouts averaged 149 ± 187 s, and 13 periods of silence between calling averaged 142 ± 390 s. However, bout lengths are highly variable, and some of the shorter bouts may be courtship behaviors. Males do not alternate calls and flights ("sing-fly" behavior; Alexander and Moore 1962, see also Gwynne 1987, Cooley and Marshall 2001) but rather remain on the same calling perch for long periods. For five males observed in the field, an estimate of the minimum time spent at a calling perch is 17 ± 16 min, but males' lack of movement, and the difficulty in determining arrival times at calling perches suggest this was an underestimate.

With few exceptions, calling male *O. canadensis* were easily startled and difficult to capture. Males emitted an alarm sound when handled, confined, or

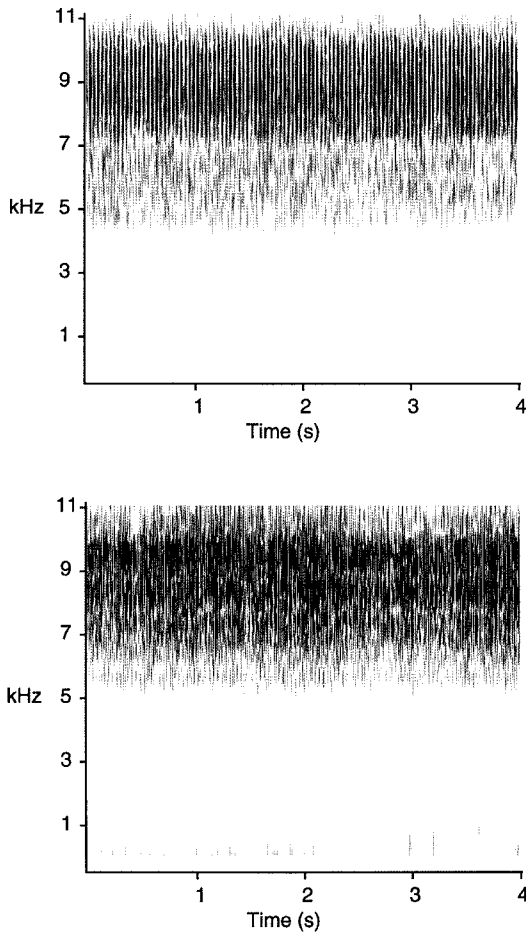


Fig. 1. Sonograms of male *Okanagana canadensis* (top) and *O. rimosa* (bottom) call fragments. Equipment was limited to a maximum of 11 KHz.

harassed. Typically, both sexes flew silently from their calling perches at the slightest provocation; rarely, calling males remained immobile and silent on their perches when startled. Immobile males were difficult to find because of their mottled coloring, and they remained immobile even if their calling tree was thrashed and shaken. These behaviors suggest that male *O. canadensis* can adopt two alternative predator avoidance strategies, escape flight or inconspicuous camouflage.

***Okanagana rimosa*.** Male *O. rimosa* behavior is generally similar to that of *O. canadensis*, except males appear less selective about calling perches, perching on woody, deciduous vegetation (often higher than three m), grass stems, or on the ground (Table 1; see also Kirby and McPhee 1963). A sonogram of a portion of a male *O. rimosa* calling bout is included in Fig. 1. In 1998, *O. rimosa* were more abundant than in previous years. Although individual male *O. rimosa* could be found calling on trees, shrubs, or even on the ground as in previous years, there were also single trees that had dense choruses. The sound intensity at

Table 1. Deciduous vegetation used by *O. rimosa* in northern Michigan

Common name	Species
Red maple	<i>Acer rubrum</i> L.
Serviceberry	<i>Amelanchier</i> spp.
White birch	<i>Betula papyrifera</i> Marsh.
Beech	<i>Fagus grandifolia</i> Ehrh.
Hop bornbeam	<i>Ostrya virginiana</i> Marsh.
Bigtooth aspen	<i>Populus grandidentata</i> Michaux
Pin Cherry	<i>Prunus pensylvanica</i> L. f.
Oak	<i>Quercus</i> spp.
Raspberry	<i>Rubus</i> spp.
Red pine	<i>Pinus resinosa</i> Aiton

the base of one *O. rimosa* chorus tree was 66 db (as measured on a Radio Shack 33-2050 sound level meter set to "A" weighting), compared to >80 db for a typical *Magicicada* chorus (J.R.C., unpublished data). Males' lack of movement unless perturbed made estimation of residence time at calling perches difficult. During 102 min. videotaped sexual interactions during the dense 1998 emergence, in which two males were generally visible at any given time, only nine spontaneous, undisturbed flights were observed, suggesting that even at high densities, calling males tend to remain on their perches and do not engage in "call-fly" behavior.

Like *O. canadensis* males, male *O. rimosa* emit an alarm sound when harassed. However, although female *O. rimosa* were easily startled, calling male *O. rimosa* were readily approachable and were more efficiently captured by hand than with a net. Unfortunately, all observations of predator avoidance behavior in *O. rimosa* were made in 1998, during a locally dense emergence. Thus, the apparent differences in predator avoidance behaviors between *O. rimosa* and *O. canadensis* could reflect different strategies at high and low densities rather than species-typical differences.

Sexual Behaviors, Both Species. Males alternated long bouts of calling with bouts of wing flicking (see Alexander 1957, Davis 1919), producing from 3-5 flicks per wing flick bout. Male *Okanagana* did not respond to artificial wing flicks produced either during their call or during periods of wing flicking. Females of both species flew to calling males, which they approached by walking. Except to approach a calling male, females remained still and passive before mating. In some cases, males made short (<20 s) calls while being approached by females. These shortened calls could be a form of courtship, although it is doubtful that females require males to make such calls because not all males did so. In some cases, mating occurred after a short (≈ 10 min) bout of wing flicking in which both male and female alternated bouts of wing flicking, and in which the male never called or made any other signal besides wing flicks. None of the wing flicking behaviors observed in either sex appeared to have a specific temporal relationship to male calls. Whether or not the male made short calls or either sex wing flicked, in all five pairs of each species observed, once the female made physical contact with the male, they mated without elaborate courtship. In

three complete mating sequences observed for *O. canadensis*, copulation lasted an average of 19 ± 4 min, whereas four *O. rimosa* copulations averaged 19 ± 2 min. These durations are shorter than those reported for *Magicicada* (243 ± 122 min, $n = 43$; Cooley 1999).

Males presented with an immobile female or similar object were persistent in investigating it and were not startled by the presence or actions of a human observer. In 9/9 cases in which a calling male *O. canadensis* and in 16/20 cases in which a calling male *O. rimosa* was presented with a model female, the male mounted, extruded his genitalia, and attempted to copulate with the model. These response rates are not significantly different from each other ($P \leq 0.28$, Fisher exact test) and are significantly different from no response to the presentation of a model ($P \leq 0.01$ for each species, χ^2 goodness-of-fit). When calling males were presented with live males of their own species, they courted them as if they were females and attempted to copulate with them. The courted male generally responded with a wing flick or an alarm sound, which, at least temporarily, deterred the courter.

Discussion

Male *O. canadensis* and *O. rimosa* signal from stationary perches, and sexually receptive females approach them. *Okanagana* females indicate their sexual receptivity by approaching advertising males and have no other specialized receptivity signals. Such a male signal/female approach mode of sexual pair formation differs from that of cicada species such as *Magicicada*, in which males both signal and search, and in which females respond to male calls with a specialized receptivity signal (Cooley and Marshall 2001).

While wing flicking in *Magicicada* is almost exclusively a female sexual receptivity signal (Cooley and Marshall 2001), in *Okanagana* its context is less specific. The risk of parasitism suggests two hypotheses for the function of *Okanagana* wing flicking. First, bouts of singing punctuated by wing flicking may make it physically difficult for acoustically orienting, parasitic sarcophagid flies (*Colcondamyia auditrix* Soper; see Soper et al. 1976) to approach cicadas. Anecdotal evidence (J.R.C., unpublished data) that touching a male provokes a bout of wing flicking supports this functional explanation. The occasional use of wing flicks by males to deter misdirected courtship by other males is consistent with the hypothesis that wing flicks in *O. canadensis* and *O. rimosa* are general deterrents to close contact or unsolicited touching. However, this functional explanation does not account for wing flicking in *O. canadensis*, upon which no parasitic attacks have been observed, nor does it explain why females wing flick even though they produce no acoustical signals attractive to parasites.

An alternative hypothesis is that wing flicking is a close-range mode of signaling. Among cicadas, males of the New Zealand genus *Amphipsalta* bang their wings as part of their calling display (Dugdale and Fleming 1969), and female wing flick responses to

male calls have been reported in the New Zealand genera *Kikihia*, *Maoricicada*, *Melampsalta*, *Notopsalta*, *Rhodopsalta* (Myers 1929, Dugdale and Fleming 1969; Lane 1995), Australian *Cystosoma* (Doolan 1981; Doolan and Young 1989), and *Cicadetta* (Gwynne 1987), European *Tibicina* (Fonseca 1991), Asian *Cicadetta* (Popov 1981), and North American Platype-diinae (Moore 1968) and *Magicicada* (Cooley and Marshall 2001). Such female signals have a specific temporal relationship to male songs, and males respond to them by courting or attempting to copulate.

Wing flicking in *Okanagana* differs from these examples in that both sexes wing flick, their wing flicks have no specific temporal relation to male calls, and female wing flicks do not provoke male courtship or copulation attempts. Even though wing flicking in *Okanagana* appears to lack the specificity of wing flick signals in other species, it may still be a form of sexual signaling. For *Okanagana*, the necessity that males signal in order for females to find them, and the risks imposed by acoustically-orienting parasites or predators may have promoted wing flicking as an unobtrusive mode of close-range signaling. Wing-flicking may enable an *Okanagana* female to alert a nearby male of her presence, allowing him to switch from risky broadcast signals to more subtle wing flick signaling that guides her approach without placing both partners in jeopardy from acoustically-orienting parasites.

Okanagana follow the generalization that the sexes divide the roles of signaling and searching. The presence of a specialized, acoustically orienting parasite is one factor that may elevate the risk of signaling relative to the risk of searching in these species. Why are other cicadas, such as *Magicicada*, seeming exceptions to the division of risk? For *Magicicada*, one possible explanation is that their unique biology makes signaling and searching relatively risk-free. Long, prime numbered life cycles and dense, synchronized emergences allow *Magicicada* to rely on the actuarial defense of being one member of a large group. Males may adopt both roles of signaling and searching, but mass periodicity may mitigate the risks inherent in each. Comparisons, such as between *Okanagana* and *Magicicada*, may allow inferences about the ancestral cicada mating system and shed light upon the evolution of the varied pair-formation patterns found in present-day cicadas.

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