

TERRITORIALITY AND SINGING-SITE PREFERENCES IN THE CRICKET, *CYPHODERRIS MONSTROSA* (ORTHOPTERA: HAGLIDAE) IN WESTERN NORTH AMERICA¹

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ABSTRACT: Many male orthopterans prefer to stridulate from certain microhabitats. However, it is unknown if such preferences exist in *Cyphoderris monstrosa* Uhler (Haglidae). Choice tests indicated that *C. monstrosa* strongly prefer to sing from large trees and clumps of trees, but a survey of singing *C. monstrosa* suggested indifference to tree species. The observed preferences may have implications for understanding the evolution of territoriality in *C. monstrosa*.

KEY WORDS: Orthoptera, Haglidae, Cricket, stridulate, conifer, habitat preference, territoriality, western North America.

The haglid crickets are represented in Western North America by three species: *Cyphoderris monstrosa* in the Cascade and northern Rocky Mountains, *C. strepitans* in the central Rocky Mountains, and *C. buckelli* in the Canadian Rocky Mountains (Morris and Gwynne 1978). Males of all three species sing at approximately 13kHz with essentially the same pulse rate, pulse duration, and amplitude (Morris and Gwynne 1978). However, two of the three species communicate differently with their songs: *C. strepitans* use song to attract mates (Dodson et al. 1983, Snedden and Irazuzta 1994) while *C. monstrosa* use song to mediate territorial disputes (knowledge of *C. buckelli* is lacking; Sakaluk et al. 1995, Mason 1996).

In *C. monstrosa*, territorial disputes can escalate from singing to biting and kicking matches (Mason, 1996), but physical aggression is absent in *C. strepitans* and *C. buckelli*. That difference in aggressiveness is puzzling – why aren't all three species alike? Mason (1996) and Sakaluk et al (1995) suggest that the answer may lie in habitat geometry. Male *C. monstrosa* sing from the branches and trunks of conifer trees, while male *C. strepitans* and male *C. buckelli* sing from bushes (Morris and Gwynne 1978). Since bushes are shorter than conifer trees and have denser branches, the cost of defending a territory in a bush may be relatively high, making territoriality disadvantageous for *C. strepitans* and *C. buckelli* but not *C. monstrosa* (Mason 1996, Sakaluk et al. 1995).

However, rather than a high cost, defending a territory in a bush may entail only a small benefit in comparison with defending a territory in a tree. All bushes could be roughly equivalent, while a limited number of conifers could offer the best protection, food, or access to females. *Cyphoderris monstrosa* may defend territories not because it is relatively “cheap,” but because it is relatively beneficial.

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According to the latter benefits hypothesis, territoriality and environmental heterogeneity should correlate: When sites are of differing quality, territoriality should be present, while when they are of equivalent quality, it should be absent. Suggesting that sites are indeed equivalent in the absence of territoriality, *C. buckelli* sing from randomly chosen bushes (Morris et al. 2002). However, whether *C. monstrosa* prefer to sing from particular trees is unknown. The aim here is to answer this question, specifically by investigating if *C. monstrosa* prefer to sing from any particular species of tree, size of trees, or size of tree clumps in meadows.

METHODS

Field Site

All experiments were conducted at the headwaters of Snow Creek in the Three Sisters Wilderness of the Cascade Mountains (U.S.A., Oregon; 121°40'5.4"W, 44°6'4.5"N). The elevation of the site ranged from 2133 to 2225 m.

For experiments, "large" and "small" trees were defined based on their circumference and height (Large Trees: circumference at 1 m = 1.74 ± 0.87 m; height = 15.79 ± 6.63 m; Small Trees: circumference at 1 m = 0.19 ± 0.084 m; height = 2.38 ± 0.72 m). Likewise, "large" and "small" tree clumps were defined based on the number of trees that they contained and the maximum height of their trees (Large Clumps: number of trunks = 24 ± 15 ; maximum height = 13.8 ± 3.5 m; Small Clumps: number of trunks = 5 ± 6.8 ; maximum height = 5.3 ± 2.1 m).

Crickets for experiments were collected from trees and tree clumps not used in trials. While in captivity, each cricket consumed apple, carrot, and staminate pinecones (Mason 1991, Snedden and Irazuzta 1994), and each one's pronotum, hind knees, and abdominal tergites VII and VIII were coated with fluorescent or phosphorescent paint (Liquitex No. 2002-981, Liquitex No. 20002-982, and Golden Phosphorescent Medium).

Tree Clump Preferences

These trials tested if male *C. monstrosa* prefer to sing from large or small tree clumps. Each trial occurred in one of five circular arenas (Fig. 1). At the center of each arena, crickets acclimated in a container for 2 hours before each trial began. Crickets were then released between 2000 and 2015 hours and observed every 5 minutes under red light, or when missing, under ultraviolet light. As a cricket crossed the perimeter of an arena, its location and the temperature on the ground were recorded. Each cricket was used only once.

The direction from the center of a given arena to its tree clumps was oriented randomly to control for the possibility that *C. monstrosa* may have tended to walk in a particular compass direction. In addition, interactions between tree size and tree species were accounted for by creating two arenas between clumps of *Tsuga mertensiana* and three arenas between clumps of mixed *Abies/Pinus* spp.

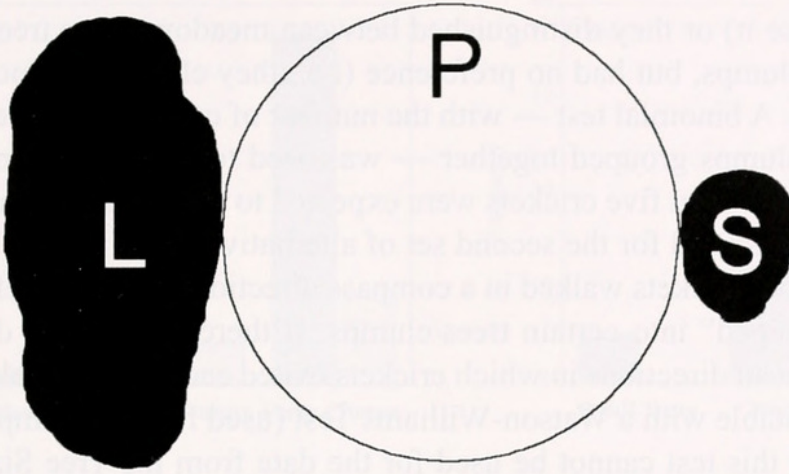


Figure 1. An arena as seen from above. Abbreviations are as follows: *S*, small tree or tree clump; *L*, large tree or tree clump; *P*, perimeter of arena. The perimeter touched each clump or tree tangentially and was marked on the ground with string tied to garden stakes. This string did not impede crickets from walking out of the arena. The mean diameters of arenas were $2.48 \pm 0.9\text{m}$ and $1.25 \pm 0.4\text{m}$ in Tree Clump Choice Tests and Tree Size Choice Tests, respectively.

Tree Size Preferences

The aim of these trials was to test if *C. monstrosa* prefer to sing from large or small trees. Trials were performed in four arenas, and followed the same protocol as for tree clumps except crickets acclimated for 45-60 minutes rather than 2 hours. In addition, if a cricket exited an arena unobserved, it was assumed to have followed a linear course from its last known location. To account for the corresponding loss of precision, these estimated locations were recorded in 30° increments. Finally, while only one cricket occupied an arena at a time, up to three were released into each arena per night, beginning at between 2100 and 2115 hours and ending by 2400 hours. Each cricket was used only once.

One variable that may interact with tree size is tree species. Hence, arenas were situated so that half were between pairs of *Pinus* trees and half were between pairs of *Tsuga mertensiana* trees. As in the tree clump experiments, the directions to the large and small trees differed for each arena.

Tree Species Preferences

To determine if *C. monstrosa* prefer to sing from a particular species of tree, logistical constraints precluded choice tests. However, surveying singing crickets was possible. To generate a null model for the survey, the relative abundance of *Pinus* sp., *Abies* sp., and *Tsuga* sp. was determined within the tree clumps that crickets sang, or within a 25 m^2 quadrat in the forest.

Analysis

To test if crickets preferred large trees and tree clumps, two alternatives are considered: crickets followed a random walk (implying that the proportion of the perimeter of the arena that a large tree/clump occupied predicted the number of

crickets that chose it) or they distinguished between meadow, large trees/clumps, and small trees/clumps, but had no preference (i.e., they chose each location one third of the time). A binomial test — with the number of crickets expected at large and small trees/clumps grouped together — was used to test the first null hypothesis because fewer than five crickets were expected to choose trees/ clumps (Zar 1996). A G-test was used for the second set of alternatives.

It is possible that crickets walked in a compass direction that they preferred and then merely “bumped” into certain trees/clumps. If there was such a directional preference, the mean directions in which crickets exited each arena would be identical, which is testable with a Watson-Williams Test (used for tree clump data; Zar 1996). However, this test cannot be used for the data from the Tree Size Choice Tests because they were grouped in 30° increments (Zar 1996). To circumvent the problem, consider that if crickets chose a compass direction, half of them from each arena would have chosen to go to either side of the median direction for all of the exits from all of the arenas, a hypothesis testable with a G-test (Batschelet 1981).

All means are reported plus or minus one standard deviation (mean \pm SD).

RESULTS

Tree Clumps Preferences

Surveys suggested that singing crickets were more abundant in large tree clumps than small tree clumps. In trials, most crickets walked directly to the large or small tree clump. *Cyphoderris monstrosa* that initially began walking towards the small tree clump usually reversed direction before they were halfway there ($n=3$). Ultimately, of the 25 crickets that exited arenas, 23 (92 percent) went to large clumps, 1 (4 percent) went to meadow, and 1 (4 percent) went to a small clump. Crickets chose tree clumps more often than is expected had they followed a random walk (Fig. 2a; binomial test, $p < 0.001$). They therefore appear to have chosen the tree clumps prior to leaving the arena. A test of whether their decision was random with respect to clump size indicates that it was not; large tree clumps were preferred (G-test, $G=38.219$, $p < 0.001$). *Cyphoderris monstrosa* moreover tended to exit arenas at the center of large tree clumps (χ^2 goodness of fit test: $\chi^2=13.272$, $p < 0.001$). Those that were permitted to continue into tree clumps commenced singing within five minutes of climbing trees therein if the ambient temperature exceeded 4°C.

The mean compass directions in which crickets exited each arena differed (Watson-Williams test: $F=38.503$, $p < 0.0005$; Zar 1996). This heterogeneity indicates that the locations at which *C. monstrosa* exited did not result entirely from a certain compass direction being preferred.

The preference of *C. monstrosa* for large tree clumps was independent of ambient temperature (Fisher's Exact Test: $p=0.708$). However, at low temperatures crickets exited arenas less frequently than at high temperatures, burrowing or becoming inactive immediately upon entering the arena (Fisher's Exact Test: $p < 0.001$).

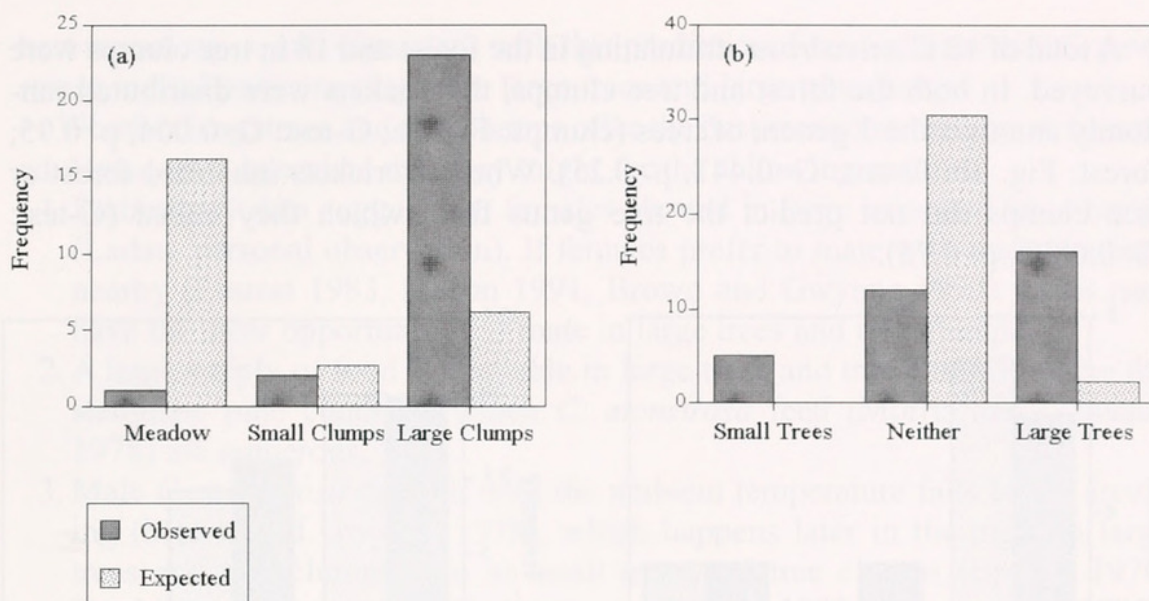


Figure 2. Number of crickets choosing (a) large clumps, small clumps, and meadow and (b) large trees, small trees, and neither. Expectations are calculated from the proportion of the perimeter of the arena that tree clumps or trees occupied.

Cyphoderris monstrosa chose large *Tsuga* clumps as often as they chose large *Abies-Pinus* clumps (Fisher's Exact Test: $p > 0.3$), suggesting that their preference for large tree clumps was unaffected by the species of trees growing in them.

Tree Size Preferences

Surveys suggested that singing crickets were more abundant in large trees than small trees. In trials, most *C. monstrosa* walked directly to the large tree, small tree, or a tree that was located outside of the arena. All told, 16 (48 percent) crickets chose to sing in large trees, 5 (15 percent) in small trees, and 12 (36 percent) chose neither, usually walking to a more distant, foreign tree. More crickets chose large trees than can be explained by the proportion of the perimeter that large trees occupied (Fig. 2b; Binomial test: $p < 0.001$). The responses of the crickets also did not conform to the pattern that was expected if they distinguished between large trees, small trees, and meadow but were not predisposed to choose any of the three (G-test: 6.194, $p < 0.05$). When crickets chose a tree, they climbed it and began stridulating.

Crickets walked in different compass directions in each arena (G-test: $G = 4.321$, $p < 0.05$; Batschelet 1981). Therefore, preference for large trees probably did not result spuriously from crickets choosing to walk in a compass direction that they preferred. Furthermore, the preference for large trees was independent of the genus of the trees (G-test: $G = 0.279$, $p > 0.5$).

Tree Species Preferences

The 14 tree clumps surveyed with singing *C. monstrosa* were composed of 7 *Abies* spp., 160 *Tsuga mertensiana*, and 92 *Pinus* spp. Within eleven 5 x 5 m quadrates centered on stridulating crickets grew 18 *Pinus* spp., 57 *Tsuga mertensiana*, and 35 *Abies* spp.

A total of 12 *C. monstrosa* stridulating in the forest and 18 in tree clumps were surveyed. In both the forest and tree clumps, the crickets were distributed randomly amongst the 3 genera of trees (clumps: Fig. 3a; G-test: $G=0.004$, $p>0.95$; forest: Fig. 3b; G-test: $G=0.447$, $p>0.25$). Whether crickets inhabited forest or tree clumps did not predict the tree genus from which they called (G-test: $G=0.0892$, $p>0.75$).

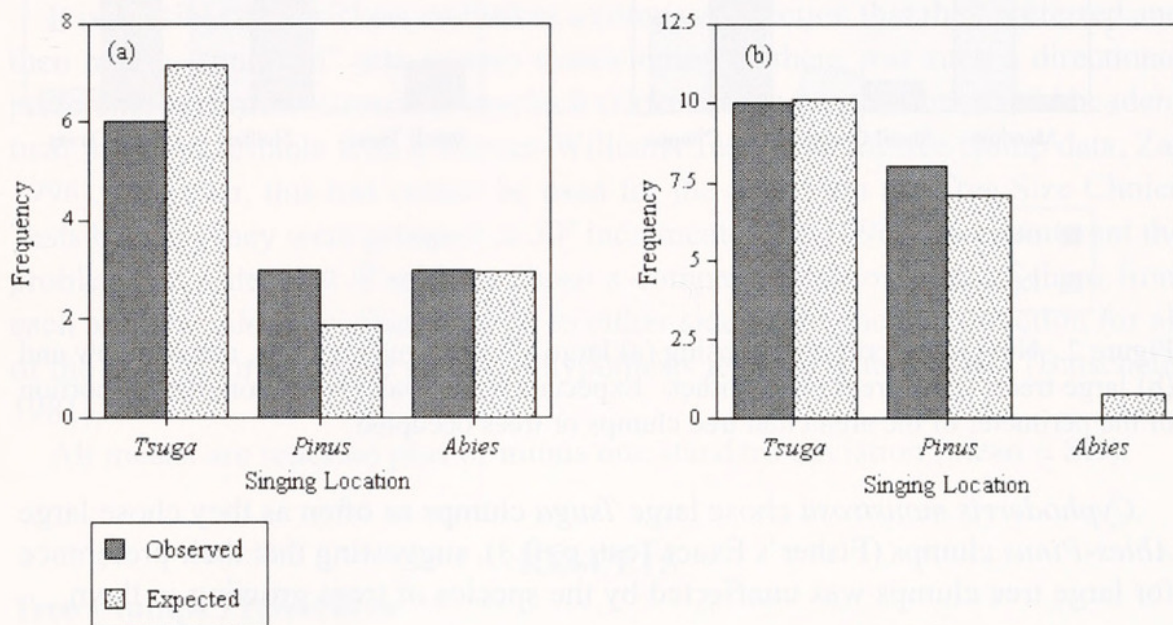


Figure 3. The number of *C. monstrosa* observed and expected (if crickets do not prefer any tree genus) to be singing from *Abies*, *Tsuga*, and *Pinus* trees in (a) tree clumps and (b) forest.

DISCUSSION

This investigation suggests that male *C. monstrosa* prefer to sing in large tree clumps, independent of the ambient temperature and local tree species. It also suggests that the crickets prefer large trees regardless of genus, and that they sing equally often from *P. contorta*, *P. albicaulis*, *Abies* spp., and *T. mertensiana*.

Natural selection is generally modeled as a balance between costs and benefits: selection favors traits only if their benefits exceed their costs (Parker and Maynard Smith 1990). This line of reasoning implies that the benefits of territoriality must exceed the costs in *C. monstrosa* but not in *C. strepitans* and *C. buckelli*. Such a difference may arise in two ways: First, territoriality may cost *C. monstrosa* more than it costs *C. buckelli* and *C. strepitans* (Sakaluk et al. 1995, Mason 1996), and second, territoriality may benefit *C. monstrosa* more than it benefits *C. strepitans* and *C. buckelli*. While these two possibilities are not mutually exclusive, they are distinct, and my results support the second one.

Specifically, I hypothesized that a limited number of sites offer *C. monstrosa* the best protection, food, and/or access to females, while for *C. strepitans* *C. buckelli*, such sites are either unlimited or nonexistent. This hypothesis predicts that *C. monstrosa* should prefer to sing from particular sites — those with the

best resources — and consistent with this prediction, I have shown that *C. monstrosa* indeed prefer to sing from large trees and large tree clumps.

Whether large trees and tree clumps offer the best resources remains to be tested. However, I speculate that they might for the following reasons:

1. Preliminary data suggest that females abound in large trees and tree clumps (Ladau, personal observation). If females prefer to mate with males that are nearby (Forrest 1983, Mason 1991, Brown and Gwynne 1997) males may have the most opportunities to mate in large trees and tree clumps.
2. A large supply of food is available in large trees and tree clumps, where the staminate pine cones on which *C. monstrosa* feed (Morris and Gwynne, 1978) are numerous.
3. Male *C. monstrosa* can call until the ambient temperature falls below freezing (Morris and Gwynne 1978), which happens later in the night in large trees and tree clumps than in small trees and tree clumps (Brooke 1970, Franklin and Dyrness 1972, Spurr and Barnes 1992, Geiger et al. 1995). Therefore, crickets can sing longer in large trees and tree clumps and possibly increase their likelihood of attracting a mate.
4. Large trees and tree clumps are considerably taller than small trees and tree clumps. Male *Anurogryllus arboreus* climb trees to increase the broadcast range of their song (Paul and Walker 1979, Walker 1983), and climbing benefits other species in a like manner (Ewing 1989). Thus, by singing from high perches that large trees or tree clumps offer, male *C. monstrosa* may optimize the broadcast range of their songs.

In sum, if *Cyphoderris* spp. differ in territoriality because of differing benefits, two predictions should hold: first, within the habitat of *C. monstrosa* certain locations should offer better resources than others, and second, within the habitat of *C. strepitans* and *C. buckelli* such heterogeneity should be lacking. Consistent with the second prediction, Morris et al. (2002) show that *C. buckelli* sing from randomly chosen bushes. Consistent with the first prediction, I here show that *C. monstrosa* prefer large trees and clumps of trees.

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