TERRITORIAL INTERACTIONS IN SYMPATRIC SONG SPARROW AND BEWICK'S WREN POPULATIONS

ROBERT E. GORTON, JR.

ABSTRACT.—The similarity in song, habits, and habitat in the Song Sparrow and Bewick's Wren stimulated a study of their interactions in western Washington. Both species respond to models and song of the other species more intensely than to the Black-capped Chickadee, but less intensely than to their own species.

Both birds showed a gradual decrease in aggressive behavior to conspecifics over the breeding season, the Bewick's Wren response rising somewhat early in the season before gradually declining over the rest of the study period. While the Bewick's Wren showed a strong decrease in response levels to the Song Sparrow over time, the Song Sparrow showed a significant drop in aggressive response toward the Bewick's Wren at the time the first brood was fledged, the response rising again at the time of the appearance of the second clutch.

The Song Sparrow and the Bewick's Wren represent a sustained bidirectional system of interspecific aggression. This system may be more sensitive to changes in breeding behavior over the season than is the intraspecific system. Where they coexist they forage at slightly different heights and on slightly different food, but overlap sufficiently so that aggression and similarity of song have evolved as still other mechanisms to reduce competition.—*Department of Biology, University of Puget Sound, Tacoma, Washington 98416. Present address: Department of Entomology, University of Kansas, Lawrence, Kansas 66045.* Accepted 27 February 1976.

A TERRITORY is defined as "any defended area" (Noble 1939). It is a fixed area from which intruders are discouraged by advertisement, threat, attack, or some combination of these behaviors (Brown 1975).

Several suggestions concerning the ultimate factors responsible for the evolution of territorial behavior have been made. Some authors stress the benefits accrued by familiarity with an area and the necessity of preventing disruption of the events between pair-bond formation and the fledging of young (Howard 1920, Nice 1941). Others view territoriality as a spacing mechanism for individuals and nests, checking predation and disease (Hinde 1956). Tinbergen et al. (1967) and Horn (1968) verified experimentally that predation increases with population density. Cody (1971) stated that predation is the single greatest cause of reproductive failure in most birds. The adaptive value of protecting potentially limiting resources has been the subject of extensive discussions (Brown 1964, Orians and Willson 1964, Immelmann 1971). Brown (1964) argued that aggressive behavior is often employed in the acquisition of defensible goals that tend to maximize individual survival and reproduction.

An increasing body of evidence exists on consistent territorial interactions between species (Orians and Willson 1964; Cody 1968, 1969, 1974; Cody and Brown 1970) as well as within them. In the cases where ecologically similar species occur together, one would expect natural selection to favor ecological divergence and a consequent reduction of competition. Lack of divergence could mean (1) that insufficient time has elapsed for the changes to be completed, (2) that some environmental conditions prevent divergence, e.g. structurally simple environments or strongly stratified feeding sites in structurally complex vegetation, or (3) that other species are already exploiting similar resources in a diversified habitat (Orians and Willson 1964). When adequate ecological divergence is not possible, convergence may occur in those behaviors and characteristics associated with spacing and territoriality. Such characteristics include song, aggressive display, and external morphology (color and

patterns). Interspecific territoriality need not be an all or nothing phenomenon. Intermediate cases may occur in which rather less ecologically similar species exhibit only partial territorial overlap (Cody 1974).

Bewick's Wren (*Thryomanes bewickii*) and the Song Sparrow (*Melospiza melodia*) commonly co-exist in broadleaf forests, riparian woodlands, shrubby thickets, parks, and gardens in northwestern Washington. The wren is mainly insectivorous and feeds its young primarily Lepidopteran larvae and adults up to about 2 cm long (Miller 1941, Bent 1948). The Song Sparrow eats both seeds and insects, although it feeds its young largely or entirely on animal matter (Schoener 1968), such as caterpillars and lacewings (Tompa 1962). According to Stiles (1973) the two species overlap somewhat in foraging heights, behavior, and technique (gleaning) in Washington state. They establish territories at about the same time and resemble each other in song through parts of their ranges (Bent 1948, 1968; Jewett et al. 1953; Peterson 1961). Spectrograms of the songs of the two species illustrate graphically a remarkable resemblance of song (Robbins et al. 1966). Miller (1941) noted that the Song Sparrow was known to pursue Bewick's Wren when it saw the latter intruding in its territory. L. S. Best, W. J. Erckmann, and L. A. Fairbanks (MS) found that Song Sparrows in the University of Washington Arboretum in Seattle could be induced to attack a Bewick's Wren mount accompanied by its recorded song. These observations suggest the possibility of sustained territorial interactions.

MATERIALS AND METHODS

This study was undertaken approximately 5 miles west of Burlington, Skagit County, Washington. Observations were made within an area of about 4.5 square miles containing a variety of habitat types: meadow, swamp, pond, dense brush, clearings, uncleared logged areas, and second-growth deciduous, evergreen, and mixed forests. The field studies were made from 12 March to 13 June 1974.

I prepared two mounts each of the Song Sparrow and Bewick's Wren and one mount of the Black-capped Chickadee (*Parus atricapillus*), all in a perching pose. The birds from which the mounts were prepared were collected from the study tract. Brown glass eyes were used in all mounts.

Songs of the Bewick's Wren were recorded in Skagit County on a Sony 110-A cassette recorder. Songs of the Song Sparrow (Cornell Cut 40) and the Black-capped Chickadee (Cornell Cut 24) were recorded in Fullerton, California, and Michigan, respectively. All recorded songs were played in the field on a Sony TC-72 cassette recorder.

The subject birds (those being tested) were located primarily by song. The model was placed within the territory of the subject as close to the singing bird as possible. The song was then played at full volume and the response of the subject to the model and song noted, along with temperature, habitat, and weather conditions. The cassette recorder was not camouflaged but was hidden whenever possible, always as close to the model as possible. I was often distant, but probably visible, assuming a low profile during the experiments, but on several occasions attacks on the model took place within inches of me, indicating no fear response interfering with the responses to the model. Individual birds were sometimes tested more than once, but never more than four times during the season. No bird was tested twice in the same day. Experiments were stopped during rain or darkness. Early in the study I paced off distances from the model to the subjects' nearest point of approach. Later I approximated the distances by eye.

The Song Sparrow was tested against models presented in the sequence Song Sparrow, Bewick's Wren, Black-capped Chickadee, Song Sparrow; the Bewick's Wren against Bewick's Wren, Song Sparrow, Black-capped Chickadee, Bewick's Wren. Models were changed after a response or a period of from 5 to 15 min, always allowing ample time for a response. A minimum of 3 min between tests was allowed the subjects. Terminal conspecific tests were used to demonstrate any habituation occurring over the experimental period, and the Black-capped Chickadee was used as a control to which neither bird was expected to react aggressively.

The responses of the subjects were scored on a scale of 0 to 4 (see Table 1). Means and standard errors were calculated for all classes of data. The sign test was used to determine differences in response data obtained from experiments involving a given subject species. The 2×2 contingency test was used to compare response data between subject species (Conover 1974).

TABLE 1

SCORING SYSTEM FOR MEASURING RESPONSES TO MODELS AND SONGS

0 = no response
1.0 = some reaction: bird comes within 25 feet of the model or begins to sing
1.5 = bird comes within 15 feet of the model and begins to sing; active flying
2.0 = stronger response: alarm calls, tail flicking, scolding, puffing up, active flying and orientation towards model, and associated behavior
2.5 = same response as 2, and bird comes within 10 feet of the model
3.0 = same response as 2, and bird comes within 5 feet of the model
3.5 = reaction just short of attack, bird comes closer than 5 feet to the model
4.0 = bird attacks model

RESULTS

Mean seasonal responses for the study period were calculated for the Song Sparrow and Bewick's Wren (Table 2). Both species exhibited a similar pattern: highest response to the conspecific song and model, minimal response to the chickadee control, and an intermediate response to the interspecific song and model. The absolute numbers and percentages of birds responding in each category are given in Table 3.

It was of interest to determine response patterns as a function of the breeding cycle. The 1974 season (12 March 1974–13 June 1974) was divided into four time periods of 18, 29, 32, and 14 days respectively, to allow a minimum of 6 individual responses in each period. No statistically significant changes in the mean response of the Song Sparrow to its conspecific song and model were noted among any of the four time periods (Fig. 1A). Likewise, no statistically significant changes in the mean response of Bewick's Wren to its conspecific song and model were noted (Fig. 1C). The Song Sparrow's response to the Bewick's Wren song and model (Fig. 1B) shows a statistically significant drop in the mean response between the second and third periods (31 March–28 April and 29 April–30 May), while the mean response of the Bewick's Wren to the Song Sparrow song and model (Fig. 1D) shows a significant drop between the first and fourth periods (12 March–30 March and 31 May–13 June).

Song Sparrows were intensely intraspecifically territorial over the study period with a gradual decline in mean aggressive response over time (Table 2, Fig. 1). Tompa (1962), working with the Song Sparrow in British Columbia, also noted a gradual decline of territorial behavior during the breeding season until late July and August when molt began in adults. Early in the breeding season during the first period (12–30 March) aggression was high in many of the subject birds, but in other birds avoidance responses were noted, in which a bird singing from its perch immediately ceased singing and flew away from the model, often into low, dense brush. Such responses were noted on four occasions during this period, one case involving what appeared to be the male of a mated pair. Numerous altercations were noted between Song Sparrows until June, when the number of such encounters decreased. On one occasion the model was placed between two adjoining territories. Two males responded aggressively to the model, but not to each other. They were very

TABLE 2

MEAN SEASONAL RESPONSES OF SUBJECTS TO CONSPECIFIC MODELS AND SONGS[1]

Subject	Model and song		
	SS (SS)	BW (BW)	BCC (BCC)
SS[2]	$2.24 \pm 0.21_{53}$	$1.32 \pm 0.19_{41}$	$0.25 \pm 0.12_{40}$
BW	$0.57 \pm 0.11_{34}$	$1.28 \pm 0.11_{39}$	$0.03 \pm 0.03_{31}$

[1] With one SE. Subscripts indicate sample size. [2] SS = Song Sparrow, BW = Bewick's Wren, BCC = Black-capped Chickadee.

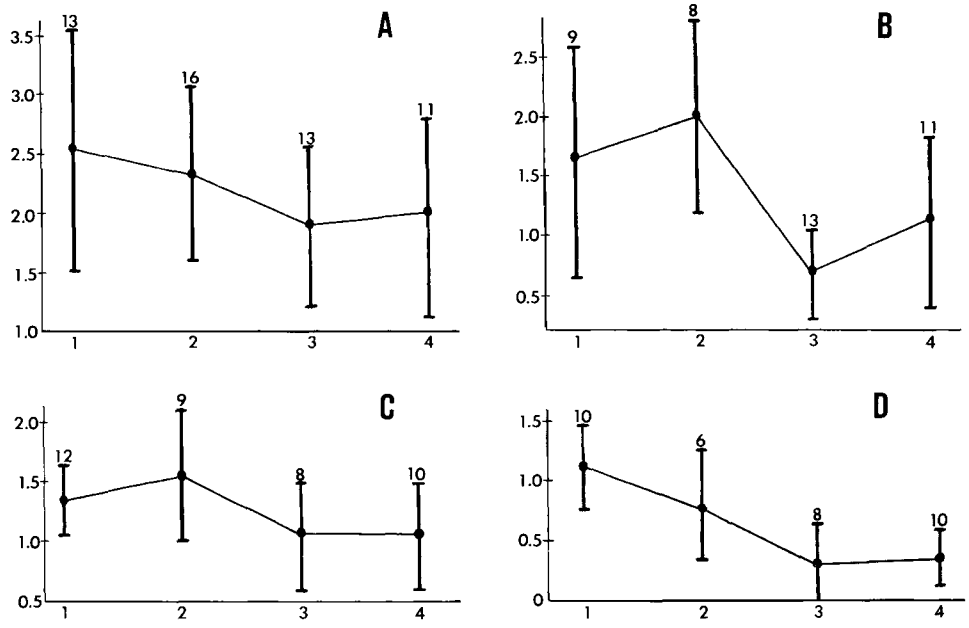

Fig. 1. A. Mean responses of Song Sparrow to conspecific song and model as a function of time, with 2 SE on either side of the mean. Numbers above SE indicate sample size in given time period. Period 1, 12–30 March; period 2, 31 March–28 April; period 3, 29 April–30 May; period 4, 31 May–6 June. B. Mean responses of Song Sparrow to Bewick's Wren song and model. C. Mean responses of Bewick's Wren to conspecific song and model. D. Mean responses of Bewick's Wren to Song Sparrow song and model.

tolerant of each other on the territorial periphery, but not to the presence of a third unknown intruder. On 7 May I noticed two pairs of Song Sparrows with beaks full of insects, indicating the presence of young. (Eggs are usually found from early April to late May, although recorded as late as mid-July (Bent 1968).) Tompa (1962) found the breeding season to extend from mid-March to late July. The first fledglings with parents were noticed on 21 May, when four Song Sparrows were seen together, one of which oriented towards the conspecific model at the onset of the recorded song. On 8 June two more groups, one of four and one of five birds, were noted in close association, some of which lacked the central brown spot characteristic of adults. The next day one of a pair of Song Sparrows walked within 3 cm of the model with no aggressive behavior, looked at it closely, and flew off. The conspecific test done hours before with another Song Sparrow resulted in a quick attack on the model. A 1-day survey on 22 June revealed few singing birds and many subadults.

The breeding cycle for the Bewick's Wren temporally approximates that of the Song Sparrow. Jewett et al. (1953) stated that nesting begins in mid-April to mid-May with broods appearing from late May to early June. Dawson and Bowles (1909) reported fresh eggs from mid-April to mid-June. Nesting may begin somewhat earlier, because I noticed an individual with a stick in its bill on 18 March. Territorial song was heard throughout March. The mean response for April was higher, coinciding with the onset of nesting. Overall, there was little change over the study period. The primary weapon in territorial disputes for this population is the song: 61.5% of the responses (24 of 39) had an absolute value of 1. Singing duels were common between adjacent individuals, and in one instance two adjacent birds pursued and attacked each other in a large tree for nearly an hour, with short recesses.

TABLE 3

NUMBER AND PERCENT OF BIRDS RESPONDING TO EACH SCORING CATEGORY

Subject model and song	Score								
	0	1	1½	2	2½	3	3½	4	Total
BW-BW (BW)[1]	6	10	14	8	0	1	0	0	39
	15.4%	25.6%	35.9%	20.6%	0%	2.5%	0%	0%	100%
BW-SS (SS)	17	12	5	0	0	0	0	0	34
	50.0%	35.3%	14.7%	0%	0%	0%	0%	0%	100%
BW-BCC (BCC)	30	1	0	0	0	0	0	0	31
	96.8%	3.2%	0%	0%	0%	0%	0%	0%	100%
SS-SS (SS)	10	6	7	4	2	3	8	13	53
	18.9%	11.3%	13.2%	7.5%	3.8%	5.7%	15.1%	24.5%	100%
SS-BW (BW)	12	11	3	7	5	0	0	3	41
	29.3%	26.8%	7.3%	17.1%	12.2%	0%	0%	7.3%	100%
SS-BCC (BCC)	35	2	0	2	0	0	0	1	40
	87.5%	5.0%	0%	5.0%	0%	0%	0%	2.5%	100%

[1] SS = Song Sparrow, BW = Bewick's Wren, BCC = Black-capped Chickadee.

As mentioned above, the Song Sparrow experiment was performed in this sequence: Song Sparrow, Bewick's Wren, Black-capped Chickadee, Song Sparrow. A Bewick's Wren in the neighborhood could thus respond to its conspecific in a sequence designed to test a Song Sparrow. In 12 of 41 tests (29.3%) for territoriality in the Song Sparrow, the Bewick's Wren responded to its conspecific. Likewise in 8 of 34 tests (23.5%) of the Bewick's Wren experiments, the Song Sparrow responded to its conspecific. Thus 26.7% of the tests (20 of 75) produced circumstantial evidence of territorial overlap. Possibly in at least a few instances the birds were near their territorial boundaries, or were attracted out of their territories by a strange conspecific song. Because no territorial mapping was done, the degree of territorial overlap in the two species cannot be determined quantitatively, but overlap often seemed to occur in transition zones between relatively open areas and structurally more complex areas. When a conspecific responded to its own song and model during a test involving the other species, it was possible to watch individuals of the two species together. In one instance the Song Sparrow drove off the Bewick's Wren. In seven other cases the Bewick's Wren either elicited a singing response from the Song Sparrow, actively avoided the Song Sparrow, or, in one case, began singing. In one of the former cases, the sparrow moved into the tree in which the Bewick's Wren was singing. Each move by the wren higher in the tree was matched by a similar move by the sparrow. This continued until the Bewick's Wren reached the top of the tree.

TABLE 4

ANALYSIS OF SEASONAL DATA TO COMPARE CONSPECIFIC AND INTERSPECIFIC RESPONSES FOR GIVEN SPECIES, USING SIGN TEST

Pop. 1	Pop. 2	Test statistic	α-level
SS-SS (SS)[1]	SS-BW (BW)	6.5	0.0001
SS-SS (SS)	SS-BCC (BCC)	6.5	0.0001
SS-BW (BW)	SS-BCC (BCC)	4.161	0.0001
BW-BW (BW)	BW-SS (SS)	3.202	0.0001
BW-BW (BW)	BW-BCC (BCC)	4.161	0.0001
BW-SS (SS)	BW-BCC (BCC)	1.716	0.0005

[1] SS = Song Sparrow, BW = Bewick's Wren, BCC = Black-capped Chickadee.

TABLE 5

ANALYSIS OF SEASONAL DATA TO TEST IF SONG SPARROW RESPONDS TO CONSPECIFIC AND INTERSPECIFIC MODELS AND SONGS AT SAME LEVELS AS BEWICK'S WREN[1]

Pop. 1	Pop. 2	Test statistic	Accept H_0?	α-level
SS-SS (SS)[2]	BW-BW (BW)	15.55	No	0.001
BW-SS (SS)	SS-BW (BW)	10.313	No	0.005
SS-BCC (BCC)	BW-BCC (BCC)	2.433	Yes	> 0.10

[1] Using 2 × 2 contingency test (class 1: responses 0–1½; class 2: responses 2–4).
[2] SS = Song Sparrow, BW = Bewick's Wren, BCC = Black-capped Chickadee.

When the sparrow made another move up the tree, the wren flew off. The Song Sparrow then sang several times and returned to its lower perch. The entire episode lasted less than 2 min. Another Bewick's Wren approached a perching Song Sparrow to sing atop a high nearby tree. The Song Sparrow took up the song, moving higher up its own perch to reply. The duel went on several minutes until the wren flew off.

Analysis of Mean Responses.—The Song Sparrow responded differently to the conspecific song and model than to the Bewick's Wren song and model and differently to the Bewick's Wren song and model than to the chickadee song and model ($P < 0.0001$, sign test for nonparametric data). Three distinct mean responses to the three model and song presentations emerge. Likewise, the Bewick's Wren responded differently to its conspecific model and song than to the Song Sparrow model and song and differently to the Song Sparrow model and song than to the chickadee model and song ($P < 0.0005$), illustrating the same three distinct response classes as the Song Sparrow (see Table 4).

The Song Sparrow reacted more vigorously to its conspecific song and model than did the Bewick's Wren to its conspecific song and model ($P < 0.001$, 2 × 2 contingency test for nonparametric data). Similarly, each responded differently to the song and model of the other ($P < 0.005$). Both responded in the same manner to the chickadee song and model, suggesting it was an effective control (Table 5).

DISCUSSION

The Song Sparrow reacted much more to its conspecific song and model than did the Bewick's Wren to its conspecific song and model. The question arises: Why should these two species show this difference in reaction intensity? The Song Sparrows picked a few favorite perches within their territories from which to sing, usually no more than 2–3 m high. Bewick's Wrens, on the other hand, seemed to have no special singing perches but sang in many places of different heights, often 3 m or more. Furthermore the Bewick's Wren seemed more active within its territory than the Song Sparrow. Even if the increased height common to the singing perches of the Bewick's Wren did not provide greater visibility, making it more difficult for an intruder to go unnoticed, it seems likely that the smaller amount of time spent in more places would increase the probability of encountering an intruder, leading to his exclusion from the area.

As mentioned above, the Song Sparrow responded at different levels to its conspecific song and model, to the Bewick's Wren song and model, and to the Black-capped Chickadee song and model. This indicates that the Song Sparrow recognizes both of these other two species and treats each one differently. (One attack on the Bewick's Wren model took place prior to the onset of the song.) This fact suggests that those individuals that react aggressively to the Bewick's Wren have a selective

advantage over those that do not. This is true if the resource supply is sufficient to support only one breeding pair of one species optimally. When response is plotted against time, a drop in response is noted between the second and third periods. The third period is the time of feeding young and fledging, a period when parent birds are busy with hungry fledglings in which they have a great deal of time and energy invested. While it should be adaptive to defend a territory vigorously against conspecifics, it should be less advantageous to defend the territory against other species, with which competition is less intense, during the period between broods. That the mean response rises again during the fourth period is suggestive. During this period, eggs are again in the nest, and an adequate food supply is again a pressing concern. Thus the interspecific aggression, primarily involving singing and active flying, is more sensitive to different activity periods over the breeding season, the Bewick's Wren being somewhat less of a threat to limiting resources than the conspecific.

The Bewick's Wren is considerably less interspecifically aggressive than the Song Sparrow. A partial proximate explanation for this is that the Bewick's Wren is generally less pugnacious. Furthermore in actual combat the smaller wren stands less of a chance of emerging victorious. Therefore selection may favor the evolution of only that level of aggression against a competitor that is most effective and least energetically expensive per unit gain. As with the Song Sparrow, Bewick's Wren responds differently to each of the models and songs; response is presumably a function of niche overlap. The mean level of aggression decreases over the breeding season. As the season progresses, greater demands are placed on the parents to bring increasingly more food to the nest as the nestlings get larger. They are then spending much of their time foraging for the nestlings and excluding conspecifics, which is more critical at this point in the breeding cycle than excluding other species. Finally when the brood is fledged, aggression should be least, as is reflected in the changes in modes of aggressive levels.

The birds divide the habitat vertically, the Song Sparrow preferring simpler, more open habitats with a lower foliage height diversity than the Bewick's Wren, so that territorial overlap refers to overlap of territorial volumes. Thus, a species that may be tolerated at one height may not be at another, while a conspecific may be excluded at any level within the territory. For example, a Song Sparrow intruding into the territory of another at 6 m high is very likely to come down to 1 m if allowed to remain; a Bewick's Wren is much less likely to do so, but would remain out of the Song Sparrow's territorial volume. Several coexistence mechanisms are at work in this system. Vertical feeding site segregation has been mentioned. Feeding behavior, and consequently foraging substrates, differ somewhat. Differences in bill morphology suggest that while they feed the young the same kinds and sizes of food, this food may be in different places so that some prey items available to the Bewick's Wren, for example in deep, narrow cracks in the trunks of trees, are unavailable to a Song Sparrow. Cody (1974) found that the Song Sparrow spends 11% more time in the 2–5 m zone in the absence of the Bewick's Wren, Orange-crowned Warbler, Yellow Warbler, Common Bushtit, and Chestnut-backed Chickadee, common competitors in this zone. It is apparent that for this population competition is pronounced enough for the establishment and maintenance of a system of interspecific aggression.

ACKNOWLEDGMENTS

I thank Howard Channing and the Cornell Laboratory of Ornithology for the song recordings. My grandmother, Mrs. Frieda Gorton, supplied me with bed and board during the fieldwork. My father-in-

law, Barrie Smith, supplied me with a tape recorder. I also thank E. L. Karlstrom, and G. Blanks of the University of Puget Sound and D. R. Paulson of the University of Washington for assistance and encouragement. M. Perrone and D. Paulson also critically read the manuscript and made many valuable suggestions. Katy Swanson and Karen Mesmer of the Quantitative Science section of the University of Washington helped with the statistical analyses. Walter Coole of Skagit Valley College provided faculty privileges and an office during my stay in Skagit County. Special thanks go to my wife, Terry Anne, who participated in one way or another in every aspect of this study and manuscript. The study was part of a Master of Science thesis at the University of Puget Sound.

LITERATURE CITED

BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull. 195.

———. 1968. Life histories of North American Cardinals, grosbeaks, buntings, towhees, finches, sparrows, and their allies, part 3. U.S. Natl. Mus. Bull. 237.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160–169.

———. 1975. The evolution of behavior. New York, W. W. Norton Co.

CODY, M. L. 1968. Interspecific territoriality among hummingbird species. Condor 70: 270–271.

———. 1969. Convergence characteristics in sympatric populations: A possible relation to interspecific territoriality. Condor 71: 222–239.

———. 1971. Ecological aspects of reproduction. Pp. 462–512 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

———. 1974. Competition and structure of bird communities. Princeton, New Jersey, Princeton Univ. Press.

CODY, M. L., AND J. L. BROWN. 1970. Character convergence in Mexican finches. Evolution 24: 304–310.

CONOVER, W. J. 1974. Practical non-parametric statistics. New York, Wiley Press.

DAWSON, W. L., AND J. H. BOWLES. 1909. The birds of Washington, 2 vols. Seattle, Occidental Pub. Co.

HINDE, R. A. 1956. Territories of birds. Ibis 98: 340–369.

HORN, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49: 682–694.

HOWARD, E. H. 1920. Territory in bird life. London, Murray.

IMMELMANN, K. 1971. Ecological aspects of periodic reproduction. Pp. 342–389 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, AND J. W. ALDRICH. 1953. Birds of Washington State. Seattle, Univ. Washington Press.

MILLER, E. V. 1941. Behavior of the Bewick's Wren. Condor 43: 81–99.

NICE, M. M. 1941. The role of territory in bird life. Amer. Midl. Naturalist 26: 441–487.

NOBLE, G. K. 1939. The role of dominance in the social life of birds. Auk 56: 263–273.

ORIANS, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. Ecology 45: 736–745.

PETERSON, R. T. 1961. A field guide to Western birds. Boston, Houghton-Mifflin.

ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1966. A guide to field identification: Birds of North America. New York, Golden Press.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123–141.

STILES, E. W. 1973. Bird community structure in alder forests. Unpublished Ph.D. dissertation, Seattle, Univ. Washington.

TINBERGEN, N. IMPEKOVEN, AND D. FRANCK. 1967. An experiment on spacing-out as a defense against predation. Behavior 28: 307–321.

TOMPA, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. Auk 79: 687–697.