

TERRITORIAL BEHAVIOR: THE MAIN CONTROLLING FACTOR OF A LOCAL SONG SPARROW POPULATION

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It has been shown frequently that territories are compressible. It is also known that the average territory size for a species in a given area may be significantly influenced by local conditions. However, it has been doubted whether territories can ever shrink to a point beyond which they can become no smaller and thus set an upper limit to the numbers of that local population.

This paper describes a situation in which a local passerine population, affected by favorable environmental conditions, could reach high densities for several consecutive years, and in which the upper limit was set by territorial behavior. It throws some light on how territorial behavior, combined with other factors, may regulate a given population. Conclusions are based in part on data already available; nevertheless, references are made to factors—food and nestling mortality—that have not yet been fully investigated.

Song Sparrows (*Melospiza melodia*), the subjects of this study, defend a territory that normally includes mating, nesting, and feeding grounds, and thus falls into the territory category "A" of Nice (1941). This study, undertaken in order to find out the regulatory mechanism in a local Song Sparrow population, was started in the spring of 1960 and is still in progress. Some data concerning this population were also available for the period between 1957 and 1960 (R. Drent and G. van Tets, pers. comm.).

STUDY AREA AND ENVIRONMENT

This study was made on Mandarte Island in the Gulf Islands archipelago, on the southern coast of British Columbia; appropriate additional small-scale habitat and population surveys were carried out also on neighboring islands (Figure 1). Mandarte Island, with an area more than five hectares, rises abruptly from sea level to an average elevation of 15 meters. A longitudinal groove in the limestone block divides the island into a northeastern and southwestern half. The SW half is a grassy plateau, and is bordered by 20- to 25-meter-high cliffs along the shoreline, while the other half slopes gradually from the groove toward three- to five-meter cliffs of the NE shore.

The vegetation of Mandarte can be divided into three main zones: barren rocks and cliffs (including rocky beaches), grassy meadows, and shrubbery. The shrubbery is of primary importance in this study; it follows the longitudinal axis of the island and is supported by the relatively thick soil

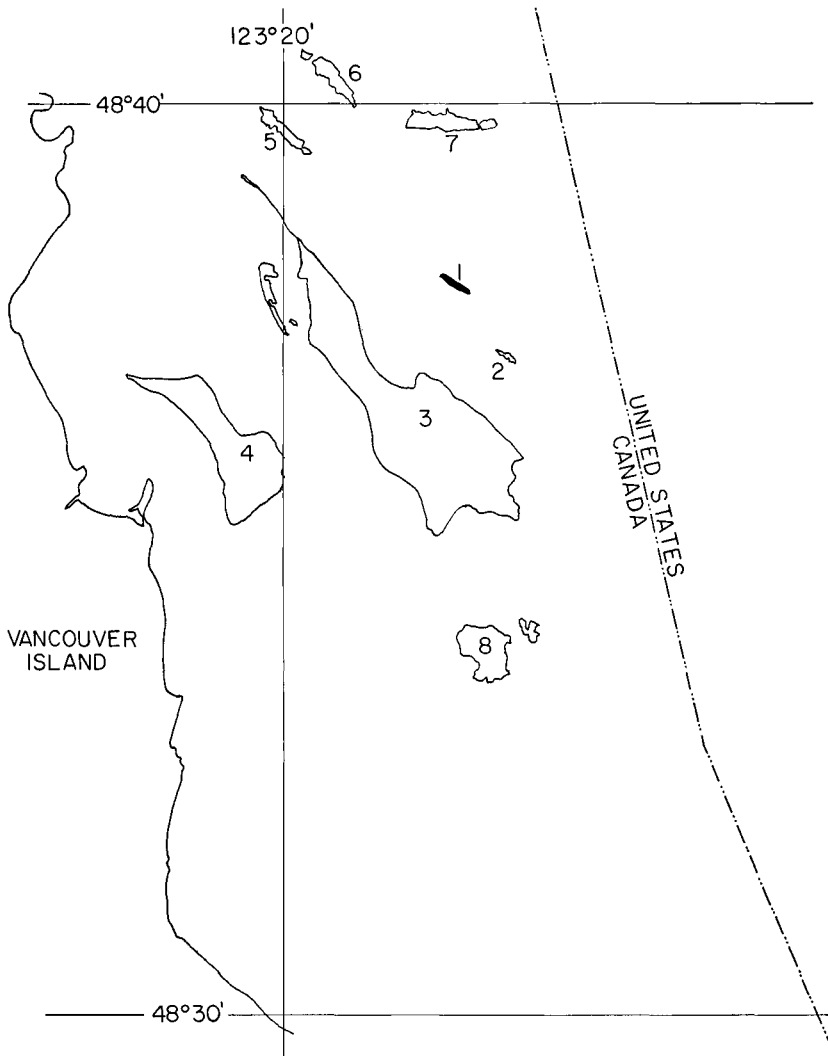


Figure 1. Mandarte Island (in black) and neighboring islands. 1. Mandarte Island; 2. Halibut Island; 3. Sidney Island; 4. James Island; 5. Forrest Island; 6. Damville Island; 7. Gooch Island; 8. D'Arcy Island.

accumulated in the groove. It reaches the NE shore at some points and altogether covers somewhat more than one hectare, while grassland covers more than 50 per cent of the island.

The composition of shrubbery is given in order of abundance: Waxberry (*Symphoricarpos albus*), Wildroses (*Rosa* spp.), Saskatoon berry (*Amelanchier florida*), Blackberries (*Rubus* spp.), Ocean Spray (*Holodiscus dis-*

color), and Fireweed (*Epilobium angustifolium*), one or another dominating at different localities. At some places the shrubbery is heavily interwoven with stems of Northern Bedstraw (*Galium boreale*). Although a few small cherry trees (*Prunus virginiana* and *P. emarginata*) are scattered through the shrubbery, taller trees can be found at one point only, where the groove has expanded and allowed more soil to accumulate. Here a group of trees—Douglas-fir (*Pseudotsuga menziesii*), Grand Fir (*Abies grandia*), and Pacific Madrone (*Arbutus menziesii*)—has established itself over an area of some 500 square meters, together with rich undergrowth of willows (*Salix* spp.), Ocean Spray (*Holodiscus discolor*), and English Hawthorn (*Crataegus oxyacantha*). It is important to note that at least during the last 50 years no substantial change has occurred in the vegetation cover of the island (Anderson, 1916).

In the summer, grasslands are occupied by breeding colonies of Glaucous-winged Gulls (*Larus glaucescens*). On the steep SW cliffs two species of cormorants (*Phalacrocorax auritus* and *Ph. pelagicus*) breed regularly, while crevices along the shoreline offer nest sites to Pigeon guillemots (*Cephus columba*). Regular breeders in the shrubbery are the crows (*Corvus brachyrhynchos*) and Song Sparrows, while Rufous Hummingbirds (*Selasphorus rufus*) are suspected to breed there. The number of breeding crows was approximately 50 in each of the last four seasons. In 1961 two pairs of Red-winged Blackbirds (*Aegialius phoeniceus*) raised single broods after failures in previous years. There are neither amphibians nor reptiles on Mandarte, and deermice (*Peromyscus maniculatus*) are the only mammals.

SONG SPARROWS

Dense vegetation cover, absence of predators and nest parasites, sufficient moisture, and favorable climate, as well as other factors, offer exceptionally good conditions to Song Sparrows, when compared with adjacent areas. Because of the usually mild winters in this region, these birds, belonging to the race *Melospiza melodia morphna* Oberholser, are residents the year around. The length of the breeding season normally extends from the second half of March to late July.

Field work was carried out during the last two summers and involved the color banding of adult and juvenile birds, and recording features of the breeding season. A total of 401 (93 adults and 308 young) birds were banded. The sexes of the birds were determined by behavioral characteristics. Population counts were made approximately every fortnight during the summers, and nearly every month through the winters 1960–1961 and 1961–1962. The number of breeding pairs remained relatively constant (46–48 in 1960 and 47 in 1961), but the number of nonbreeding adults

was unknown for the first summer, because at that time they were not all banded. In 1960 the total adult population was 98–100. In 1961, 47 pairs of Song Sparrows started breeding on Mandarte. Five additional territories were occupied by unmated males throughout the season, while two unmated males composed the floating population. Thus the total number of adults at the onset of breeding was 101.

Survey of territories. Every available place in the shrubbery was utilized by Song Sparrows during the course of the study. Helped by obvious perching trees and singing posts, territory-owner males kept sharply defined boundaries throughout the breeding seasons, although the aggressiveness of the birds gradually decreased toward the end of the summers. Territorial activity reached its minimum in late July and early August, when adults entered their postnuptial molt. Suthers (1960) distinguished between utilized area and maximum territory occupied by Song Sparrows inhabiting a lakeshore environment; on Mandarte territories the shrubbery were too small and tightly packed for this distinction to be made.

When they were feeding nestlings, adults mainly searched for food in the shrubbery. However, when foraging for themselves, they frequently entered the grassland adjacent to their territories, and occasionally the tidal zone also—the latter, to a certain extent, serving as a common feeding ground. It was only at the end of the breeding season, when caterpillars became scarce, that parents collected food items, mainly lacewings and other insects, from the grassland.

Territory boundaries in the meadows, unlike those in the shrubbery, were difficult to define. Areas in the former used by adults often overlapped; occasional fights occurred, although never with such vigor as in the shrubbery. These observations, and the obvious insignificance of the area of utilized grassland compared with the area of shrubbery defended by a pair (as will be shown later), suggest that these grassy areas should not be considered as part of territories, but rather as a constituent of home ranges.

In 1961, before the territories were measured, daily observations were made throughout the season to determine the boundaries. During that period the size of individual territories proved to be constant. Measurements were made with a 33-meter (100-foot) tape. Certain errors are due to the very irregular shape of some territories, especially at places where the dense vegetation precluded accurate measurements. However, estimations showed that these errors were not more than 5 per cent. Measurements of grassy areas for the calculating of home ranges were rather approximate, because the boundaries here were not sharply defined, there were no obvious landmarks, and the ranges overlapped.

Territory and home range measurements are shown on Table 1. Considering the shrubbery part of home range as real territory, the average

TABLE 1
 TERRITORY AND HOME RANGE MEASUREMENTS FOR BREEDING AND
 UNMATED MALES IN 1961
 (Measurements given in square meters)

<i>Status of males</i>	<i>Number</i>	<i>Area of territories</i>			<i>Area of home ranges</i>		
		<i>Min.</i>	<i>Max.</i>	<i>Av.</i>	<i>Min.</i>	<i>Max.</i>	<i>Av.</i>
Breeding	47	110	400	288	167	822	473
Unmated	5	65	105	82	(98	135	120) ¹

¹ Home range measurements for four unmated males. The fifth, which possessed 65 m² of shrubbery, utilized some 300 m² of grassland. However, the home range boundaries were too loose to take accurate measurements.

territory size for 47 breeding pairs was one tenth of the minimum for Ohio as reported by Nice (1943). Including grassy areas, the average home range size was still one fifth of the size of the Ohio minimum. Territories of the five unmated males were without exception smaller than the minimum for breeding pairs. Four of these males defended their territories throughout the season; in fact, they were still singing in late June and early July, when breeding males were very rarely heard. However, the fifth male did not show any sign of aggressiveness toward neighboring males. Two additional males were unable to establish territories; they stayed in the same general area of the island throughout the summer, apparently tolerated by territory-owning males.

As mentioned before, there was no correlation between the area of utilized grassland and that of defended shrubbery. Even when the latter was well below average, breeding pairs were able to rear two or three broods without any sizable grassland. On the other hand, one male was unable to obtain a mate with only 65 square meters of shrubbery, even though he also used more than 300 square meters of grassland with a home range area of ca. 365–375 square meters. Although features of the shrubbery might influence the size of individual breeding territories, the five unmated males, each defending an area of shrubbery of 105 square meters or less, possessed territories distributed over the island in a way that covered the range of all vegetation types. This suggests that the determining factor of successful mating was the amount of shrubbery defended by a male rather than the total area utilized.

Site tenacity and emigration. During the first summer 55 adult birds were banded—somewhat more than 50 per cent of the total adult population. Of these birds 29 survived the winter and started to breed in 1961. With one exception they all kept their old territories, apart from minor changes in boundary lines. One male, which stayed unmated through the summer of 1960, in the next summer moved to a neighboring territory where the owner had perished during the winter.

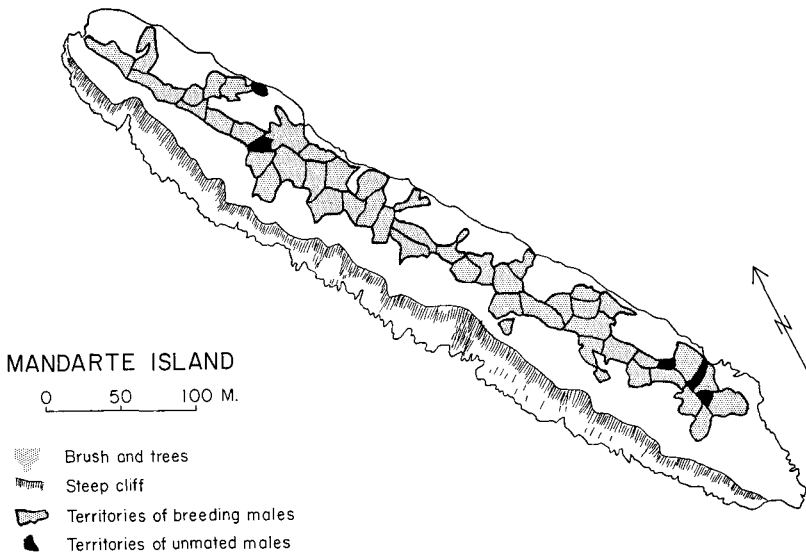


Figure 2. Map shows the arrangement of Song Sparrow territories.

Of the 113 young banded in 1960, 21 were recovered in 1961. Nineteen of these stayed on Mandarte Island, while two had emigrated to adjacent islands. Those young that stayed can be further divided in the following way: six breeding males, 11 breeding females, and two unmated males. All of them occupied places left vacant through adult mortality. In one area of the island, following a heavy loss of adults and their replacement by yearlings in 1961, the territories were completely rearranged, although the number of territories for this area remained unchanged. (Figure 2 shows the subdivision of shrubbery into individual territories in 1961.)

During the summer of 1961 there was only one example of territory desertion by a female, whose mate had disappeared in July. This female settled down in September on a territory ca. 150 meters away, where the owner had lost his mate in August. From the beginning of breeding in 1961 to the end of January 1962, the loss in adult population was 22 per cent. Vacant places caused by adult mortality during the summer were filled by young birds in the fall, which once their postjuvenile molt had been completed, showed signs of territoriality.

Emigration of young birds first occurred in late summer and lasted until October. In late August two Mandarte young, both from the first brood, were observed on Halibut Island, ca. 1,300 meters to the south. They showed definite signs of territoriality. These birds were followed shortly by one young from the second and three from the third brood, which also established themselves on Halibut Island. The males obtained territories, and stayed there through the winter. One young of unknown sex from the

second brood was recovered on 1 September six km to the west of Mandarte on James Island. Both of these islands are forested and support local Song Sparrow populations with lower densities when compared with Mandarte Island.

This first phase of emigration was markedly correlated with the revival of territoriality in autumn. It affected those young that already showed signs of increasing aggressiveness, even though they were unable to establish themselves on Mandarte, since previously vacant places had been filled by other young males. Following this period, territoriality gradually decreased, reaching its minimum during November and December. During this time territory owners, both old and young, usually stayed on their home ranges, although the surplus young population gathered in loose feeding groups of 5-10, frequenting the meadows and the abandoned nesting grounds of cormorants.

At the end of January 1962 definite signs of the revival of territoriality were observed. Singing was often heard, and frequent chasing occurred. Vacant places caused by winter mortality were already filled by first-year birds. There had been no further sign of emigration since the fall. There were approximately 55 young in excess, when compared with the breeding population in 1960 and 1961. As indicated by data from 1961, the second phase of emigration occurs in February and mainly in March, which is the period of spring territorialism and includes the final spacing and mating, before the onset of breeding. This spring emigration concerns young males left without a territory, as well as first-year females that could not settle down on an already established territory. It is worthwhile to note that there was no detectable immigration of Song Sparrows to Mandarte Island during 1961, and no indication that this had happened in 1960.

DISCUSSION AND CONCLUSIONS

Howard's original theory of the functions of territory has been continuously argued and modified since 1920, partly because of different ways of interpreting it, partly because of the very complex nature of territorialism. The object of territory defense—nest site, mating and feeding ground, etc.—varies from species to species, and even within a given species it is under the influence of seasonal changes and features of the habitat. Nevertheless, most contemporary authors agree on two main functions of the territory, *i.e.*, behavioral and ecological. The former mainly concerns pair formation and maintenance of a pair, while the latter may include the assurance of adequate food supply during certain parts of the annual cycle and/or the regulation of population densities. However, the behavioral and ecological functions are often so closely related that distinction between the two becomes very difficult.

Based upon these considerations the following questions suggest themselves:

1. Does territorial behavior play any significant role in the control of the Mandarte Island Song Sparrow population?
2. If so, is the minimum required territory size for successful mating and/or breeding determined by:
 - a. the amount of food available;
 - b. other features of the habitat, such as type and density of the vegetation, number of perching posts, exposure to prevailing wind, etc.
3. Or is the regulation mainly behavioral, the size of the territories depending upon the aggressiveness or tolerance of the individuals, thus assuring the owners of permanent mates, sufficient nesting sites, and the avoidance of interference during the breeding season.

On Mandarte Island the Song Sparrow population has remained at a high density for at least the last two years, presumably as a result of the suitable habitat, and the absence of severe mortality factors during the annual cycle, especially in the breeding season. Although quantitative data are not available for the years previous to 1960, observations carried out by other students do not indicate any significant changes in the population since 1957 (Drent and van Tets, pers. comm.). The unchanged environmental conditions on the island during the past 50 years would also favor relative stability in population numbers.

The territories, as shown above, have been remarkably smaller than those reported for this species on the continent. The fledging success during the last two years was higher (more than 60 per cent of the eggs laid) than in Ohio (ca. 36 per cent, Nice, 1937) and San Francisco Bay (49.3 per cent, Johnston, 1956). Nest destruction, nest parasitism, and predation did not play any important role in nestling mortality. The abundance and availability of food might be influenced by the vegetation, which varies from one territory to another; thorough investigation is necessary to find out whether starvation plays any substantial role in the less than 40 per cent egg and nestling losses, especially as the numbers of caterpillars, the main food item of nestling Song Sparrows, show a gradual decrease toward the end of the breeding season. Although there is no indication that the size of breeding territories is affected directly by the availability of food supply, the data are not quantitative enough to support final conclusions on the food value of territories on Mandarte Island.

On the other hand, observations, population counts, and the survey of territories suggest that territorial behavior plays an important, if not the main, role in the control of this local population. Under different conditions this function of the territory is not always obvious enough to be recognized. In an area with yearly changing physical and biological con-

ditions, with less suitable habitat, and with a significant annual immigration, the fluctuations in the breeding population may be substantial. In one year, because of favorable conditions, the habitat may become overcrowded, the territories will be relatively small and tightly packed, and hostility of the individuals will increase. On the other hand, following a bad year with low reproductive success, heavy mortality, and/or decreased rate of immigration, the population will be scarce, the territories loosely attached to each other with vacant places in the habitat, and the chance for encounter between neighboring birds relatively low.

Very rarely are conditions favorable for a length of time in one area for the same species, thus permitting high numbers for consecutive years with little fluctuations. But when this happens, the so far latent or less obvious function of territorial behavior in population control becomes operative. Where the suitability of habitats has been artificially raised, *e.g.*, by the provision of nest boxes, significant increase in breeding populations has occurred. This phenomenon was well demonstrated by experiments of Kluyver and Tinbergen (1953) in European titmice, and of von Haartman (1956) in Pied Flycatchers (*Muscicapa hypoleuca*). However, such an increase cannot be indefinite. With higher densities, under favorable conditions, the size of territories will decrease. This shrinkage in size is accompanied by an increasing resistance on the part of individuals, which in time will reach a point, beyond which no further decrease in territory size can occur. This procedure has been described in detail by Tinbergen (1957) in his discussion of the role of hostility (including both aggressiveness and avoidance) in the mechanism of dispersion.

That the same phenomenon can occur also under natural circumstances was shown again by Kluyver and Tinbergen (1953). In their study of titmice they found differential regulation of densities in neighboring, but basically different, habitats. In mixed woods, described as desirable for titmice, territories were relatively small, boundaries well defended, and the population showed small-scale yearly fluctuations. On the other hand, in adjacent, less favorable pine woods, territories were larger, with loose boundaries and less fighting, and the number of breeding birds changed significantly from one year to the other. Also, there was a detectable emigration from the mixed woods to the less favorable habitats with lower densities.

A similar situation due to habitat selection was described by Glass (1960) in the European Chaffinch (*Fringilla coelebs*). In this study, the difference in population densities between the stable populations in desirable habitats and the unstable ones exhibiting yearly fluctuations in less favorable habitats (and one-way emigration as a result of population

pressure) was still more pronounced than in the study of Kluyver and Tinbergen.

Apparently the same is true on Mandarte Island, where favorable conditions allowed a stable population with high density during at least the last two but presumably five or more years. The territories have become extremely small. They are tightly packed, and all available space in the shrubbery is being utilized. Because of the increased pressure, the yearly population surplus emigrates to adjacent islands with less desirable habitats for Song Sparrows, in a manner similar to that shown with the titmice and chaffinch. The emigration of Song Sparrows occurs in two steps as shown by population surveys and field observations. The first phase begins in late summer and reaches its peak during the autumnal territoriality. This involves mainly young males, which already show signs of territoriality, and cannot settle down since places vacant as a result of adult mortality have been filled. The second phase of emigration occurs during late winter and early spring, when territory establishment and mating takes place prior to the onset of breeding, and affects those yearlings that are still in excess and have a lower tolerance threshold toward crowdedness than the others. Similar two-phase emigration is characteristic of several territorial passerine species (Kalela, 1958).

This emigration of yearly surplus from Mandarte into less suitable habitats, with no detectable immigration from those areas, reveals the real importance of territorial behavior in the mechanism of population control at high density levels. While the size of individual territories is determined by the aggressiveness and tolerance of the neighboring males, and to a certain extent is under the influence of the vegetation cover, the success of obtaining a mate for the breeding season is dependent upon the amount of shrubbery defended by a male. Thereby the females, when rejecting or accepting a particular part of the habitat, may also play an important role in population control. By the acceptance of an appropriate amount of vegetation cover, the chance for successful breeding is increased, by preventing interference and possibly by assuring shelter and adequate food supply for the young. However, the role of the food on Mandarte Island is still to be investigated.

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SUMMARY

In 1960 a study was undertaken to reveal the controlling mechanism of

a local Song Sparrow population on Mandarte Island, British Columbia. The present paper discusses the role of territorial behavior in the regulation of breeding numbers.

This population is at a high density, and has showed relative stability over the past years. The survey of territories, observations on behavioral aspects, population counts, and the emigration of yearly surplus into neighboring, less attractive habitats indicate that territorial behavior plays the most important role in the regulation of Song Sparrows on this island. It has been concluded that the size of individual territories is determined by the aggressiveness and tolerance of the individuals, while the chance for successful mating is apparently dependent upon the size of shrubby area defended by a male.

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