

## CATASTROPHIC MORTALITY AND ITS POPULATION CONSEQUENCES

FRANK S. TOMPA

ADVERSE environmental conditions may be expected to affect the survival of surplus individuals to a greater extent than the well-established segment of a population (see Brown, *Wilson Bull.*, 81: 293-329, 1969). This assumption may apply especially to a species with a spatially closed territorial system that forces reserve individuals into peripheral habitats or otherwise into a subordinate position. Situations contrary to this may be treated as unplanned "natural" experiments without introduced arbitrariness and may provide valuable additional information on population processes.

In my discussion of the dynamics of an insular population of the Song Sparrow, *Melospiza melodia* (*Acta Zool. Fennica*, 109: 3-73, 1964), I referred to a late spring snowstorm that eliminated one-third of the adult population leaving the young surplus relatively intact and was the indirect cause of a substantial population increase one year later. This increase followed a period of relative stability at a high population level. In reference to this Lack (*Population studies of birds*, Oxford, Oxford Univ. Press, 1966, pp. 135-137) argues that "on the view that territorial behaviour operates like a partly compressible rubber disc, one would have expected the upper limit of numbers on Mandarte to be nearly constant. This appeared to be so in the first three years of Tompa's study, when the number of breeding pairs was respectively about 47, 47 and 44, . . . but in the final season 69 pairs bred, an increase of 50 per cent," and concludes that territorial behavior was ineffectual in regulating breeding density.

To evaluate Lack's argument I subjected to analysis hitherto unpublished material relating to movements, status, and fate of individual birds before and after the storm. These results, presented here, clarify some of the previously published inferences and illustrate other interesting aspects of the functioning of social systems (see also Brown, *ibid.*, pp. 306-308). For background information the reader is referred to the general discussion of this population (Tompa, *ibid.*). I have tried to avoid unwarranted repetition of facts and arguments.

Although the island, 6.26 ha in extent, lying off the Pacific Coast of southern British Columbia, is generally free of snow during the winter, a heavy snowfall in early March 1962 covered the most exposed parts of the island with a thick wet snow layer for 4 days, and particularly the northeast half of the island where the elongated shrubbery zone con-

tains practically all Song Sparrow territories. The southwest half with high cliffs and an open grassy plateau remained largely void of snow and accessible to ground feeders. The minimum temperature while the snow remained was  $-2.8^{\circ}\text{C}$ .

The storm occurred at the peak of the spring territorial activities, preceding by 2 or 3 weeks the usual onset of breeding on the island. One week before the snow the adult population contained 41 males and 25 females, all color-marked, and also a few unmarked birds whose sex and territorial status were known because of their strong site tenacity. The young population consisted of 73 color-marked yearlings. All the young females (19) were settled, and were mated to territorial males.

The status of the 54 young males was yet largely undetermined. Approximately one-third stayed constantly within the shrubbery zone, and were involved in active territorial contest. Changes in their territorial status and location over the island occurred frequently. A high hierarchical dominance position for several of these young males was noted as early as the preceding autumnal territorial period. The remaining two-thirds majority of the young males showed a low level of territorial motivation and were effectively kept away from the shrubbery zone by the more dominant and territorially active adult and young males. This apparently subordinate young population was concentrated in loose groups along the high cliffs and over the grassy plateau of the southwest half of the island. In addition there were approximately 15 unmarked young whose sex ratio and territorial status appeared similar to those of the marked young.

Before the storm a minimum of 44 territorial pairs were established over the island; unmarked birds brought this number closer to 50. The population contained no excess females, as all those that could not settle within a pair bond had left earlier. While the number of pairs was therefore about the same as during the previous years, the number of excess young males was still relatively high. The bulk of this surplus was expected to leave the island within a few weeks' time, by the start of general breeding in the population (Tomp, *ibid.*, pp. 17, 28).

*Losses.*—A complete population survey carried out as soon as the snow melted showed heavy losses (Table 1). Within the marked adult population male and female mortality was 34 and 36 per cent respectively, and as many as 42 per cent of young females perished. The 24 per cent losses among the young males were seemingly the lowest in the population.

As the territorial status of all other age and sex groups was stable before the storm, mortality was then further related to the varied social status of the young males. I was surprised to find that all the 13 missing

TABLE 1  
DIFFERENTIAL SURVIVAL OF SONG SPARROWS DURING THE SNOWSTORM

	Adults		Young males			Young
	♂ ♂	♀ ♀	Active	Inactive	Total	♀ ♀
Originally	41	25	(18)	(36)	54	19
Survived	27	16	5	36	41	11
Losses	34%	36%	(72%)	—	24%	42%

individuals had belonged to the territorially active minority, and made up roughly 70 per cent of its membership. As the status of some males in the group was uncertain, an exact percentage could not be calculated, but all three young males that had established themselves on territories before the storm perished. On the other hand all the nonterritorial, subordinate majority of the young males survived.

Direct exposure to the storm was not responsible for all the losses. As mortality affected only the territorially active population, and the partaking young males in particular, a high motivational state with resulting strong site attachment and lowered physiological conditions was presumably a critical factor. During the winter nonterritorial period adult and young birds fed regularly and freely over the grassy areas and along the cliffs of the southwest half of the island (Tompa, *ibid.*, p. 14). By the time the snow came only territorially inactive young males were regularly using these areas, which also remained relatively accessible to ground feeding while the snow covered other parts of the island.

Mortality presumably affected the unmarked birds similarly, as no significant change in the relative proportions of marked and unmarked birds was noted after the storm.

*Population changes.*—Six territorial pairs were eliminated, while females alone perished on 11 territories. Similarly, including the 3 young males that settled on territories before the storm, males alone died on 11 territories. With the unmarked birds included, nearly 30 territorial pairs were completely or partially eliminated, or almost 60 per cent of the total number of pairs.

As a consequence, well-established neighbor relationships in a tightly packed population were broken up all over the island. About a half-dozen individuals deserted their territories after losing their mates and settled some distance away. The stable territorial system that had characterized the population during the previous years was destroyed.

*Population recovery.*—Once the snow melted the population's recovery

was fast, though incomplete. With the survival of the nonactive majority of young males outside the territorial zone, the island had a substantial reserve male population. During the previous years, and presumably even before the study began, the tight territorial system effectively prevented excess intrusion and disturbance by young males in the spring, and forced most of them to emigrate before the onset of general breeding. Now with the resistance of the established population impaired, the surviving young males invaded the shrubbery. While 21 of them settled within a few days, in time nearly all the 41 marked excess males, and some unmarked, gradually established territories. Six marked young males that overwintered on neighboring islands also returned, and some of them settled. During this readjustment period a few territorial males died and about seven young males that had previously been subordinates left the island before the onset of general breeding (Tomba, *ibid.*, pp. 28-31).

This uninhibited settling of young males more than replaced the losses, increased the number of territories nearly 40 per cent, and lowered the average territory size. This shrinkage of the territories may be explained in part by the way new males establish themselves within the population under more usual conditions—the intruder first gains a small foothold and then gradually extends its boundaries. As all these newly settled males were nonterritorial yearlings and apparently subordinate before the snowstorm, a general submissiveness on their part may be another explanation.

With no surplus female population on the island, replacement of their losses was incomplete. Seven marked yearling females that overwintered on neighboring islands returned before breeding started, and about the same number of unmarked new females entered the territorial population. As the number of the latter was proportionally high, these spring returns probably included a few females born outside the population. Neighboring islands had a denser and more protective vegetation cover, which supported a sparser Song Sparrow population than Mandarte Island.

By the time conditions became relatively stable after the delayed start of breeding that year, the island had 44 breeding pairs, or slightly fewer than the number of pairs including unmarked birds before the snow. Altogether 17 established males were left without females, while 8 young males remained "floaters." These nonterritorial males, concentrated at the northwest point of the island, were recorded there before the storm. As that was the only part of the island where old territories remained intact, these males were prevented from settling there. Some of the floaters moved to other parts of the island later in the summer.

The effect of the highly unbalanced sex ratio, 69 males and 44 females, on the breeding season is described elsewhere (Tompa, *ibid.*, pp. 34–35).

*Delayed consequences.*—As the breeding season progressed, all non-territorial males still on the island were able to enter the shrubbery and settle, though they remained nonterritorial until the autumnal period of social activities. This passive way of settling by reserve males during the summers appeared regular within the population. Hence despite the death of a few territorial males during the summer, the number of established males showed a slight increase by the end of the breeding season.

During the autumnal territorial period, characterized by spacing movements and emigration of the young of the year, young females settled in larger than usual proportions on the island, filling vacancies on single male territories. Although final territory adjustments normally occur during the spring territorial period preceding breeding, this settling of young females in the fall temporarily increased the number of territories to an unusually high level and also restored a balanced sex ratio.

Thanks to an extremely high winter survival of both adult and young birds (Tompa, *ibid.*, pp. 42–47), the high population level remained unchanged when spring came in 1963. Moreover, as the chances for the most dominant young males to settle by simple replacement were now lowered, several of them established themselves through intrusion and by occupying small patches of shrubs away from the central shrubbery zone that had been unoccupied the previous years. The usual spring return of young females that had overwintered on neighboring islands filled a few of these new peripheral territories.

Thus when breeding started in 1963 the total number of pairs was 69, 57 per cent higher than in 1962, and 47 per cent higher than the more "normal" 1960 and 1961 level. In spite of the restored sex ratio among the territorial birds and the very low number of unsettled young males still on the island, the population showed signs of stress, indicating that the extreme population level was only a temporary situation. The onset of breeding was delayed by 1 week, and fights were frequent among neighboring birds. Hatching failure increased to 13.7 per cent from the 3.8 per cent level of the previous years. Seven territory desertions caused directly by interference and inadequate vegetation cover occurred in late spring and early summer, in contrast with the one desertion recorded in 1961 and four in 1962 after the snowstorm. These disturbances were the most pronounced early in the breeding season.

Although irrelevant to the general problem, it is of interest that when the island was revisited in September 1966, at least 12 marked birds

from the 1963 population were still alive and occupying parts of the island where they had been recorded before.

#### CONCLUSIONS

The differential mortality among the various sex, age, and social groups caused by the storm indicated the increased degree to which populations may be exposed to harmful environmental variables during periods of intense social activity. If such activity is to have a selective value, then long-term gains for the partaking individuals and/or their offspring must exceed temporary disadvantages.

Considering the more than 50 per cent increase in the breeding population of 1963, it is important to note that the effective increase in the number of territories occurred as early as the spring of 1962. Then the high number of small nonbreeding territories was the direct consequence of the storm that broke up the tight territorial system, making it possible for an extremely high number of previously nonterritorial and apparently subordinate young males to establish themselves. To this were added those nonterritorial males able to settle passively later in the summer after the breeding season was in progress. Thus the total number of established males within the population by the end of the summer (65-67) was only slightly below the number of breeding pairs (69) at the start of the season the following spring. As noted earlier, some of these pairs broke up soon afterwards, decreasing the number of effectively breeding pairs to 67.

One may speculate that most of these single males of the 1962 season would have deserted their territories in the prolonged absence of mates. As it was, they became stabilized by the passive settling of young females during the autumnal spacing movements. Thus the factors causing the increase in the number of territories and in the number of breeding pairs were clearly distinct. The first arose from a catastrophic situation that in turn prepared the ground for the secondary increase, which was part of a very regular spacing process. Although the overall increase in the number of breeding birds proved to be disadvantageous to the population, as shown by increased social intercourse, delay of breeding, and breakup of territories, the settling of females on single male territories also restored the balanced sex ratio evidently essential to the normal functioning of the population.

The primary functional value of territories and their forms may vary from species to species. Nevertheless because of its essential exclusiveness, territoriality may give the individual certain secondary advantages that have a significant positive feedback to the system. Such advantages are elimination of interference with mating and breeding, enhanced

population movements into unoccupied areas, and increased chances for finding a mate. All these are important aspects of population processes. In this light, instead of providing negative evidence to the occasional role of territorial behavior in the control of upper population levels as Lack (*ibid.*) implies, the circumstances under which the present population increase occurred pointedly emphasize such a role.

#### ACKNOWLEDGMENTS

While working in the field I enjoyed a Scholarship of the National Research Council of Canada. Logistic support of the Song Sparrow project was provided from National Research Council grants to M. D. F. Udvardy.

#### SUMMARY

A late spring snowstorm in front of the breeding season eliminated one-third of an insular Song Sparrow population. Territorially active young males were the most affected, while the survival among nonterritorial surplus males was complete. The disrupted territorial system contributed to the subsequent establishment of a very high number of small single male territories, as the replacement of female losses was incomplete. All these unmated territorial males obtained mates during the autumnal spacing movements of the young, causing a substantial increase in the number of breeding pairs for the following season in an already high population. Changes within the population following the storm, and the way the population increase occurred, emphasize the role territorial behavior may play in the control of upper population levels.

*Department of Zoology, University of British Columbia, Vancouver, British Columbia. Present address: Department of Biology, Memorial University, St. John's, Newfoundland, Canada. Accepted 8 June 1970.*