

“Prairie Grouse”, *Tympanuchus cupido* × *phasianellus*, Hybridization on Manitoulin Island, Ontario

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Greater Prairie Chickens started their range expansion from Wisconsin about 1900. They reached Sault Ste. Marie, Ontario, by 1925 and completed colonization of Manitoulin Island by 1945. In the fall of 1932, an irruption of Northern Sharp-tailed Grouse from the Hudson Bay Lowlands occurred. Residents of Manitoulin distinguished the two species and reported the presence of “square-tails” and “sharp-tails” in the winter of 1932-1933. There is no specimen evidence or verbal reports that Northern Sharp-tailed Grouse reached Michigan during that irruption. Prairie Sharp-tailed Grouse were in the northern peninsula of Michigan by 1930. In 1941, Michigan Department of Natural Resources made a planting of 37 Prairie Sharp-tailed Grouse on Drummond Island. Thence they spread east and the first lek was found at the west end of Manitoulin Island in 1952. By 1960, these birds had virtually colonized the whole island. Development of a hybrid index from the morphology of specimens of skins and skeletons from Manitoulin indicated that more than 50% of all birds in the 1960s were hybrids. In Michigan, less than 1% of the birds necropsied or checked in hunters’ bags were hybrid. It seems likely that ethological isolation broke down on Manitoulin Island. The booming display of the Prairie Chicken and the tail rattling display of the Sharp-tailed Grouse can be broken down into their component parts. They appear to be homologous to five discrete displays of the Spruce Grouse, grouped in different patterns in each of the two lek species. There was little hybridization between Prairie Sharp-tailed Grouse and Prairie Chickens that had lived sympatrically for thousands of years. Northern Sharp-tailed Grouse had probably never lived sympatrically with Prairie Chickens and the evolution of the perception of species distinctions may not have evolved to the point where hybridization was restricted to a rare event.

Key Words: Greater Prairie Chicken, *Tympanuchus cupido*, Sharp-tailed Grouse, *Tympanuchus phasianellus*, hybrids, behaviour, Manitoulin Island Ontario, Michigan.

In Ontario during the last 150 years the ranges of many species of birds have changed dramatically (Snyder 1957), mostly as a result of introduction and later intensification of European farming methods and logging. Their effect in Michigan and the adjacent areas of Ontario have altered the habitat and allowed the sequential invasion of Manitoulin Island by Greater-Prairie Chickens (*Tympanuchus cupido*) and two races of Sharp-tailed Grouse (*Tympanuchus phasianellus*).

Land use in the Manitoulin area is largely dictated by the geology of the Island. Almost horizontally bedded ordovician limestone slightly tilted toward the south is generally covered with shallow soils. Only about 12% of the island has soils deep enough for farming. Over 40 500 ha (about 25% of the island) is limestone plain which is largely open because of grazing by cattle and pulp-wood cutting. Both of these uses created and have steadily enlarged the prairie-like appearance of the landscape (Braffette and Brown 1948*). However, that land use is changing today and there is less grazing and pulp-wood cutting.

Although unlike the traditional range occupied by Prairie Chickens and Sharp-tailed Grouse prior to European settlement, it proved to be suitable and was colonized. In this paper I outline the history of the three invasions of Manitoulin Island by three forms of “Prairie Grouse” and offer some hypotheses concerning the development of the hybrid population. Although not

an inhabitant of prairie, I shall refer to the Northern Sharp-tailed Grouse (*T. p. phasianellus*) and the mixed population of Manitoulin Island collectively as “Prairie Grouse” in this paper.

History of Prairie Grouse on Manitoulin Island

Prairie Chickens and Sharp-tailed Grouse were sympatric over a wide area in southern Wisconsin in pre-and early settlement times (Schorger 1944). They were ecologically isolated, with the Prairie Chicken occupying the open Long-Grass Prairie and the Sharp-tailed Grouse confined to the Oak openings and brushy areas. With the advent of lumbering and settlement, new range appeared to the north, east and west of their historic distribution and extraordinary range expansions took place. Prairie Chickens moved west almost to the foothills of the Rocky Mountains and as far as one hundred and fifty kilometres north of Edmonton (Houston 2002). They also spread to the northeast, followed twenty years later by the Prairie Sharp-tailed Grouse (*T. p. campestris*), terminating on Manitoulin Island, Ontario.

Between 1875 and 1920 the original range of both species was being converted to farmland and new range in the north was being created by lumbering followed by fire (Hamerstrom et al. 1957). Parts of every county but not all townships in Wisconsin were affected.

Prairie Chickens

The first Prairie Chickens to enter the Upper Peninsula of Michigan presumably came from Wisconsin about 1900 (Ammann 1950*, 1957). They spread across the Peninsula reaching the western half of Chippawa County in 1923-1924. This county includes the north-eastern part of the Upper Peninsula adjacent to St. Joseph's Island and the Sault Ste. Marie area of Ontario.

Baillie (1947) wrote, "The first indication that these birds were expanding their range eastward from Michigan came from the west side of St. Joseph's Island, south of Sault Ste. Marie, where a few appeared about 1925. R. H. Burns of Sault Ste. Marie assured us that by 1946 the birds, although not plentiful, had moved over onto the Canadian mainland and were in occupation of a narrow belt of cleared land along the St. Mary's River up to a distance of three miles inland where the edge of the Pre-Cambrian Shield prevents their further progress." W. E. Gimbley (Ontario Department of Lands and Forests, now Ministry of Natural Resources, personal communication) saw some Prairie Chickens at Echo Bay, twelve miles east of Sault Ste. Marie in the late 1930s and W. St. John (L & F personal communication) said that they also reached the Kirkwood area north of Thessalon about that time. This invasion of this part of Algoma including Manitoulin Island by Prairie Chickens occurred a few years before the spectacular irruption of Northern Sharp-tailed Grouse of 1932-1933.

Some of the residents of Manitoulin Island still remembered in the 1950s the 1932 invasion of Sharp-tailed Grouse. John and Cecil Merrylees saw a flock of "Prairie Grouse" feeding on grain spilled from sleighs on Christmas Eve 1932, on the road west of Indian Point Bridge in Burpee Township. "The flock consisted mostly of 'sharptails' but some 'square' tails were included" (Baillie 1947). This was the first eyewitness account of both Prairie Chickens and Sharp-tailed Grouse occurring together on the Island. The Indian Point bridge is about 56 kilometres from the western end of the Island. It is unlikely that the Prairie Chickens reached this point during the first year of their presence on the Island. They had been advancing at an average rate of 13.5 kilometres per year in Michigan. Ammann (1950*) reported that they reached the lower Seney marshes in 1910-12 about 270 kilometres to the west. If their rate of advance was relatively steady they may have arrived on Manitoulin Island about four years earlier, about 1928. By 1932 there were probably several leks with breeding populations established on suitable range that lies between Meldrum Bay and Indian Point.

Baillie (1947*) also recorded five additional observations in the 1930s. Only one, from Larry Donaldson, refers definitely to "square" tails being seen near Gore Bay in Gordon Township about 1937. By 1939 they had apparently reached Great Cloche Island near Lit-

tle Current in Howland Township where W. Wilkinson reported seeing six to eight. They had moved about 55 km in seven years or at an average rate of eight kilometres per year. By 1942, they were reported on Ten Mile Point in Sheguiandah Township and at Manitowaning in Assiginack Townships by C. J. Young (Ontario Lands and Forests, personal communication). They had virtually colonized the entire island.

The only specimen of a Prairie Grouse preserved from the early invasion of the north shore of Lake Huron east of Sault Ste. Marie was collected by Professor N. Rae Brown in the Kirkwood Forest Management Unit north of Thessalon on 13 September 1942. It is a hybrid Prairie Chicken \times Sharp-tailed Grouse. Figure 1 maps the advance of the Prairie Chicken in the Michigan-Manitoulin area.

Northern Sharp-tailed Grouse

The breeding distribution of the Northern Sharp-tailed Grouse in Ontario, based largely on the reported location of leks, is confined to peatland muskegs and burns in the north. The First Nations people report leks within a few km of the Hudson Bay coast. Along the southern fringe of their breeding range they breed regularly south to the northern Canadian National Railway line. In some areas they breed further south to where better drained land-forms permit development of forest within which there are a few outlying muskegs large enough to support breeding populations; for example, near Matheson, Tionaga, and the Black Sturgeon area near Lake Nipigon.

There are areas of abandoned or little used cultivated land that lie adjacent or close to occupied muskegs but the Northern Sharp-tailed Grouse seems to be unable to colonize them. Their inability to adapt to grassland habitat perhaps explains their failure to persist in areas to which they irrupted in 1932-1933.

There are about 260 000² km of muskeg country in northern Ontario which forms the range of the Northern Sharp-tailed Grouse. In the northern part of this range there are annual fall migrations of these birds into the river courses and to the south particularly in the rockier western parts of Ontario.

Every few years some birds move into the Cochrane area where they come to the gravel roads for grit and are easily shot. When populations are exceptionally high, these fall migrations take the form of irruptions that carry the birds far to the south. Snyder (1935) suggests an irruption in 1865-1866. Fleming (1906) documents an irruption in 1896-1897 that carried birds as far south as Muskoka and Parry Sound Districts.

Snyder (1935) described in detail the irruption of Northern Sharp-tailed Grouse that started in mid-October 1932. By March 1933 the birds had penetrated to many localities in the Parry Sound District. A specimen was preserved which was taken as far south as Bracebridge in Muskoka District, but Snyder did not mention that they reached Manitoulin Island.

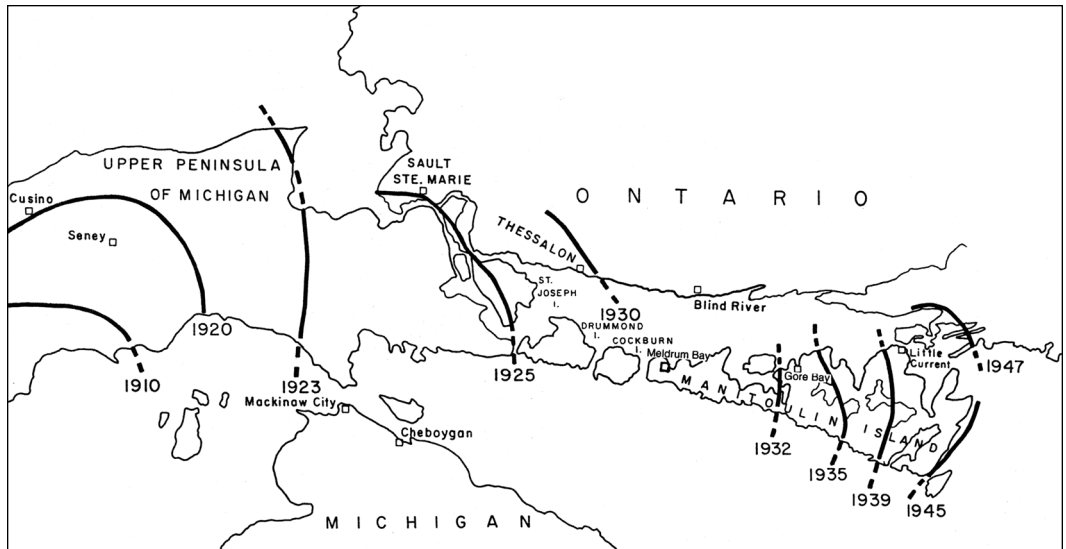


FIGURE 1. Approximate speed of advance of Prairie Chickens in northern Michigan and Manitoulin Island, Ontario.

Although no specimens of Northern Sharp-tailed Grouse from the Island were preserved from the 1932-1933 irruption, there is confirmation in the surviving files of the Department of Game and Fisheries¹ that they did reach Manitoulin Island in 1932. In a letter dated 20 February 1933 J. M. Parks, Superintendent at North Bay, writing of Sharp-tailed Grouse, "On November 5th last it was estimated that several hundreds of birds alighted in the town of Elk Lake, and at the present time small flocks are to be found in the vicinity of North Bay, Sudbury and the Manitoulin Island." He wrote a second letter on 6 March 1933, "Flocks have again been reported in the vicinity of Webbwood and the Manitoulin Island." During this irruption Northern Sharp-tailed Grouse spread over an area of approximately 100 000 square kilometres to the south of their normal breeding range in Ontario. That did not include the area south of the French and Mattawa Rivers where only a few flocks appeared, nor did it include the area the birds occupied in Quebec.

In the Sault Ste. Marie area, a flock of Sharp-tailed Grouse appeared near the school on Lot 11 Concession A of St. Joseph's Township during the winter of 1932 according to Murray Smith (Lands and Forests, personal communication). His brother, F. B. H. Smith, saw a flock of "Prairie Grouse" (species uncertain) about a hundred strong, in the same place in 1935.

Snyder (1935) listed seven observations of young birds or nests with eggs reported from south of the

normal breeding area in the summer of 1933. Although there may be an error in any one of these reports, Snyder pointed out, that the aggregate provides "unquestionable evidence that the species nested in territory occupied by the immigrants". However, by the summer of 1934 they had virtually disappeared from their irruptive range.

Prairie Sharp-tailed Grouse

The eastward spread of the Prairie Sharp-tailed Grouse occurred about twenty years after that of the Prairie Chicken. They were assisted in their movement by a release made by the Michigan Department of Conservation. Ammann (1947*) wrote of the Upper Peninsula: "By the early thirties Sharptails had spread to and become abundant in most suitable areas in the western third of the peninsula. Except for Drummond Island, however, they were not commonly noted in the extreme eastern end (Eastern Chippawa and MacKinac Counties) until 1949." Thirty-seven banded Sharp-tailed Grouse were trapped, moved and released in February and March 1941 near Johnstown on Drummond Island (Ammann 1947*). They undoubtedly bred that spring. In 1942 only one bird of fifteen shot was found to have been banded. The population resulting from this successful planting was probably responsible for the subsequent invasion of Cockburn and Manitoulin Islands. Four specimens preserved by H. McQuarrie and B. Smith were shot on Cockburn

¹ Amalgamated in 1946 with the Department of Lands and Forests, the name was later changed to the Ministry of Natural Resources (M.N.R.)

Island in November 1950. The birds were abundant there and had evidently been present for some years.

The first specimen of a Prairie Sharp-tailed Grouse on Manitoulin Island was a female shot by W. Ritching on the east bluff at Gore Bay in Gordon Township in 1948. This specimen, given to the author without a label, is now in the Royal Ontario Museum. It is a female in extremely worn plumage. Searches and intensive observations from blinds were carried out between 1949 and 1952 on known leks. No Sharptails were discovered until 1952; it seems likely that this female penetrated well ahead of the main invasion.

On 26 April 1952, I found a Sharp-tailed Grouse lek four kilometres west of Meldrum Bay in Dawson Township, Manitoulin. On 28 April 1952, there were fifteen birds present, four of which were females. Two birds were collected: one was a Sharp-tailed Grouse, and the second was a hybrid. Prairie Sharp-tailed Grouse probably had established their first leks on Manitoulin Island about 1950. On 25 April 1952, a single Sharp-tailed Grouse hen appeared at the lek at the airport near Gore Bay about 50 km from the west end of the Island. H. McQuarrie collected the first male Sharp-tailed Grouse recorded on the central part of the Island on the lek at Britainville, Campbell Township in 1953. Probably about this time males first arrived at the airport at Gore Bay. By 1960, Sharp-tail-like birds were abundant at the Gore Bay airport, Britainville, and in Billings Township where six specimens were collected on 24 September 1960.

In the spring of 1962 the first Sharp-tailed Grouse appeared at the east end of Manitoulin Island in Sheguiandah Township. John Budd (Lands and Forests, personal communication) found a dead bird that may have hit telephone wires beside the road but the species was still scarce. Only Prairie Chickens and hybrids appeared on the two leks in Sheguiandah Township that were studied in 1962. Figure 2 maps the advance of Prairie Sharp-tailed Grouse from Michigan to Manitoulin Island.

The Prairie Chicken stock had colonized, from St. Joseph's Island to eastern Manitoulin, a distance of 187 km in 20 years, an average of about nine km per year. It took the Prairie Sharp-tailed Grouse 21 years to spread from Drummond Island in their year of release to the eastern end of Manitoulin Island, a distance of 137 kilometres at an average speed of six km per year. They were substantially slower than the Prairie Chickens twenty years earlier.

The Hamerstroms (1951), summarizing Wisconsin recovery data, concluded, "...we are convinced... that Prairie Chickens really are somewhat more mobile than Sharptails most of the year." It would appear that if fidelity to the home lek or other behavioural factors did not interfere with changes in home range, Prairie Chickens could be expected to colonize new areas at a faster rate than Sharp-tailed Grouse. Another factor

must be considered. Prairie Sharp-tailed Grouse have replaced Prairie Chickens in most of Northern Michigan and the adjacent parts of Ontario. This would suggest that there is competition between the two species in this kind of range. It is likely that the Prairie Chicken was only able to colonize the Sault Ste. Marie-Manitoulin part of Ontario in the absence of competition from Prairie Sharp-tailed Grouse. The mechanisms of competition are at present unknown. It is possible that Sharp-tailed Grouse did not colonize this new range at the same rate as they might have done had the range been vacant of competitors.

History of Prairie Grouse in Northern Michigan

The same genetic stocks of Prairie Chickens and Prairie Sharp-tailed Grouse over-ran the Upper Peninsula of Michigan a few years before they reached Manitoulin Island but there seems to be no evidence that the northern race of the Sharp-tailed Grouse reached Michigan during its irruption in 1932-1933.

I have used Ammann's (1950*) unpublished report on the spread of both species in Michigan as a basis, with modifications according to his (personal communication) subsequent suggestions to estimate the years during which both species were present at the same time in each county.

Using only those years, Table 1 summarizes the data resulting from necropsies by game division biologists and checked in hunters' bags in the field in the Cusino area. Ammann (personal communication) suggested that some hybrids could have been missed before staff were aware that hybrids might be present. In the necropsy sample, 6 of 420 (1.4%) of the birds checked were identified as hybrids. In the Cusino field checks, only 4 of 1206 (0.3%) were identified as hybrids. Combining these hunter bag checks in fall with observations of living birds on their leks in spring, sixteen positive and eight probable hybrids were identified. There were three additional hybrid specimens shot in fall and one seen in spring on Drummond Island.

Johnsgard and Wood (1968) reported many hybrids from three provinces and seven states where the two species occur sympatrically. Their report indicates widespread casual hybridization but nowhere was a hybrid population described. It is clear that the hybrids recorded in Northern Michigan were similarly products of casual cross matings and that at no time did a hybrid population similar to that of Manitoulin Island develop.

We have two areas of range, both of which were occupied by the same genetic stock of Wisconsin Prairie Chickens, but those areas were initially invaded by a different stock of Sharp-tailed Grouse. Casual hybridization occurred in Northern Michigan with the Prairie Sharp-tailed Grouse, whereas a hybrid population resulted on Manitoulin Island with the Northern Sharp-tailed Grouse.

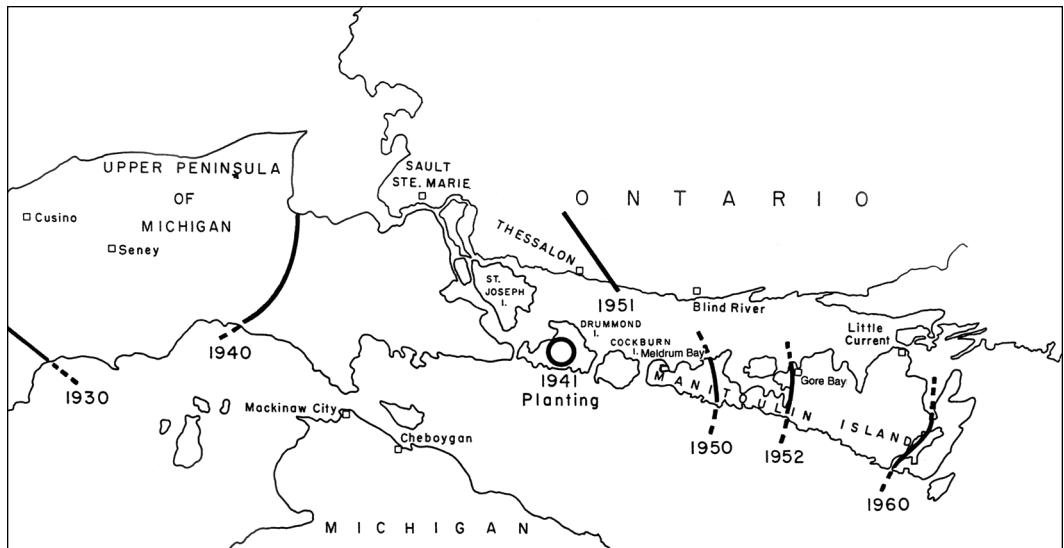


FIGURE 2. Approximate speed of advance of Sharp-tailed Grouse in northern Michigan and Manitoulin Island, Ontario.

Observations on Leks

Starting in 1951, watching from a blind on selected leks on Manitoulin Island, I made judgements on whether each male was a hybrid, a Prairie Chicken, undetermined or a Sharp-tailed Grouse. I used their plumage markings, aberrations in their displays and the colour of their booming sacks and toes. By 1951, Prairie Sharp-tailed Grouse had only reached the extreme western end of Manitoulin Island and none had appeared on the four leks intensively studied. Counts of these leks (Table 2) suggested that of 48 males present, 28 (58%) were hybrids, 16 (33%) were Prairie Chickens, 4 (8%) were undetermined, and none were Sharp-tailed Grouse. Those in the undetermined category had the appearance of Prairie Chickens but slight shortening of the pinnae, or occasional peculiarities of behaviour caused me to question their identity.

By 1962, Prairie Sharp-tailed Grouse had taken over at Gore Bay Airport. There were only 3 (23%) hybrids, no Prairie Chickens, but 10 (7%) apparently pure Prairie Sharp-tailed Grouse.

In 1961, on the extreme eastern end of the Island at the Sheguiandah lek, there were still 10 (83%) hybrids, 2 (17%) Prairie Chickens, and no Sharp-tailed Grouse. Much the same ratios prevailed at Sheguiandah in

1962 when 6 (85%) were hybrids and there was only 1 (15%) Prairie Chicken. However in 1964, Prairie Sharp-tailed Grouse had appeared at Sheguiandah and in 1966 at Ten Mile Point. The proportions of hybrids in each year for each lek studied ranged from 23% to 85% (Table 2).

Discussion

The hybrid frequency on Manitoulin Island amounts to more than 50% of the population (Lumsden in preparation) but in northern Michigan far less than 1%. There are thus significantly different rates of hybridization in these two areas. Prairie Chickens and Sharp-tailed Grouse do not produce hybrid populations wherever they have been sympatric. Mayr (1942) outlined four categories of isolating mechanisms, one or more of which can operate to maintain the genetic integrity of a population. They are: (1.) ecological isolation; (2.) ethological isolation; (3.) mechanical isolation; (4.) genetic isolation.

The hybrid population that developed on Manitoulin Island indicates that there could be no genetic, mechanical or ecologically isolating mechanisms operating. It is likely that ethological isolating mechanisms provided the most effective barrier between the species else-

TABLE 1. Number of Prairie Chickens, Sharp-tailed Grouse and hybrids from the upper peninsula of Michigan necropsied by Game Division biologists 1935-1957 and checked by field staff at Cusino 1939-1954.

	Prairie Chickens	Sharp-tailed Grouse	Hybrids
1935-1957 necropsies	49	371	6 ¹
1939-1954 field checks	110	1096	4 ²

¹ first hybrid identified in 1939

² two hybrids identified by G. A. Ammann

TABLE 2. Number of male hybrids, Prairie Chickens, Undetermined, and Prairie Sharp-tailed Grouse tallied on various leks in 1951 and 1952 and 1964–1966.

Lek	Hybrid	Prairie Chicken	Undetermined	Sharp-tailed Grouse
1951				
Gore Bay Airport	10 (55%)	4 (22%)	4 (22%)	0
Billing's Township	2 (33%)	4 (66%)	0	0
Britainville	6 (75%)	2 (25%)	0	0
Tustians Farm	10 (63%)	6 (37%)	0	0
Total	28 (58%)	16 (33%)	4 (8%)	0
1952				
Gore Bay Airport	6 (42%)	4 (29%)	4 (29%)	0
Sheguiahdah	6 (85%)	1 (14%)	0	0
Total	12 (57%)	5 (24%)	4 (19%)	0
1964				
Sheguiahdah	8 (67%)	1 (8%)	0	3 (25%)
1965				
Sheguiahdah	6 (60%)	1 (10%)	0	3 (30%)
1966				
Sheguiahdah	4 (50%)	2 (25%)	0	2 (25%)
10 Mile Point	4 (57%)	0	0	3 (43%)
Total	8 (53%)	2 (13%)	0	5 (33%)

where and that this broke down on Manitoulin Island.

In non-lek species, such as the Spruce Grouse (*Canachites canadensis*) males that display in isolation on their territories usually must respond at one time to no more than a single visitor of their own species. Thus, on the approach of a rival male the territory holder could react with one or more displays. On the approach of a female the male might respond with courtship displays (Lumsden 1961) and finally by copulation if the hen were receptive.

In a lek-species, however, where territories are very small and many males may be displaying in close proximity, a single male may have to respond simultaneously to a challenge from a dominant neighbour, to an invasion by a subdominant rival or to a visit by a receptive female. Each lek species has a complex display which seems to be appropriate in a variety of circumstances and which is performed endlessly. The lek display of the Prairie Chicken and the tail-rattling display of the Sharp-tailed Grouse are the multi-purpose displays which function in these complex social situations.

Schenkel (1956 and 1958) proposed that these multiple purpose displays of the above species are homologous with the tidbitting displays of many species of pheasant. I cannot agree with this. First, the tidbitting displays so far described for pheasants are all frontal displays, while the booming and tail-rattling displays are lateral in orientation. Second, one can hardly find a single component element in common between tidbitting and the grouse displays.

If we break down these multipurpose displays of lek species into their component parts and look for homologies in the displays of a solitary species (e.g., the Spruce Grouse), we find elements from four different Spruce Grouse displays – hooting, tail flick, strutting

and head and tail down displays are telescoped into the booming display of the Prairie Chicken. In the case of the Sharp-tailed Grouse, tail-rattling display elements from the tail swishing, strutting, head-jerk, and head and tail down displays appear. Table 3 summarizes how these elements are grouped. It is important to note that the multipurpose displays of Prairie Chickens and Sharp-tailed Grouse, while homologous with several displays of a solitary species, have the component elements so grouped that the two displays present totally different sounds and appearances to an observer. These differences constitute the behavioural isolating mechanism. Anyone who is familiar with the two species will recognize that it is possible to identify the lek, whether Prairie Chicken or Sharp-tailed Grouse, as far away as the birds can be heard, perhaps two kilometres. Sexually active hens would have no difficulty in locating the lek of their own species in an area of sympatry. Similarly, should a hen make a mistake and visit a lek of the wrong species, the courtship behaviour directed at her would normally tend to correct her mistake.

If these species-specific displays constitute the main isolating mechanism, it is likely that perception by the female of the differences must be present to make them effective. I suggest that the Prairie race of the Sharp-tailed Grouse (*Tp. campestris*) that may have lived sympatrically with Prairie Chickens for thousands of years, through selection, produced a biotype of female in which perception was very sharp. Females of the muskeg-dwelling Northern Sharp-tailed Grouse (*Tp. phasianellus*), which may never have lived in sympatry with the Prairie Chicken, were not subjected to this kind of selection. This may explain the breakdown of species isolation on Manitoulin Island and the production of a hybrid population.

TABLE 3. Elements in Spruce Grouse displays grouped in the booming and tail-rattling displays of Prairie Chickens and Sharp-tailed Grouse.

Spruce Grouse	Prairie Chicken		Sharp-tailed Grouse		
	Booming	Nuptial Bow	Tail Rattling	Cooing	Nuptial Bow
Hooting Display					
inflation of oesophagus	X		Seldom	X	
hooting vocalization	X		Seldom	X	
Tail Flick					
(inhibited locomotion)					
Rapid steps	X		X		
Tail Flicked open	X				
Wings lowered	X				
Strutting/Tail Swishing					
Spreading alternate sides of tail			X		
Wings lowered	X			X	
Inflation of oesophagus	X			X	
Head-Jerk or Squatting					
Wings held open and away from the body		X	X		X
Head and Tail Down					
Head and neck extended forward	X		X		

There are further factors that may have contributed to the production of hybrids. Snyder (1935) reported that the sex ratio of Northern Sharp-tailed Grouse that irrupted in 1932 was grossly distorted. Of the 65 specimens that were preserved in museums, the sex ratio was 74% females to 26% males, most of which were in their first year. Furthermore, the birds that reached Manitoulin Island had no traditional leks at which they could seek matings in the spring of 1933. It is apparent that leks of the resident Prairie Chickens in western Manitoulin attracted traditionless Northern Sharp-tailed Grouse. This occurred again when Prairie Sharp-tailed Grouse invaded Manitoulin Island in the early 1950s. They did not immediately establish leks of their own but appeared at the existing Prairie Chicken and hybrid leks.

An additional factor may have enhanced the opportunity for hybridization and perhaps reduced the influence of the male Sharp-tailed Grouse on the 1933 year class. A lek is composed of a group of males in which an hierarchy of dominance prevails. Repeated observations on both Sharp-tailed Grouse and Prairie Chicken leks have confirmed that only very few males perform all the matings. In some cases, a single alpha male may copulate with 75% of the females that visit the lek (Lumsden 1965*). Among Prairie Chickens, Robel (1967, 1970) reported that two males performed 89% of 121 copulations. The extent to which the Sharp-tailed Grouse males contributed to the 1933 year class would depend on their ability to achieve high status in the lek hierarchies. This would be difficult for them since most were less than one year old.

Snyder (1935) wrote that the Northern Sharp-tailed Grouse disappeared from their acquired range very rapidly and that by the winter of 1933-1934 there were

very few left. This population from the muskeg is apparently not adapted to life in grassland and it is likely that most disappeared from Manitoulin within a year. Some may have returned to the north and others died. The hybrids produced in 1933 and the Prairie Chickens were left to continue to interbreed and to colonize the rest of the Island.

Table 2 shows that during the invasion by Prairie Sharp-tailed Grouse (*Tp. campestris*), no males had reached the Gore Bay Airport by 1951. However, by 1962 77% of the 13 males present were Sharp-tailed Grouse. At the same time at Sheguiandah on the extreme east end of the island in 1962, there were no Sharp-tailed Grouse among the seven males present. By 1964, 25% of 12 males tallied there were Sharp-tailed Grouse. By 1966, the proportion of Sharp-tailed Grouse had risen to 33% at Sheguiandah and 10 Mile Point.

Field studies were not continued after 1970 but naturalists have maintained an interest in the "Prairie" Grouse of Manitoulin since. Observations made by Jerry Guild (Ontario Field Ornithologists News 1997) on the Gore Bay Airport on 15 April, 1997 yielded a count of 50 Sharp-tailed Grouse. Jean Iron (personal communication) recorded 75-100 Sharp-tailed Grouse on 15 April 2000; 30 on 12 April 2003; and 60 on 11 April 2004 at the Gore Bay Airport. No Prairie Chickens or hybrids were recorded in these years. No naturalist seems to have checked the "Prairie" Grouse on the eastern end of the island. In view of the success of Sharp-tailed Grouse in the Gore Bay area and the time lapse since the last checks, it seems likely that Sharp-tailed Grouse have now displaced Prairie Chickens and hybrids throughout the island.

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