

Plumage and Internal Morphology of the “Prairie Grouse”, *Tympanuchus cupido* × *phasianellus*, of Manitoulin Island, Ontario

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I made comparisons among populations of Greater Prairie-Chickens, Sharp-tailed Grouse and their hybrids on Manitoulin Island of pinnae length, breast, flank and tail feather patterns, tail graduations, wing chord, and skeletal characteristics. Estimates of the proportion of hybrids from these individual characters ranged from 32% to 60%. Lek behaviour of hybrids was a mixture of the patterns of the parent species. The colour of the booming sacks varied and displayed the range between the parent species. There was a tendency with time for the characters of Prairie Chickens to decline coincident with an increase in Sharp-tailed Grouse characters. Both Prairie Chickens and Sharp-tailed Grouse are lek species in which an alpha male may consume most of the matings. The speed with which morphological change took place in Manitoulin Island is to be expected where a non-random mating system of this kind prevails.

Key Words: Greater Prairie-Chickens, *Tympanuchus cupido pinnatus*, Sharp-tailed Grouse, *Tympanuchus phasianellus*, proportion of hybrids, morphology, behaviour, population changes, Heath Hen, *Tympanuchus cupido cupido*, species relationships.

The occupation of Manitoulin Island, Ontario, by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) and their hybrids with Northern Sharp-tailed Grouse (*T. p. phasianellus*) was essentially complete by 1945 and offers clues to species relationships. Trapping of these birds started in the winter of 1948-1949 and field studies continued intermittently until 1966, with hunting season collections continuing until 1970. Between 1943 and 1946, Prairie Sharp-tailed Grouse (*Tympanuchus p. campestris*) moved into the western end of the island and reached the eastern end about 1960 (Lumsden 2005).

Specimens of hybrids showed the full range of characters between Greater Prairie-Chickens and Sharp-tailed Grouse. The purpose of this study is to estimate the proportion of hybrids present in the Manitoulin Island population, its change with time and to describe its morphology. Manitoulin specimens are curated at the Royal Ontario Museum in Toronto.

Methods

Manitoulin specimens were sorted into three groups. The samples taken from 1949 to 1959 consisted of Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) and their hybrids with Northern Sharp-tailed Grouse (*Tympanuchus phasianellus phasianellus*). They included specimens from the western end of the island and later the eastern end near or on leks where no Prairie Sharp-tailed Grouse (*Tympanuchus p. campestris*) to that time had been recorded.

From 1960 to 1963, Prairie Chickens, hybrids and Prairie Sharp-tailed Grouse were present in all parts of the island. Between 1964 and 1970, Prairie Chickens had disappeared and the earlier hybrids were interbreeding with Prairie Sharp-tailed Grouse. For compar-

ison with the Manitoulin specimens, Prairie Chickens were borrowed from five museums with specimens from Manitoba, Saskatchewan, Alberta, Michigan, Wisconsin, Minnesota, Iowa, Montana, North and South Dakota, Nebraska, Illinois and Oklahoma. All the Northern Sharp-tailed Grouse were collected in northern Ontario.

Morphological Characters

Pinnae, breast, flank and tail feathers were collected from trapped birds that were released elsewhere. On the pinnae feathers from 9 to 11 mm of the proximal end of the shaft were white and were embedded in tissue. Measurements were taken from the terminus of the white on the shaft to the tip of the feather. Measurements were taken from study skins by sliding a thin ruler under the longest feather and reading from the skin to the tip.

The pinnae lengths were divided into five groups: Class 1: 84-72 mm; Class 2: 71-59 mm; Class 3: 58-46 mm; Class 4: 45-33 mm; and Class 5: 32-20 mm (Table 1). Feathers from the upper breast (Figure 1) (Table 2) and the lower flanks (Figure 2) (Table 3) were selected to represent the range of pattern variation seen in the three populations. These were arranged into five pattern classes ranging from the barred Prairie Chicken pattern (Class 1) to the acute-angled arrow-shaped pattern (Class 5) of the Sharp-tailed Grouse. The equivalent feathers on all specimens were matched with these patterns and a relevant value assigned. Figure 3 illustrates the steeply graduated tail of a male Sharp-tailed Grouse. Graduation was the length of the outer tail feathers subtracted from the length of the central tail feathers. Measurements were taken from where the feather emerged from the skin to the tip.

Division of the measurements of the degree of graduation of the tail into five groups were Class 1: 30-44 mm,

TABLE 1. Classes of length of the pinnae of male Prairie Chickens, the Manitoulin population and Northern Sharp-tailed Grouse.

Class	1	2	3	4	5	Total
Prairie Chicken	100 (77%)	30 (23%)	0	0	0	130
Manitoulin 1949-1959	7 (11%)	30 (39%)	11 (14%)	4 (5%)	24 (32%)	76
Northern Sharp-tailed Grouse	0	0	0	0	19 (100%)	19

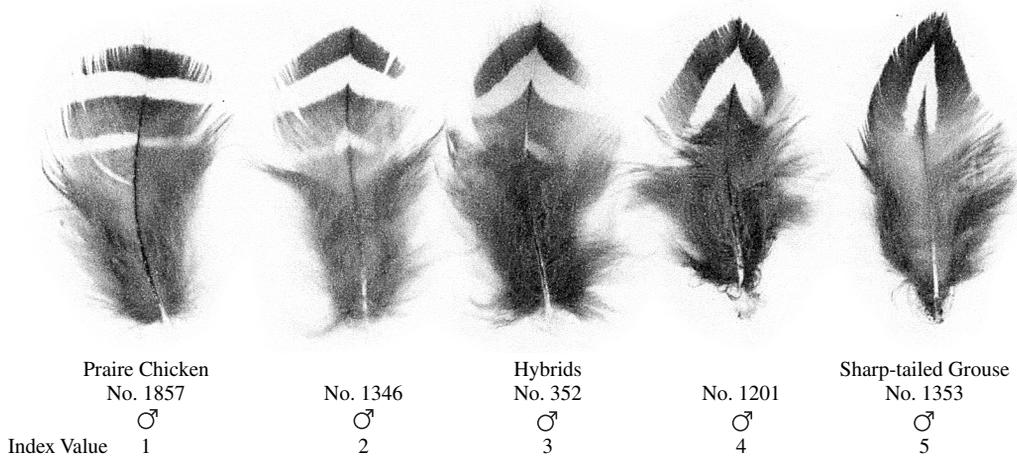


FIGURE 1. Upper breast feathers from a Prairie Chicken, three hybrids and a Sharp-tailed Grouse showing range of variation.

Class 2: 45-58 mm, Class 3: 59-73 mm, Class 4: 74-87 mm and Class 5: 88-102 mm (Table 4). Figure 4 illustrates the pattern on the tail feathers of a male Prairie Chicken, a female and four male Sharp-tailed Grouse. The pattern on the latter varies in males and is often an indicator of sex (Table 5).

There was a small overlap in the length of the wing (chord) between Prairie Chickens and Northern Sharp-tailed Grouse. The wing lengths were divided into Class 1: 239-230 mm; Class 2: 229-220 mm; Class 3: 219-210 mm; Class 4: 209-200 mm; and Class 5: 199-190 mm (Table 6).

Skeletons were saved from as many specimens as possible. Measurements were taken from the tip of the ilium process to the ventral surface of the pubic bone. In cases where the ilium process projected below the pubic bone, a minus value was assigned. Figure 5 shows the lateral view of the ilium and ischium of Prairie Chickens, Heath Hens (*Tympanuchus cupido cupido*), (see note page 000) and Northern Sharp-tailed Grouse. Size classes summarized in Table 7 were as follows: Class 1: -2.5- +0.7 mm; Class 2: 0.8-4.0 mm; Class 3: 4.1-7.3 mm; Class 4: 7.4-10.6 mm; and Class 5: 10.7-13.9 mm. The vertebral column consists of a

TABLE 2. Classes of patterns on the upper breast feathers of male Prairie Chickens, the Manitoulin Island population and Northern Sharp-tailed Grouse.

Class	1	2	3	4	5	Total
Prairie Chickens	175 (100%)	0	0	0	0	175
Manitoulin 1949-1959	14 (42%)	9 (27%)	6 (18%)	3 (9%)	1 (3%)	33
Manitoulin 1960-1963	8 (12%)	8 (12%)	12 (19%)	9 (14%)	27 (42%)	64
Manitoulin 1964-1970	2 (4%)	5 (9%)	11 (21%)	11 (21%)	24 (45%)	53
Northern Sharp-tailed Grouse	0	0	0	0	66 (100%)	66

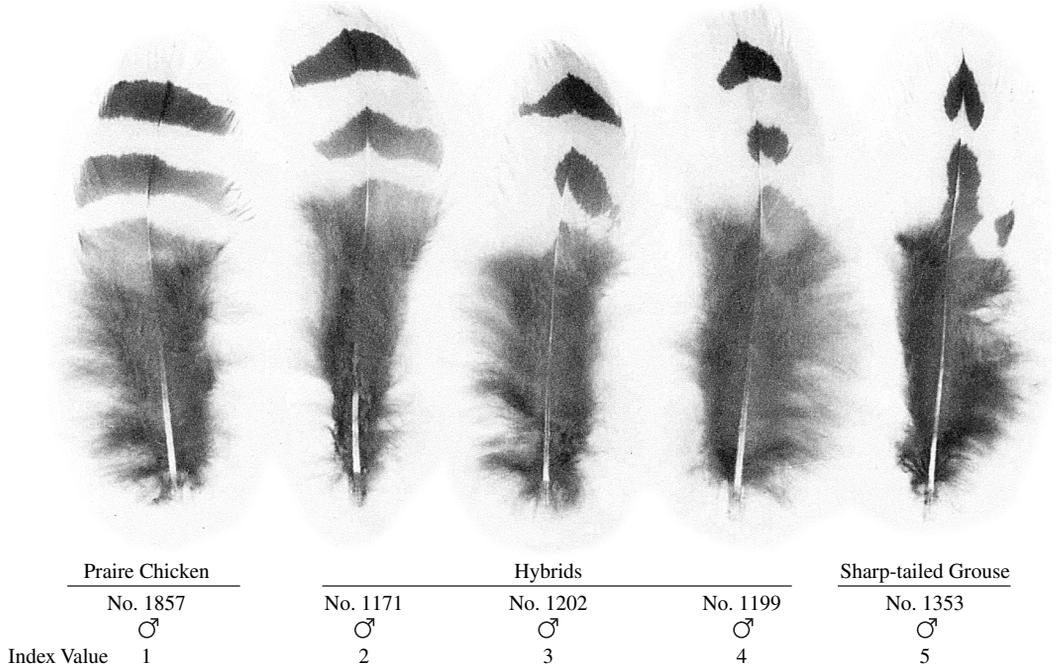


FIGURE 2. Lower flank feathers from a Prairie Chicken, three hybrids and a Sharp-tailed Grouse showing range of variation.

TABLE 3. Classes of patterns on the feathers of the lower flank feathers in male Prairie Chickens, the Manitoulin Island population and Sharp-tailed Grouse.

Class	1	2	3	4	5	Total
Prairie Chickens	174 (100%)	0	0	0	0	174
Manitoulin 1949-1959	11 (33%)	11 (33%)	2 (6%)	2 (6%)	7 (21%)	33
Manitoulin 1960-1963	5 (8%)	3 (4%)	7 (11%)	7 (11%)	42 (66%)	64
Manitoulin 1964-1970	0	4 (7%)	3 (6%)	8 (15%)	38 (72%)	53
Northern Sharp-tailed Grouse	0	0	0	3 (4%)	63 (95%)	66

TABLE 4. Degree of graduation of the tail of male Prairie Chickens, the Manitoulin population and Northern Sharp-tailed Grouse.

Class	1	2	3	4	5	Total
Prairie Chickens	144 (99%)	2 (1%)	0	0	0	146
Manitoulin 1949-1959	39 (67%)	13 (22%)	4 (7%)	2 (3%)	0	58
Manitoulin 1960-1963	5 (16%)	3 (9%)	13 (40%)	7 (22%)	4 (13%)	32
Manitoulin 1964-1970	0	2 (11%)	8 (42%)	9 (47%)	0	19
Northern Sharp-tailed Grouse	0	0	0	29 (39%)	45 (61%)	74

TABLE 5. Frequency of males from Manitoulin Island classified as Sharp-tailed Grouse by criteria other than the tail pattern and as hybrids, which showed a pattern of lines parallel to the shaft on the central tail feathers.

	Classified as Sharp-tailed Grouse		Classified as Hybrids	
	With Pattern	Without Pattern	With Pattern	Without Pattern
1949-1959	1	0	0	39
1960-1963	4	13	2	28
1964-1970	7	3	5	21
Total	12 (43%)	16 (57%)	7 (7%)	88 (93%)

TABLE 6. Classes of the length of the wing (chord) of male Prairie Chickens, the Manitoulin population and Northern Sharp-tailed Grouse.

Class	1	2	3	4	5	Total
Prairie Chickens	31 (20%)	105 (69%)	17 (11%)	0	0	153
Manitoulin						
1949-1959	0	11 (36%)	14 (47%)	5 (17%)	0	30
Manitoulin						
1960-1963	0	8 (13%)	37 (60%)	16 (26%)	1 (2%)	62
Manitoulin						
1964-1970	0	2 (4%)	16 (31%)	22 (42%)	12 (23%)	52
Northern Sharp-tailed Grouse	0	0	2 (2%)	58 (73%)	20 (25%)	80

TABLE 7. Distance from the tip of the ilium process to the ventral surface of the pubic bone in male Prairie Chickens, the Manitoulin population, and Sharp-tailed Grouse.

Class	1	2	3	4	5	Total
Prairie Chickens	27 (87%)	4 (13%)	0	0	0	31
Manitoulin						
1949-1959	12 (36%)	11 (33%)	7 (21%)	3 (9%)	0	33
Manitoulin						
1960-1963	2 (4%)	5 (10%)	6 (12%)	9 (18%)	28 (56%)	50
Manitoulin						
1964-1970	0	0	3 (9%)	12 (34%)	20 (57%)	35
Northern Sharp-tailed Grouse	0	0	0	11 (28%)	28 (72%)	39

variable number of bones, particularly among the hybrids. I follow Campbell and Lack (1985) in their definitions of subdivisions. The cervical or neck vertebrae are free with the posterior one carrying a floating rib. The thoracic or dorsal vertebrae carry ribs articulated through sternal ribs with the sternum.

Four thoracic vertebrae are normally fused to one another but a fifth is free. The sixth is fused to the lumbar vertebrae and carries a rib that articulates with the neighbouring sternal rib but not directly with the sternum. The lumbar and sacral vertebrae, which form the synsacrum, are fused to one another but some to the ilium. I have counted as caudal or tail vertebrae those that are free. However, the number varies with age. The anterior one may fuse with the synsacrum in old birds. I did not include in Table 8 very young birds that

had not completed fusion of the synsacrum. The vertebral column ends with the pygostyle.

Results

Length of the Pinnae

Prairie Chickens have a tuft of feathers 70-85 mm long on the sides of the neck above the anterior edge of the booming sac. On the Sharp-tailed Grouse, the equivalent feathers are only about 23 mm long. Table 1 presents the number of birds with pinnae in each class for Prairie Chickens, Manitoulin Island specimens, and Northern Sharp-tailed Grouse. Because 77% of the Prairie Chickens are in Class 1, we should consider that 77% of 7 Manitoulin birds are also Prairie Chickens leaving only two hybrids in that class. In Class 2, there are 30 (23%) of the Prairie Chickens. Therefore, 23%

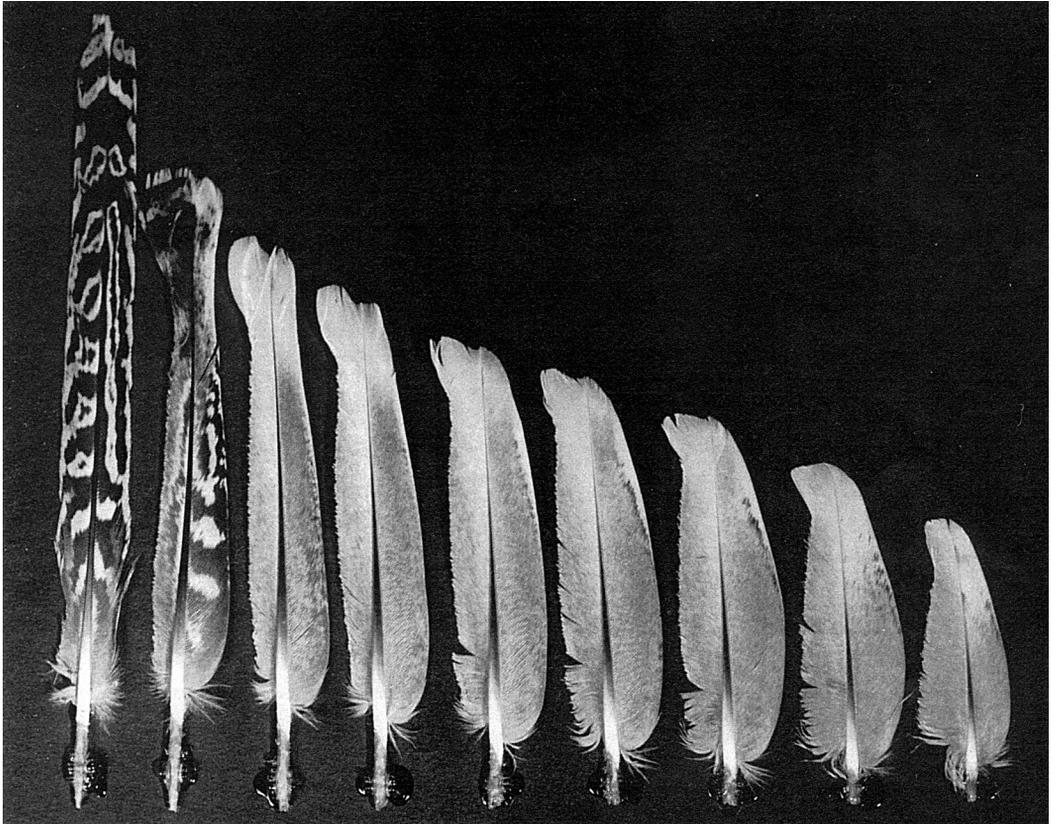


FIGURE 3. Feathers illustrating the steeply graduated tail of a male Sharp-tailed Grouse.

of 30 Manitoulin birds must be considered to be Prairie Chickens, leaving 23 hybrids. All the Manitoulin birds in Class 3 and 4 must be considered hybrids, totalling 15. All the Sharp-tailed Grouse were placed in Class 5 so we must consider the 24 Class 5 Manitoulin Grouse as Sharp-tailed Grouse. Left are 40 probable hybrids out of 76 specimens from Manitoulin or 52%. It was unfortunate that nearly all specimens collected in fall during hunting seasons of 1960 to 1970 were molting with pinnae and tail feathers not fully grown.

Fred and Frances Hamerstrom graciously let me measure their collection of 275 pinnae of Prairie Chickens collected in Wisconsin. The mean for those Wisconsin specimens was 77.7 mm whereas the maximum for Manitoulin birds was 75 mm.

Pattern on the Upper Breast Feathers

As all Prairie Chickens were assigned to Class 1 (Table 2), we must assume that all Manitoulin specimens in Class 1 were also Prairie Chickens. All Sharp-tailed Grouse fell into Class 5, therefore all Manitoulin birds in Class 5 should be considered to be Sharp-tailed

Grouse. The remaining 74 Manitoulin grouse constituting 49% of the sample can be regarded as hybrids.

Patterns on the Lower Flank Feathers

All Prairie Chickens were placed in Class 1 (Table 3), so we must consider all the Manitoulin specimens falling into this class as being Prairie Chickens. In Class 4 only 4% were Sharp-tailed Grouse leaving 16 hybrids. With Class 5 birds from Manitoulin, all but 3 (5%) must be considered as Sharp-tailed Grouse. There were 49 hybrids among the Manitoulin sample or 32%.

Tail Graduation

The tail feathers of a Sharp-tailed Grouse are very steeply graduated. The outer pair is only about 35% of the length of the central ones. In the Prairie Chicken, the tail is almost square with the outer rectrices measuring about 71% of the pair at the centre. The degree of graduation was the difference in length between the outer and central pair. It should be noted that the central pair of tail feathers in both species does not emerge from the tissue on the same plane as the eight pairs of rectrices. They grow on the same plane as the upper tail

TABLE 8. Counts of cervical, thoracic, synsacral and caudal vertebrae of Prairie Chickens, the Manitoulin populations and Sharp-tailed Grouse, all years and both sexes combined.

	Cervical Vertebrae		Thoracic Vertebrae			Synsacrum			Unfused Caudale			Number of birds in the sample
	15	16	5	6	7	11	12	13	5	6	7	
Greater Prairie Chicken	33	0	0	38	0		13	31	19	11	0	38
Manitoulin Population	56	2	1	28	6	2	21	16	19	24	1	58
Sharp-tailed Grouse	53	0	0	47	1*	4	46	3	0	31	8	53

* one extra thoracic but missing one lumbar

coverts and should properly be recognized as modified tail coverts. Table 4 presents the measurements broken down into five classes. As 44 of the Manitoulin birds were placed in Class 1 with 99% of the pure Prairie Chickens, there is a possibility that none of them were hybrids. Two (1%) of the Prairie Chickens were placed in Class 2. A few of the Class 2 Manitoulin birds may have been pure Prairie Chickens. Adjusting their numbers by 1% should provide an estimate of 17 hybrids, 29 (39%) of the Sharp-tailed Grouse were placed in Class 4. The number of hybrids in Class 4 must be reduced from 18 to 11. In Class 5, the number of true hybrids is likely to have been 2. Most of the specimens in Class 5 were collected during the molt hence the small sample size. Out of 109 Manitoulin specimens, 55 or 50% do not conform to this character of either parent species and can be considered hybrids.

Tail Pattern in Sharp-tailed Grouse

The central tail feathers of many male Sharp-tailed Grouse (e.g., #217, Figure 4) are distinctive with lines running parallel to the shaft. Females have irregular bars running across the feather. A proportion of the males lack the line pattern and have a barred pattern that is somewhat similar to that of a female (Figure 4). About 86% of the Prairie Sharp-tailed Grouse males have the distinctive line pattern; 14% do not (Snyder 1935; Manwiler 1939). In the male Northern Sharp-tailed Grouse I have examined, 12% are lacking the lines running parallel to the shaft. Examination of the specimens from Manitoulin Island did not adhere to the above pattern. Of 28 males classified as Sharp-tailed Grouse by other criteria, one would expect that 3 (12%) or 4 (14%) would lack the line pattern. In fact, 57% were without this character, a rate four or five times higher than expected. Of males classified as hybrids, 93% lacked the line pattern (Table 5).

The dorsal surfaces of the rectrices of male Sharp-tailed Grouse are very pale grey and are white at the tips. In hybrids, this part of the tail is a darker grey even in

those that approach Sharp-tailed Grouse in other characters. Prairie Chickens have all the rectrices and even the central modified tail coverts dark in colour with some lighter coloured bars or spots.

Length of the Wing

The lengths of the wings of Prairie Chickens and Northern Sharp-tailed Grouse overlap slightly, but the former average distinctly larger (Table 6). There were no Manitoulin birds in Class 1. In Class 2, 69% were Prairie Chickens, leaving 7 probable hybrids. In Class 3, of the 67 Manitoulin specimens, about 14% could be either Prairie Chickens or Northern Sharp-tailed Grouse, leaving 58 probable hybrids. Class 4 contained 43 Manitoulin specimens but there were 58 (73%) Northern Sharp-tailed Grouse, leaving 12 probable hybrids. Class 5 contained 25% of the Northern Sharp-tailed Grouse, therefore 10 of 13 Manitoulin birds were most likely to be hybrids. Those adjustments produced an estimate of 60% hybrids.

Distance from the Tip of the Ilium Process to the Pubic Bone

There is a substantial difference in the shape of the pelvic area between the Prairie Chicken and the Northern Sharp-tailed Grouse. In the former, the ilium process projects ventrally so that it overhangs the ischium and occasionally even projects beyond and below the pubic bone (Figure 5). In the Northern Sharp-tailed Grouse it projects laterally, barely obscuring the ischiadic foramen. Table 7 records that 87% of the Prairie Chickens were in Class 1. We can assume that only 2 of the 14 Manitoulin birds in Class 1 were hybrids. In Class 2, 13% must be regarded as Prairie Chickens leaving 14 probably hybrids. All 16 Class 3 Manitoulin birds were hybrids. Among the Sharp-tailed Grouse, 28% were in Class 4, so our estimate of hybrids is 17. As Class 5 contained 72% of the Sharp-tailed Grouse, we can estimate only 14 of 48 from Manitoulin as hybrids. Thus, 63 Manitoulin specimens were probable hybrids constituting 53% of the 118 samples.



FIGURE 4. Central rectrices from a male Prairie Chicken, one female and four male Sharp-tailed Grouse showing variation in markings.

Vertebral Column

Skeletons available, not all complete, were 38 Prairie Chickens, 58 from the Manitoulin population and 53 Northern Sharp-tailed Grouse. Table 8 summarizes the numbers of vertebrae in each sector of the spine for the three populations. The only variation in the cervical vertebrae occurs among the Manitoulin birds, 2 of which had an extra cervical vertebra. Counts of the thoracic vertebrae among the Manitoulin specimens revealed that one bird possessed only 5 but six had 7 (17% of the series). Among the caudal vertebrae of all three populations there was variation. None of the Prairie Chickens had seven, none of the Northern Sharp-tailed Grouse had five, but nineteen hybrids had five and one had seven.

Not only is there variation in the number of vertebrae in each sector of the spine of the Manitoulin birds, but there is also variation in the structure of the bones. Table 9 summarizes six categories of aberrations that appeared in the vertebral columns. Of the 38 Prairie Chickens studied, three (8%) had aberrant structures. Of the 58 Manitoulin specimens, 24 (41%) were abnormal in structure. Among the Northern Sharp-tailed Grouse, two (4%) of 53 showed abnormalities. Many of those aberrations might not affect the functioning of the bird as far as survival was concerned. More serious abnormalities such as fusion or missing vertebrae might influence survival, possibly in situations of escape from avian predators. More serious but unmeasured in this study would be possible aberrations in

TABLE 9. Number of specimens with aberrant structures in the vertebral column in Prairie Chickens, the Manitoulin population and Sharp-tailed Grouse.

Category of aberrance	Prairie Chicken	Manitoulin Population	Sharp-tailed Grouse
Five dorsals fused	1	2	0
All six dorsals fused	0	3	0
Vestigial rib on the anterior lumbar	0	9	1
One missing lumbar	0	1	0
Incomplete parapophyses connecting the lumbar with the ilium	2	8	1
Posterior dorsal not properly fused to the lumbar	0	1	0
Total	3	24	2

muscle tracts, mixed behavioural signals or improper responses to external threats.

In mature Prairie Chickens there are five or six free caudal vertebrae (Table 8). In Sharp-tailed Grouse there are six or seven. The evolution of the tail rattling display in the latter would likely have carried with it a change in the mobility and muscular structure of the tail, hence the increase in the length of the tail and its capacity for movement. The pygostyle is generally considered to be composed of a number of fused caudal vertebrae. As both these species have eight pairs of rectrices, it may be reasonable to assume that the pygostyle is composed of at least eight fused caudal vertebrae.

Behaviour

Schwartz (1945) gave a very complete description of the booming display of the Prairie Chicken. Typically its component parts consist of raising the pinnae vertically above the head, rapid stomping of the feet while standing still or running forward, raising or lowering the head, inflating the oesophagus so that the orange "booming sacs" are distended; a rapid opening of the tail feathers, which produces an audible click, slight lowering of the wings but retaining the carpal joint within the covering flank feathers, and uttering three "booming" notes which sound like blowing over the open neck of a large bottle. This call may carry for several kilometres. The homologous tail rattling display of the Sharp-tailed Grouse consists of holding the horizontal body high off the ground on extended legs, lowering the head, raising the feathers dorsal to the cervical apteria, exposing the purple booming sacs, extending the wings from the body sometimes at full stretch with a downward curve of the primaries, erecting the tail at least vertically and often tilted slightly forward, spreading each side of the tail alternately at high speed making a loud rattling sound, and uttering a note that sounds like a cork being withdrawn from a bottle or a shrill "chilk" or hoarse "cha" call.

A second display homologous with the "booming" segment of the Prairie Chicken display is called "cooing". The bird stands still, extending the neck forward and slightly upward, inflating the oesophagus and hence distending the purple cervical apteria, bowing

the neck slightly downward and uttering a loud cooing note, usually keeping the carpal joint of the wing covered by the flank feathers (Lumsden 1965*).

Those hybrids that most nearly resembled Prairie Chickens produced the booming display, sometimes typically but frequently with three weak notes and some omitted the third note. One hybrid boomed with a single note, drooping his wings as he uttered and spread his tail with an audible hissing sound.

Another hybrid cooed instead of booming: he held his wings slightly open but flicked them fully open, spreading his primaries while vibrating his tail without the volume of rattling in a pure Sharp-tailed Grouse. He produced an audible click with his tail at the end of this performance. Another hybrid, when cooing, uttered a double note. A Prairie Chicken-like hybrid made a rustling sound with his tail when booming and extended his wings slightly, retracting them at the third booming note. A Sharp-tailed Grouse-like hybrid produced three wheezy notes in his tail-rattling display. There was much confusing variation in the displays of hybrids and individuals were not as consistent in the component parts of their display as the two parent species.

Colours of Booming Sacs and Feet

The resonance of the booming and cooing calls is produced by inflation of the oesophagus that distends the coloured skin of the cervical apteria. In Prairie Chickens, these booming sacs, or timpani as they are sometimes called, are orange in colour with a narrow pink rim adjacent to the feathers. In Northern Sharp-tailed Grouse (*T. p. phasianellus*), the booming sacs are smaller than in Prairie Chickens and are purple. At the height of the mating season they may be almost as dark as blueberries. Those of the Prairie Sharp-tailed Grouse (*T. p. campestris*) are much paler and are pinkish-purple in colour. The timpani of hybrids are very variable in colour. Those in the middle of the cline between the species may have a muddy violet edge with one to three small dull orange patches. Others may have a reduced orange-yellow patch with an enlarged dusky pink rim.

Prairie Chickens have dusky orange toes during the breeding season. In Sharp-tailed Grouse, they are grey. Hybrids varied from orange through yellowish orange, to yellowish-grey to grey coloured feet. All these Prairie Grouse seem to molt the pectinations of their toes in mid-April and the displaying males, toward the end of the display period, show considerable wear on their nails.

Discussion

The hybrid indices summarized in Tables 1-4, 6-7 suggested that the proportion of hybrids in the Manitoulin population was between 32% and 60%. Certain features of the pinnae and tail suggest that hybridization may have been more extensive than this. Unexpected in the morphology of the Manitoulin Prairie Grouse was the relatively short pinnae of the population. That none reached the mean length of 77.7 mm of Wisconsin Prairie Chickens was a surprise. The longest measured 75 mm. Genetically, the Manitoulin birds are descended from the Wisconsin stock, 20 to 30 years before this study began and several hundred kilometres removed. This strongly suggests that hybridization on the island was more extensive than indicated by the other hybrid indices. The line pattern on the tail of Northern Sharp-tailed Grouse was missing in a proportion 4 or 5 times that expected of Sharp-tailed-type Manitoulin Grouse. Perhaps it is not unexpected that 93% of those classified as hybrids should lack the line pattern. This feature is a secondary sexual character that may be more readily modified by hybridization than primary characters.

The steep graduation of the tail occurs in both sexes of Sharp-tailed Grouse and is therefore not a secondary sexual character. The trends in measurements do not completely conform to the pattern shown in other characters. One might expect that in Class 5 (Table 4) in 1964–1970 the influence of Prairie Sharp-tail genes might produce a more steeply graduated tail. Perhaps this unusual tail structure is not sufficiently integrated in the gene matrix of the species to resist the more conventional square tail of the Prairie Chicken genes in hybrids.

Tables 2-4, 6 and 7 showed a number of trends. In the first period, 1949–1959, there was a tendency for hybrids to cluster toward Class 1 and 2 on the Prairie Chicken end of the scale. By the third period, 1964–1970, the clustering was toward Class 4 and 5 or the Sharp-tailed Grouse end of the scale.

In Class 1 and 2 there was a strong tendency for the number of specimens to decline in each period while the number in Class 4 and 5 showed an increase. The latter is probably because Prairie Sharp-tailed Grouse had completely colonized the island and were contributing their genes to the mix. Observations indicated that the alpha males at Sheguiandah and at Billings lek in 1966 were probably Prairie Sharp-tailed Grouse (Lumsden 2005).

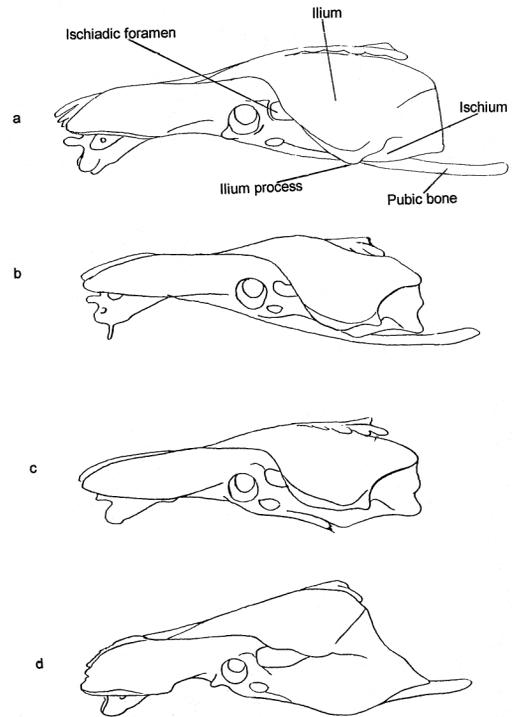


FIGURE 5. Ilium process of (a) Greater Prairie Chicken (b) and (c) Heath Hen and (d) Northern Sharp-tailed Grouse.

The speed with which change took place in the morphology of the Manitoulin population over time was perhaps largely due to the fact that "Prairie" Grouse are lek species. The particular bird that succeeds in becoming the alpha male in the hierarchy of dominance on a lek would consummate most of the matings. His genes would dominate in the subsequent year class. The absence of male Prairie Chickens on the Airport lek in 1962 and the presence of 10 male Prairie Sharp-tailed Grouse would have had a profound effect on the 1962–1963 year class. It is perhaps not surprising that Guild (1997*) saw 50 Sharp-tailed Grouse there on 19 April 1997. J. Iron (personal communication) saw 75–100 on 15 April 2000, 30 on 12 April 2003 and 60 Sharp-tailed Grouse there on 11 April 2004. Those observers made no mention of Prairie Chickens or hybrids. Being skilled naturalists, they are unlikely to have missed them.

Note: The extinct Heath Hen (*Tympanuchus c. cupido*) is of interest in that its ilium process does not project as far as that of the Greater Prairie Chicken (*Tym-*

panuchus c. pinnatus) (Figure 4). The two specimens I have examined would be placed in Class 2 and 3 of Table 7. Gutiérrez et al. (2000) judged the Heath Hen to be a species level taxon. The structure of the ilium may support that judgement.

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