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Etho-Ecological Apects of Hybridization in the Tetraonidae

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ETHO-ECOLOGICAL ASPECTS OF HYBRIDIZATION IN THE TETRAONIDAE

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As is apparent from the review of Gray (1958), natural hybridization among the grouse has been documented on many occasions. Gray reported some 36 types of alleged or apparent hybridization involving at least one species of grouse. Although of course most of these were intrafamily hybrids with other grouse species, several alleged cases of hybridization with domestic fowl *(Gallus gallus)*, partridge *(Perdix perdix)*, ring-necked pheasant *(Phasianus colchicus)*, silver pheasant *(Gennaeus nycthemerus)* and even the turkey *(Meleagris gallopavo)* are among the examples summarized by Gray. The authenticity of some of these interfamilial hybrids is doubtful at best, and they have little if any relevance to the general problem of isolating mechanisms and ecological interactions among wild grouse. Thus, this review will deal only with natural interspecific hybridization within the grouse family.

As part of a forthcoming book on the grouse and ptarmigans of the world, I have prepared range maps for all of the extant species of Tetraonidae, and have also adopted the generic limits that were proposed by Short (1967). Further, the sequence of species I have adopted differs only very slightly from that recommended by Short, specifically with respect to the position of the genus *Centrocercus*, which is placed adjacent to *Dendragapus* in my sequence, and between *Bonasa* and *Tympanuchus* in Short's. In any case, the basis for the sequence of discussion of genera in this paper and their arrangement in Table 1 is that of my proposed taxonomy.

As may be seen from Table 1, at least 15 types of natural interspecific hybridization have thus far been reported in the Tetraonidae, involving 12 of the 16 species accepted by Short and myself. In theory, these 16 species should be capable of producing some 120 different hybrid combinations, assuming that every species has an opportunity to hybridize with every other one. This, however, is impossible on the basis of each species' distributional characteristics, and obviously only those species that are geographically and ecologically sympatric with one another somewhere in their respective ranges have any opportunities for natural hybridization. This situation greatly restricts opportunities for hybridization, and reduces the theoretical opportunities for hybridization from 120 to probably somewhere in the neighborhood of 25–30 combinations, depending on the accuracy of available range maps. Thus, the 15 reported probable hybrid combinations actually represent perhaps at least half of the

Table 1. Summary of Reported Cases of Hybridization (X) Among Species of Grouse and Ptarmigans

	Spruce Grouse	Willow Ptarmigan	Rock Ptarmigan	Black Grouse	Capercaillie	Black-billed Capercaillie	Hazel Grouse	Ruffed Grouse	Sharp-tailed Grouse
Sage Grouse	–	–	–	–	–	–	–	–	X
Blue Grouse	X	–	–	–	–	–	–	–	X
Spruce Grouse		X	–	–	–	–	–	X	–
Willow Ptarmigan			X	X	X	–	X	–	–
Rock Ptarmigan				X	–	–	X	–	–
Black Grouse					X	–	X	–	–
Capercaillie						X	–	–	–
Greater Prairie Chicken							–	–	X

total potential natural hybrid combinations that could have occurred under natural conditions. Six of the 15 combinations involve intrageneric hybrids on the basis of the taxonomy used here; thus the majority of combinations are actually intergeneric crosses. However, if actual frequency of individual cases are considered, then by far the majority are intrageneric as might be expected. In fact, given the known range patterns, nearly all potential intrageneric hybridizations have actually been reported, with the single obvious exception of the black grouse *(Tetrao tetrix)* x black-billed capercaillie *(T. parvirostris)*. The white-tailed ptarmigan *(Lagopus leucurus)* has also not yet been implicated in hybridization, but it is questionable whether the white-tailed ptarmigan comes into local contact with any other ptarmigan species except perhaps the rock ptarmigan *(L. mutus)*.

Intrageneric Hybrids

Dendragapus. The only opportunities for intrageneric hybridization within this genus are between the blue grouse and the spruce grouse *(D. canadensis)*, which are fairly extensively sympatric in western North America, from Yukon Territory south through British Columbia, western Alberta, northern Idaho and western Montana. So far only a single specimen of this combination has been reported (Jollie, 1955). This individual was shot in Benewah County, Idaho, where both of the parental species are relatively rare, and where the habitat consists of

heavy forests of pines, firs, cedars, and other conifers. The hybrid was a young male, and no information on its behavior or fertility is available.

These two species are not isolated ecologically, and must come into fairly frequent contact during the breeding season. They exhibit a considerable number of plumage and display differences among the males, but females are distinctly similar, and it seems probable that males would not discriminate between females of the two forms.

Lagopus. As noted earlier, the white-tailed ptarmigan has so far not been implicated in hybridization, but both of the other two ptarmigans have hybridized on several occasions. The willow ptarmigan (including the "red grouse") and rock ptarmigan have extensive geographic overlap both in North America and in Eurasia. Apparent hybrids between them have been reported from Norway and Sweden on various occasions (Kihlen, 1914; Schaanning, 1920; Gray, 1958), and also from Great Britain (Collette, 1886; Ogilvie-Grant, 1908). However, there is no convincing example from North America. Todd (1963) mentioned one specimen from Labrador that he thought might be an abnormally colored willow ptarmigan or possibly a hybrid. Harper (1953) also described a subadult male ptarmigan collected in Keewatin that had intermediate bill depth measurements but unusually low weight and wing measurements. He concluded that it must be a hybrid or a highly aberrant willow ptarmigan. These two species certainly exhibit extensive local contacts over wide areas, although their habitat preferences do tend to maintain ecological segregation between them. Further, they establish relatively monogamous pair bonds, which also probably helps to facilitate reproductive isolation between them.

Tetrao. Three Eurasian species of *Tetrao* exhibit widespread overlap with one another, namely the black grouse, capercaillie, and black-billed capercaillie. As noted earlier, the black-billed capercaillie has not yet been reported to hybridize with the black grouse, although such hybridization seems quite likely, but on the other hand the other two hybrid combinations are well verified. The combination of the black grouse and capercaillie has been known to occur in Norway and Sweden from as early as 1744, and is sufficiently common there as to be given a specific vernacular name (Rakkelfugl). Farther south in Europe it is called the Rackelhahn and Rackelhane. Hybrids have also been produced in captivity, and both sexes of the hybrids appear to be reproductively active. Backcrosses between the male F_1 hybrid and the capercaillie have been bred, but F_1 female hybrids are evidently infertile in spite of sometimes laying eggs (Gray, 1958). Hybridization is believed to sometimes result from conditions of range expansion when the capercaillie moves into new areas. Females are apparently more mobile than males, and thus may move into an area first. On finding no male capercaillies with which to mate, they mate with male black grouse. In other areas where male capercaillies have been heavily hunted the females may also be prone to hybridize. More than 200 individual examples of this hybrid

combination are known, and probably only the reduced fertility of the F_1 generation and the ecological differences of the parental species prevent more extensive gene exchange (Mayr, 1942). Apparently the males of the F_1 hybrids often join leks of black grouse where, because of their large size, they are easily able to dominate the resident male black grouse, and often send them fleeing. The birds display more actively than do the black grouse, and their loud, raucous call (the basis for their vernacular name) is faintly reminiscent of that of the male capercaillie (Muller-Using, in Grzimek, 1972).

Similarly, natural hybridization between the capercaillie and the black-billed is known to occur in the rather limited area of geographic sympatry between these two very closely related forms. In one area of overlap in western Siberia 12 percent of the courting male birds were identified as hybrids (Kirpichev, 1958, cited by Short, 1967). As recent observations by Andreev (1979) indicate, the male behavior patterns of these two species are actually very similar, especially as to posturing, and general lek behavior. However, acoustic characteristics are quite different in the two species, and there are a few plumage and soft-part coloration differences that may have some significance as isolating mechanisms.

Tympanuchus. In North America, hybridization between the sharp-tailed grouse and greater prairie chicken *(Tympanuchus cupido)* has been previously surveyed (Johnsgard and Wood, 1968), and has been documented for every state and province where natural contact between these species has occurred. These include four Canadian provinces from Ontario to Alberta, and eight states (the Dakotas, Colorado, Nebraska, Iowa, Minnesota, Wisconsin and Michigan). The highest known incidence of hybridization was reported from Manitoulin Island, Ontario, where the two species rather recently came into contact and where from 5 to 25 percent of the total population may be of hybrid origin. On the Great Plains the incidence of hybridization is considerably lower, but probably in Nebraska the minimum rate is between 0.3 and 1.2 percent of the combined population (Johnsgard and Wood, 1968). In a study area in western Minnesota the rate of hybridization increased from 1.0 to 3.7 percent as the ratio between the two species increased. In that area, studies of hybrids indicated that their displays were intermediate in form between those of the parental species, and may have repulsed females (Sparling, 1979). However, apparently both the F_1 hybrids and backcrosses are fertile, and thus reproductive isolation is largely dependent upon behavioral mechanisms in areas of local sympatry.

Intergeneric Hybrids

Centrocerus x Tympanuchus. The sage grouse *(C. urophasianus)* has a distribution in North America that closely approximates that of various species of sagebrush *(Artemisia* spp.), and it exhibits little ecological or geographic overlap with any other grouse species. The only species with which it is fairly widely sympatric is the sharp-tailed grouse *(Tympanuchus phasianellus),* and over much

of eastern Montana and parts of adjacent Wyoming the two species are in contact. Two hybrids were obtained from central Montana in 1969 (Eng, 1971) in an area of transitional habitat between these two species. More recently, a hybrid male was found on a sharp-tailed grouse display ground in Sheridan County, Wyoming, during March of 1979 (Williams, 1979). This bird performed several sharptail-like displays on this ground, which was about a quarter-mile from a sage grouse strutting ground. Later the bird was seen in company with two sage grouse hens, to which it also displayed. The male was seen again on the display ground in 1980, so it survived at least a year (Robert Williams, pers. com.), but there is no indication that it managed to reproduce successfully.

Although both of these species are lek-forming types, their plumages and sexual display patterns are distinctly different, and the considerable difference in their adult body weights would also tend to militate against successful hybridi-

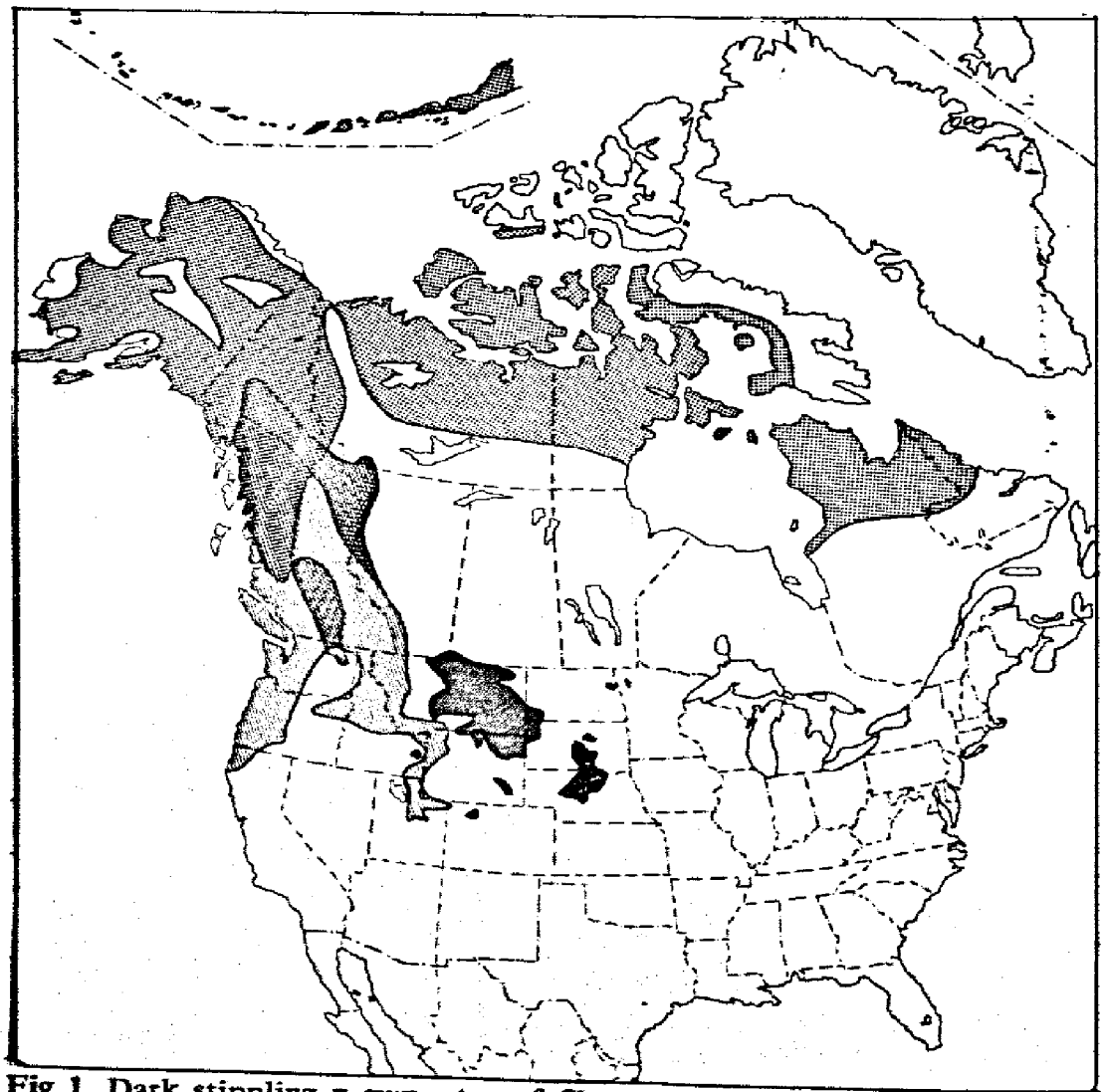


Fig 1. Dark stippling = sympatry of Sharp-tail & Greater Prairie Chicken
Wavy Hatching = sympatry of Sage Grouse & Sharp-tail
Cross hatching = sympatry of Blue Grouse & Sharp-tail
Hatching = sympatry of Blue & Ruffed Grouse
Shading = sympatry of Willow & Rock Ptarmigan

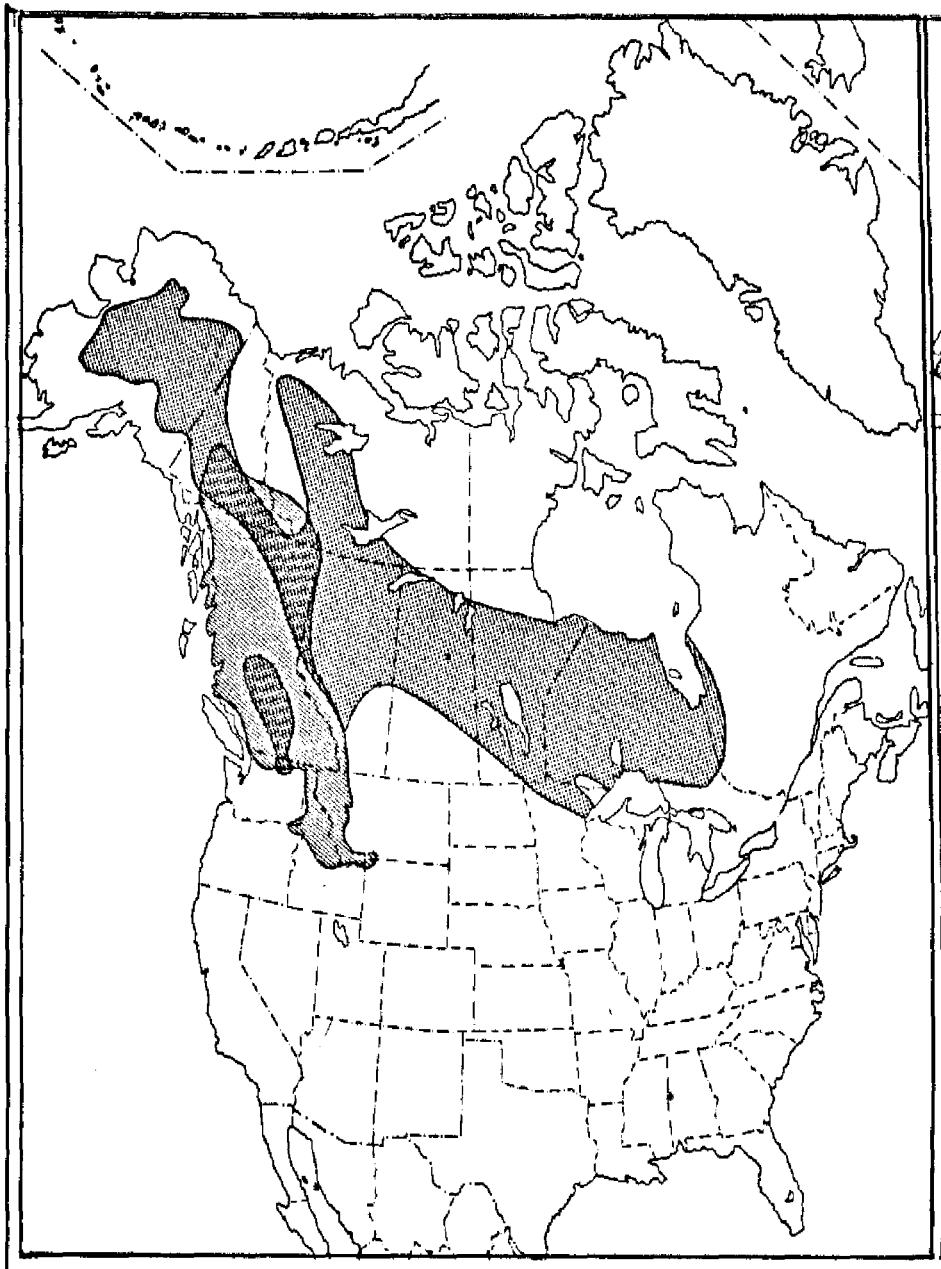


Fig 2. Shading = sympatry of Spruce Grouse & Sharp-tailed Grouse
Hatching = sympatry of Blue Grouse & Spruce Grouse

Fig 3. Hatching = sympatry of Spruce Grouse & Willow Ptarmigan
Shading = sympatry of Spruce & Ruffed Grouse

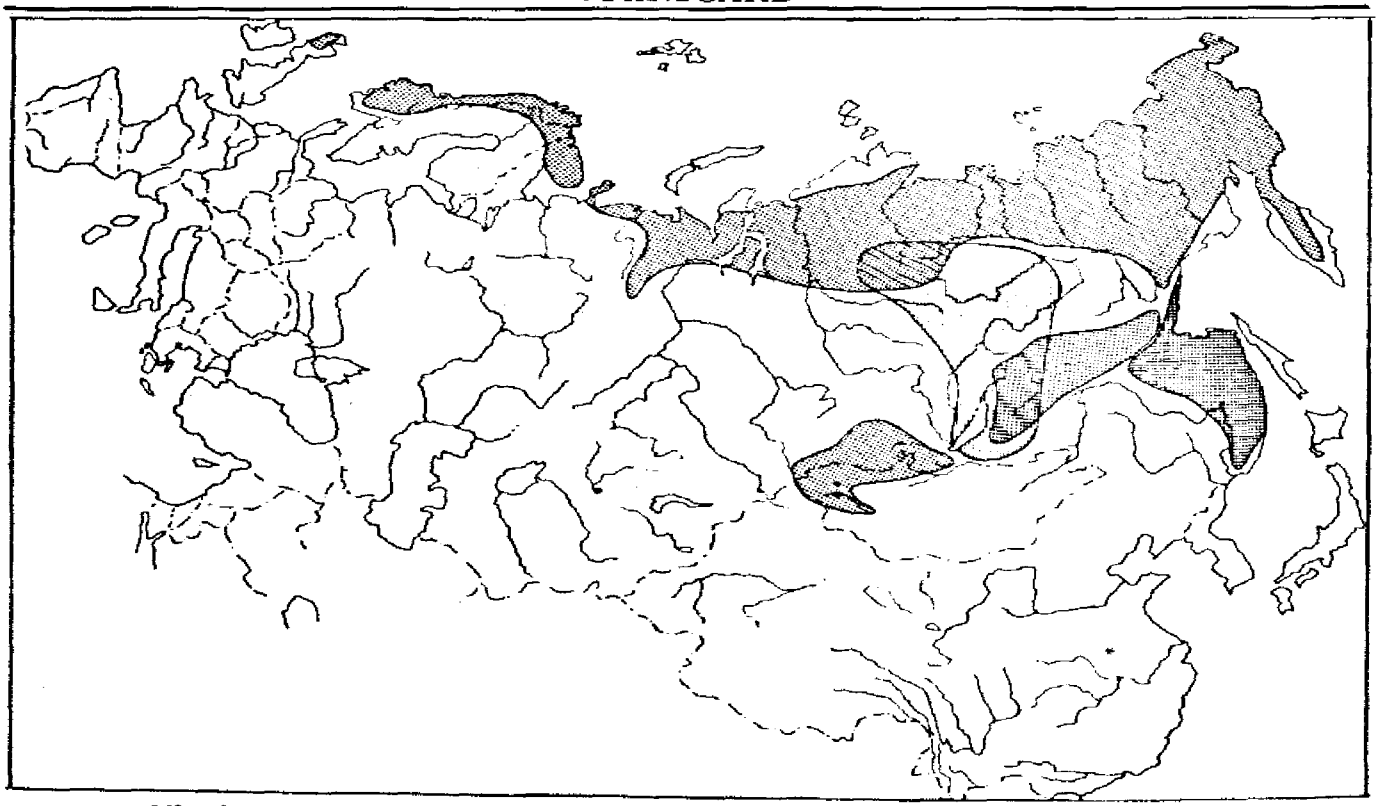


Fig 4. Shading = sympatry of Willow Ptarmigan & Rock Ptarmigan
Hatching = sympatry of Capercaillie & Black-billed Capercaillie
Cross-hatching = sympatry of Hazel Grouse & Sharp-winged Grouse

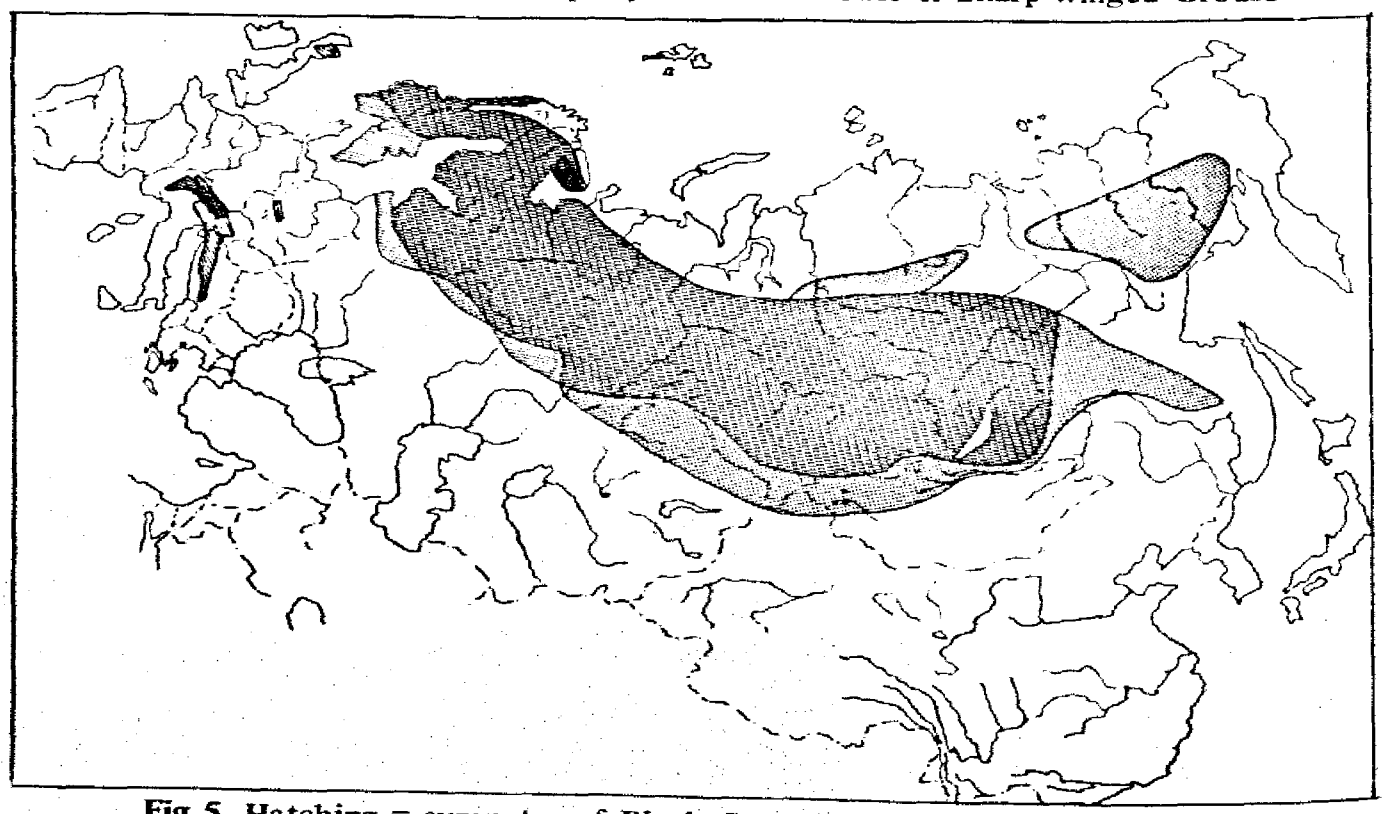


Fig 5. Hatching = sympatry of Black Grouse & Capercaillie
Shading = sympatry of Black Grouse & Willow Ptarmigan
Cross-hatching = sympatry of Rock Ptarmigan & Hazel Grouse

Fig 6. Cross-hatching = sympatry of Black Grouse & Rock Ptarmigan
Hatching = sympatry of Capercaillie & Willow Ptarmigan
Shading = sympatry of Hazel Grouse & Willow Ptarmigan

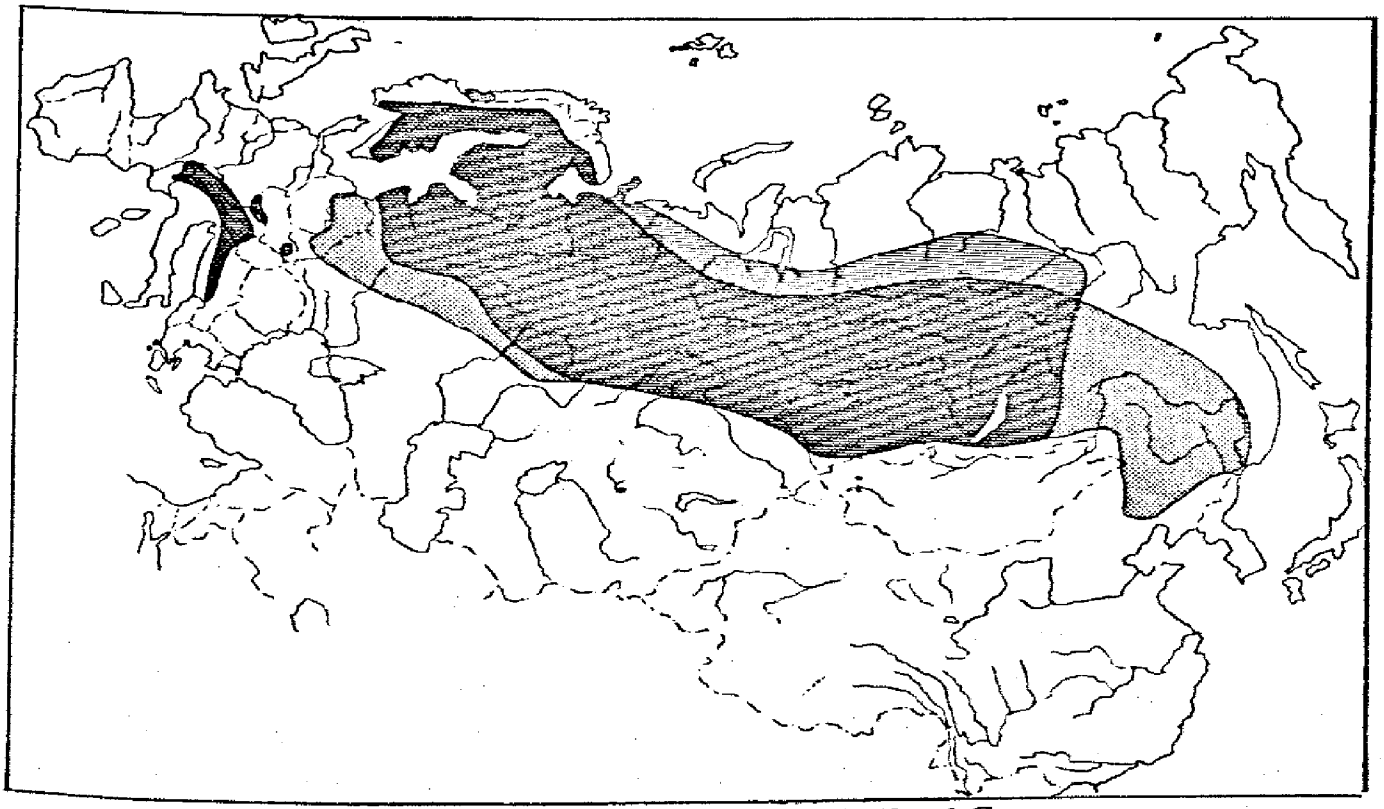


Fig 7. Shading = sympatry of Black Grouse & Hazel Grouse
Hatching = sympatry of Capercaillie & Hazel Grouse

zation between them. Further, the two species are probably not very closely related, since it is probable that the sage grouse is more closely allied to the blue grouse *(Dendragapus obscurus)* and other "forest" grouse than to the "prairie" grouse of the genus *Tympanuchus* (Johnsgard, 1973). It seems likely that reproductive isolation between *Centrocerus* and other grouse is largely maintained by ecological and geographic isolation, complemented by the distinctive structural features and behavioral aspects of male display. Rather surprisingly, the hybrid observed by Williams (1979) exhibited such typical features of sharp-tail display as foot-stamping, running parallel and flutter-jumping, none of which occur in the sage grouse repertoire, although the major display approached the typical strutting of sage grouse.

Lagopus x Tetrao. In addition to its contacts with the rock ptarmigan, the willow ptarmigan is also sympatric with the black grouse *(Tetrao tetrix)*, the capercaillie *(T. urogallus)* and the hazel grouse *(Bonasa bonasia)*. Rather surprisingly, wild hybrids involving all three of these combinations have been described. The most frequently reported of these combinations involve the black grouse; Gray (1958) lists 21 references that relate to such hybrids. According to her, wild hybrids have "often" been reported from Norway, and additionally a brood of seven hybrids was hatched in the Stockholm Zoo, most of which survived at least two weeks. There is some indication of reduced fertility in this cross, since males sometimes exhibit only rudimentary right testis, and in females the ovary is poorly developed. The cross has apparently occurred in both directions (reciprocal hybridization), and in Norway the Sweden is sufficiently common to have a special vernacular name "Rype-Orre". Collette (1886) reported locating at least 12 specimens from Sweden, and at least 22 from Norway. He also noted that they are "not unusual" in Russia and mentioned that one possible example involving *L. l. scoticus* is known from Scotland. According to Dresser (1876) male willow ptarmigan sometimes attend the leks of black grouse, which probably accounts for the frequency of hybrid combination.

A seemingly less likely hybrid combination is between the willow ptarmigan and the capercaillie, but these two species have also apparently hybridized repeatedly in Norway (Collette, 1906). At least three specimens of the combination have been preserved (*Ibis*, 1894, p. 447). As is the case with the black grouse, ecological separation between the willow ptarmigan and capercaillie should normally provide complete reproductive isolation, and the patterns of mating (monogamous versus complete promiscuity) also would seem to make this an extremely unlikely match.

The rock ptarmigan, in addition to hybridizing with the willow ptarmigan, is also sympatric with the black grouse, and the hazel grouse, and has hybridized with both of these species. It is also seemingly geographically sympatric with the capercaillie and black-billed capercaillie, but has not yet been reported to

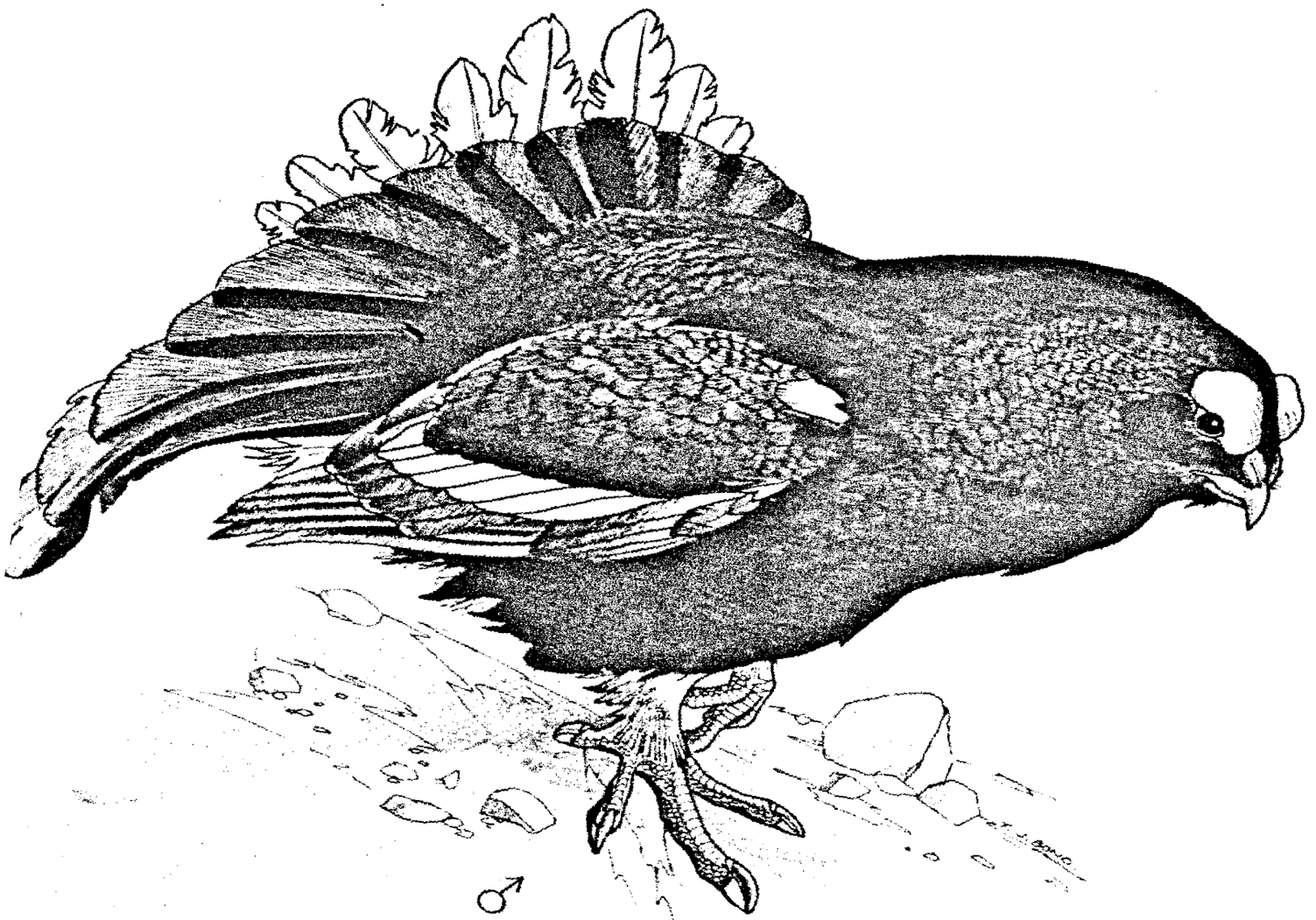
hybridize with either of these two species. Of the two hybrid combinations that have been described, the one involving the black grouse has been more frequently reported. In Norway this cross is known as the "Fjeldrype-Orre" (Collette, 1898; Schaanning, 1920), and several apparent examples have been reported from there.

Lagopus x Bonasa. Equally surprising is the hybrid cross between the willow ptarmigan and the hazel grouse, as isolation is facilitated by their ecological preferences, although they are geographically sympatric over an extremely broad range. Collette (1886) described a male specimen with "well defined" testes from Sweden, and this cross is reportedly "not uncommon" in Scandinavia (Gray, 1958). Both of the species have essentially monogamous pair bonds, which would seem to allow for "correction" of incipient pairing mistakes between the time of pair formation in late fall or winter and breeding the following spring.

Geographic overlap between the rock ptarmigan and hazel grouse is extremely slight, and besides occurring in the Alps it may also locally exist in central Norway, northern Finland, and especially in northern and northeastern Siberia. However, the more widespread overlaps are mostly areas where exact distributions are uncertain, and it seems unlikely that actual ecological contacts between these two species would be quite frequent. Gray (1958) mentions three apparent hybrids of this combination, but I have not been able to see either original citation provided by her.

Dendragapus x Tympanuchus. The blue grouse is extensively sympatric with the ruffed grouse *(Bonasa umbellus)* and with too a lesser extent with the sharp-tailed grouse. There are several hybrids known of the former combination, (Ouellet, 1974; Tufts, 1975), and a single example of the latter cross has been reported (Brooks, 1907). The blue grouse and sharp-tailed grouse exhibit considerable geographic sympatry in the Yukon Territory, northeastern British Columbia, south-central British Columbia and north-central Washington, and few areas of local contact in Idaho, colorado and possibly elsewhere, but ecologic differences tend to keep the species fairly well separated. Nevertheless, male blue grouse do often move into fairly exposed areas when displaying, and perhaps under such circumstances come into local contact with female sharp-tailed grouse. The only known example of this cross was obtained near Osoyoos, British Columbia, near the Washington border, and Brooks believed it to be the result of a male blue grouse mating with a female sharp-tail. The hybrid was sexually active, since it had been observed the previous spring displaying in the company of sharp-tailed grouse.

Dendragapus x Lagopus. The spruce grouse is sympatric with several North American grouse in addition to the blue grouse. These include the sharp-tailed grouse, and also the ruffed grouse and willow ptarmigan *(Lagopus lagopus).* The areas of geographic sympatry are extensive in all three cases, but the best case of



♂

BLACK GROUSE. (Tetrao tetrix)

♀

resulting hybridization is with the willow ptarmigan (Lumsden, 1969). At least three specimens of natural hybrids of this combination have been reported, and two of them came from the Hudson Bay area of Ontario, where spruce stands near rivers that provide spruce grouse habitat are in close proximity to heath and lichen communities that support willow ptarmigans. The last of the known hybrids came from York Factory, Manitoba, which is also near Hudson Bay and probably represents similar habitat interdigitation. No information is available on the possible fertility or the sexual activity of this cross. The mating systems of the two species are rather different, with the spruce grouse essentially promiscuous, while the willow ptarmigan establishes monogamous pair bonds, so this would tend to reduce further the probability of frequent hybridization.

Dendragapus x Bonasa. In North America, the ruffed grouse is widely sympatric with the spruce grouse and the blue grouse, but so far hybrids have only been described for the spruce grouse. Ouellet (1974) reported on a hybrid specimen that had been shot in Champlain County, Quebec, in an area of intensive logging, where spruce grouse habitat and probably their numbers were declining, and where ruffed grouse were thriving. Tufts (1975) later pointed out that this cross had been documented several times in the late 1800's from Nova Scotia, and that one specimen from there was known to be still extant.

Tetrao x Bonasa. Both the black grouse and the capercaillie are extensively geographically sympatric with the hazel grouse, but only the former species is believed to have hybridized with this species. One such male hybrid was described by Dresser (1876), and Pleske (1887) described and illustrated a male and female of this combination. The combination has also been illustrated by Schaanning (1920–1923). The combination is probably relatively rare, but indicates a surprising potential for breakdown of reproductive isolation, considering that one of the parental species is a promiscuous, lek-forming type and the other exhibits a monogamous pair-bonding breeding system. Dresser (1876) suggested that it most probably results when a wandering unmated hazel grouse male encounters a female black grouse rather than the reverse.

Discussion

Of the 15 kinds of interspecific hybrids summarized here, 6 are among strictly North American species, 8 involve strictly Old World species, and the remaining case consists of the two Holarctic ptarmigan. In only one situation of probable extensive intrageneric sympatry (black grouse and black-billed capercaillie) is there still no definite evidence of natural hybridization, while in five other cases of intrageneric sympatry the rate of hybridization ranges from relatively rare (willow and rock ptarmigans) to extremely frequent (sharp-tailed grouse and greater prairie chicken). There are two situations of extensive intergeneric sympatry in North America where hybridization is unreported but might be expected (ruffed grouse with blue grouse, and the spruce grouse with the

sharp-tailed grouse), while in Eurasia extensive intergeneric sympatry without known hybridization occurs between the hazel grouse and the two species of capercaillies, also with the Siberian spruce grouse *(Dendragapus falcipennis).* This last species in turn is likewise sympatric with the black-billed capercaillie, but hybridization is unknown. Any hybridization involving these east Asian grouse could well go undetected, as for example the apparently fairly common hybridization between the capercaillie and black-billed capercaillie was unreported until fairly recently.

If the cases of known grouse hybridization are arranged in descending order of apparent frequency, some interesting trends emerge, as indicated in the following table.

Hybrid Combination	Occurrence of Hybrids	Mating Types
Sharp-tail x Prairie Chicken	From under 1.0—3 percent of combined population, rarely to 25 percent.	Lek x Lek
Capercaillie x Black-billed Capercaillie	Up to 12 percent of males in one local area	Lek x Lek
Black Grouse x Capercaillie	More than 20 specimens known	Lek x Lek
Willow Ptarmigan x Black Grouse	At least 34 specimens known	Monogamous x Lek
Willow Ptarmigan x Hazel Grouse	Many specimens known	Monogamous x Monogamous
Rock Ptarmigan x Black Grouse	Several specimens known	Monogamous x Lek
Rock Ptarmigan x Willow Ptarmigan	Several specimens known	Monogamous x Monogamous
Willow Ptarmigan x Capercaillie	Several specimens known	Monogamous x Lek
Black Grouse x Hazel Grouse	Several specimens known	Lek x Monogamous
Ruffed Grouse x Spruce Grouse	Several specimens known	Promiscuous x Promiscuous Solitary Solitary
Willow Ptarmigan x Spruce Grouse	Three specimens known	Monogramous x Promiscuous Solitary
Rock Ptarmigan x Hazel Grouse	Three specimens known	Monogamous x Monogamous
Sage Grouse x Sharp-tail	Two specimens known	Lek x Lek
Blue Grouse x Spruce Grouse	One specimen known	Promiscuous x Promiscuous Solitary Solitary
Blue Grouse x Sharp-tail	One specimen known	Promiscuous x Lek Solitary

Thus, lek species are involved in 13 of the combinations, promiscuous but solitary species are associated with 5 combinations, and monogamous species are involved in 11 of the combinations. This is rather surprising, and suggests that monogamous are little if at all more immune to possible hybridization than are lek-forming species, particularly inasmuch as there are six species of lek-forming grouse and probably only four monogamous species. However, all three of the most frequently occurring hybrid combinations involve pairings by two lek-forming species, as might be expected.

Summary

A review of records of intrafamilial hybridization in the Tetraonidae indicates that at least half of the potential natural hybrid combinations that could in this family on the basis of known distribution patterns actually have been reported at least once. These include 15 interspecific hybridization combinations that involve 12 species and all of the genera currently recognized by taxonomists. The three most commonly reported hybrid combinations all involve lek-forming species of grouse as parental types, while the remaining 12 combinations are all considerably rarer and involve lek-forming parental species in 7 cases, promiscuous but solitary species in 6 cases, and monogramous species in 11 cases. The results suggest that monogamous grouse species are only slightly less prone to hybridization than are the non-monogamous forms, and that in all grouse species habitat separation is probably a major isolating mechanism.

ZUSAMMENFASSUNG/RÉSUMÉ

Es wird über verschiedene Inzuchtkombinationen berichtet und dass monogam lebende Rauhfusshuhnarten weniger geneigt sind zur Inzucht als nicht monogam lebende. Bei allen Schneehuhnarten ist die Isolierung von Lebensräumen eine grosse Gefahr für das Fortbestehen einer Art.

En examinant les archives de l'hybridation interfamiliale chez les Tétraonidés l'on constate qu'au moins la moitié des combinaisons potentielles naturelles des hybrides de cette famille, sur base de la répartition connue, ont été notées au moins une fois. Ceci comprend 15 combinaisons d'hybrides concernant 12 espèces et tous les genres généralement reconnus par les taxonomistes. Les trois combinaisons d'hybrides le plus notées comprennent toutes des espèces "lek-forming" de Tétraonidés comme type de parents alors que les 12 combinaisons restant sont toutes nettement plus rares et concernent dans sept cas des parents des espèces "lek-forming", des espèces mêlées mais solitaires dans six cas et des espèces monogames dans onze cas. Des résultats acquis on peut déduire que les espèces monogames de Tétraonidés ne sont que légèrement moins enclines à l'hybridation que les formes non-monogames et que pour toutes les espèces de Tétraonidés la séparation des habitats est probablement un mécanisme majeur pour l'isolement.

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