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4 Hybridization

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Hybridization

THE study of hybridization between species, under either natural or artificial conditions, provides information of value for a variety of reasons. In general, it may be expected that the incidence of crossbreeding between populations existing under natural conditions will be related to their nearness of relationship, and information of taxonomic interest may be obtained from such study. Furthermore, the relative survival and fertility of the resulting hybrids should provide an indication of the degree of genetic difference between the parental types, and thus genetic information may be available through experimental hybridization studies. Hybrids provide favorable material for studying the chromosomal numbers and configurations among related species, and when they are fertile the degree of phenotypic variation in second or backcross generations may be used to estimate genetic differences controlling specific traits. Finally, the presence or absence of natural hybridization between closely related forms occurring in the same habitats may provide a clue as to the degree of niche overlap and interspecies competition for habitat resources. Therefore, if the basis for periodic or local hybridization between two forms that normally do not hybridize can be established, the ecological differences that normally prevent hybridization may possibly be deduced.

For various reasons, the grouse and quails of North America exhibit a rather surprisingly high tendency to hybridize, even among species belong-

ing to seemingly different genera. Peterle (1951) reviewed the cases of intergeneric hybrids reported in gallinaceous birds, and Cockrum (1952) provided a more complete survey of hybridization in North American birds. Sibley (1957) commented on the taxonomic significance of hybridization in grouse, and a similar review of the significance of hybridization in the New World quails is available (Johnsgard, 1970). For a complete listing of all known hybrids of gallinaceous birds, including those reported from Europe and Asia, the summary by Gray (1958) may be consulted.

GROUSE HYBRIDS

Virtually all known cases of hybridization among the North American grouse species have involved naturally occurring hybrids. This is largely a reflection of the difficulties of keeping and breeding grouse in captivity. The only case of hybridization among North American grouse under captive conditions known to me is the production of several hybrids (including reciprocal crosses) between greater and lesser prairie chickens in 1969 and 1970 by William Lemburg of Cairo, Nebraska.* He has also attempted, without success, to obtain backcross hybrids from a wild-caught female greater prairie chicken × sharp-tail grouse mated to males of both of these species.

All of the North American genera of grouse (as recognized here) have been involved in intergeneric hybridization except for *Bonasa* and *Centrocercus*.[1] In addition, intrageneric hybridization has occurred in *Tympanuchus*, *Dendragapus*, and probably also in *Lagopus*.

Intrageneric Hybrids

Hybridization within the genus *Lagopus* has still not been certainly proved, but would seem highly probable on the basis of the extensive area of geographic contact between the willow and rock ptarmigan. Gray (1958) summarized references to British specimens of possible hybrids between these two species but questioned their authenticity. Todd (1963) mentioned one specimen from Labrador that he examined, which he thought might be an abnormally colored willow ptarmigan or possibly a hybrid. Harper (1953) described a subadult male ptarmigan collected in Keewatin that had a bill depth of 8.5 millimeters (vs. 7.75 maximum for his series of rock, and 9–10.5

*William Lemburg, 1970: personal communication.

1. A record of hybridization between the sage grouse and the sharp-tailed grouse has recently been published (*Wilson Bulletin* 73:491–93).

for willow ptarmigan). Its upper tail coverts were longer than are typical of rock ptarmigan, but its weight and wing measurements were less than are typical of rock ptarmigan. Some black feathers were present at the base of the bill and behind the eye. Harper concluded that it must be a hybrid or a highly aberrant willow ptarmigan.

A single reported specimen representing hybridization between the blue grouse and spruce grouse has been reported (Jollie, 1955). This bird was obtained in Idaho where, although the ruffed grouse is common, both of the parental species are evidently rare. These two species overlap extensively in their ranges from western Montana through Idaho and Washington, and north to the Yukon Territory and apparently occupy generally similar habitats through much of this range.

The other genus of grouse that has been involved in intrageneric hybridization is *Tympanuchus*, and in this case there is no question that hybridization between the sharp-tailed grouse and the greater prairie chicken has occurred repeatedly under natural conditions. In a recent summary, Johnsgard and Wood (1968) pointed out that natural hybridization has been reported in every state and province where natural contact between these species has occurred. These include four Canadian provinces from Ontario to Alberta and the Dakotas, Colorado, Nebraska, Iowa, Minnesota, Wisconsin, and Michigan. The highest known incidence of hybridization so far reported is on Manitoulin Island, Ontario, where the two species have recently come into contact and between 5 and 25 percent of the total grouse population may be of hybrid origin. The complete spectrum of plumage patterns exhibited by such birds would indicate a clear capacity to produce second-generation or backcross offspring, but so far little information is available on the relative reproductive success of hybrids as compared to the parental types. The few observations made so far (Lumsden, 1965; personal observations) suggest that hybrids are usually able to occupy only peripheral territories on display grounds that are dominated by pures of either species, and are probably at a considerable reproductive disadvantage in spite of their apparent fertility.

Lagopus × *Dendragapus Hybrids*

At least three specimens of natural hybrids between willow ptarmigan and spruce grouse have been reported so far (Lumsden, 1969). These two species overlap extensively in their breeding ranges in eastern Labrador, northern Ontario, the Northwest Territories, Yukon Territory, British Columbia, and Alaska, but are ecologically isolated during the breeding season. Lumsden noted that in the area where two of the hybrids occurred, the Hudson Bay

region of Ontario, spruce stands near rivers are in close proximity to heath and lichen communities. The last of the three reported hybrids came from York Factory, Manitoba, which is also near Hudson Bay and presumably represents similar habitat. Lumsden suggested that the measurements of one of the two preserved hybrid skins would suggest that hybrid vigor has influenced its size, but no information is available as to the possible fertility of this cross.

Dendragapus × *Tympanuchus Hybrids*

Only a single specimen representing this cross has so far been reported. Brooks (1907) described an apparent blue grouse times sharp-tailed grouse hybrid taken at Osoyoos, British Columbia. In spite of a seemingly substantial overlap in the breeding ranges of these two species, extending from the Yukon southeast through parts of British Columbia, Washington, Idaho, western Montana, Utah, and western Colorado, it appears that ecological differences in breeding habitats rarely would allow for possible interbreeding. Additionally, these two genera do not appear to be especially closely related.

Grouse × *Pheasant Hybrids*

In spite of the fact that the ring-necked pheasant is regularly placed in a separate subfamily from the grouse, many instances of apparent hybridization between these two groups have been reported. In North America several apparently authentic hybrids between the blue grouse and the ring-necked pheasant have been described, and one was captured and kept alive for several years (Gray, 1958; Hudson, 1955). There was also a case of probable hybridization between the ruffed grouse and the ring-necked pheasant in New York (Bump et al., 1947). In Europe, several reported hybrids between pheasants and ptarmigan have been reported (Gray, 1958), in spite of marked habitat differences exhibited by these species.

QUAIL HYBRIDS

Intrageneric Hybrids

All known natural hybrids among the New World quails involve the genus *Callipepla*, as recognized in this book.

The range of the scaled quail overlaps fairly extensively with that of the Gambel quail, primarily in New Mexico but also in western Texas along the Rio Grande, southeastern Arizona, and adjacent Mexico. Introduc-

tions of the scaled quail into central Washington have also resulted in a small amount of contact with California quail, and two hybrid specimens have been reported from that area (Jewett et al., 1953). Shore-Baily bred and reared a number of such hybrids, finding them to be fertile, and I have also reared fourteen first-generation hybrids of this cross (plate 114). Although I have not produced any second-generation offspring, several backcrosses to the California quail have been reared to maturity.

Wild hybrids between the scaled quail and the Gambel quail have been known to occur for some time; apparently the earliest published record is that of Bailey (1928), who described a hybrid shot in Grant County, New Mexico. This hybrid was the basis for a painting by Louis A. Fuertes, now in the collection of the Laboratory of Ornithology, Ithaca, New York. The laboratory very kindly gave me permission to reproduce this painting (plate 97), on the back of which is the following inscription:

An interesting half-breed Quail. Probably Gambels × Scaled. This bird was sent me by Mr. W. E. Watson of Pinos Altos, having been killed by him from a flock of Gambels Quail November 26, 1916 on Whiskey Creek a few miles from Pinos Altos, Grant County, New Mexico. It is a male, and brief description is:—Crest somewhat shorter than male Gambels and feathers not clubbed. Chin and throat, crest, and middle of belly patch rich chestnut. Thus chestnut taking the place of black in Gambels. Forehead light gray, hind head chestnut. Fore-breast color of Gambels but showing the shelled edgings and black shaft lines of Scaled in a lesser degree.

I have just sent the skin to Mr. L. A. Fuertes and he comments thereon, in part, as follows:—"This is the second instance I have known of wild hybridization of American partridges of different genera. The other was a male hybrid Mountain Plumed Quail and California Valley Quail. I painted the bird for Loomis but both the specimen and the picture were burned in the San Francisco fire."

R. T. Kellogg
Silver City, New Mexico
August 11, 1927

More recently, Phillips, Marshall, and Monson (1964) reported wild hybrids of this combination from various localities in southeastern Arizona, and Hubbard (1966) described an apparent backcross hybrid that had also been collected in Grant County. A hybrid was recently collected in Otero County by New Mexico game personnel. Captive hybrids of this cross have been obtained on several occasions. These were originally thought to be sterile, but second-generation embryos were brought nearly to the point of hatching at the Arizona–Sonora Desert Museum, and William S. Huey informed me that he reared about twenty apparent backcross hybrids. I have

not been able to produce any second-generation or backcross hybrids from the three males and one female of this cross that have been present in my laboratory.

The Gambel quail also exhibits a very limited degree of natural contact with the California quail in southern California, and wild hybrids between these species have been reported from there (Miller and Stebbins, 1964). One male hybrid representing this cross that is in my laboratory has exhibited sexual activity but has not fathered any backcross offspring in either direction. It would nevertheless seem highly likely that this hybrid combination will prove to be fertile.

Two other intrageneric hybrid combinations have been reported in this genus. One is the cross between the California quail and the elegant quail, represented by hybrids reared in the London zoo, and the other is a cross between the scaled quail and elegant quail that was also produced under captive conditions (Banks and Walker, 1964).

Colinus × *Callipepla Hybrids*

Natural contact between the bobwhite and the scaled quail exists over a fairly broad zone extending from northern Mexico through west-central Texas, the Oklahoma panhandle, possibly extreme southwestern Kansas, and southeastern Colorado. Wild hybrids have been reported from three counties in Texas, and probable hybrids have also been seen in Oklahoma. Captive hybrids have been produced on a variety of occasions, including a considerable number that have been reared in my laboratory (plate 117). The females of this cross produce abnormally small eggs, which usually have exhibited no embryonic development. Most attempted matings with males of the parental species have proven unsuccessful but a few backcrosses have hatched.

Natural contact between the bobwhite and the other *Callipepla* species is virtually nonexistent, but introductions of the bobwhite into Washington, Oregon, and Idaho have resulted in some possible recent contact with the California quail. Furthermore, introductions of the bobwhite and California quail into Utah produced a relatively short-lived period of contact and resulted in the only known case of naturally occurring hybridization between these species (Aiken, 1930). This cross has also been obtained in captivity, and the hybrids evidently exhibit a very limited degree of hybrid fertility. A pair of such hybrids raised at the San Joaquin Game Bird Farms of Reedley, California, produced over one hundred eggs, of which four second-generation birds were successfully reared (plate 116). These hybrids were maintained in my laboratory for about two years, and the females produced

uniformly small eggs that exhibited little or no embryonic development. Attempts to backcross the males to both parental species were also unsuccessful.

Although no wild hybrids between the bobwhite and Gambel quail are known, I have reared two hybrids representing this cross to maturity (Johnsgard, 1970). These two, a male and female, established a firm pair bond and exhibited normal sexual behavior (Prososki, 1970), but the female's eggs were somewhat smaller than normal and all of them were either infertile or exhibited early embryonic death. At least ten skins representing captive-raised hybrids between the elegant quail and the bobwhite, which is a hybrid combination previously unreported in the literature, are in the J. S. Ligon Collection at the University of New Mexico. Some of these specimens were the result of hybridization of the elegant quail with the masked bobwhite, while others involved one of the white-throated races, and the differences in body as well as throat pigmentation have been clearly transmitted to the hybrids, particularly the males.

Callipepla × *Oreortyx Hybrids*

The area of geographic overlap between the California quail and mountain quail is considerable, and includes much of California, Oregon, and Washington. The earliest record of hybridization between these species is that of Peck (1911), who described a specimen taken in Harney County, Oregon, which is now in the Museum of Vertebrate Zoology, Berkeley, California. A second specimen of unknown origin was painted by L. A. Fuertes (Peterle, 1951). I have reared to adulthood a male of this cross (male mountain × female California) but have been unable to obtain fertile eggs with attempted pairings with female California quail. There are no other reported cases of natural or artificial hybridization involving the mountain quail, although one unidentified skin in the J. S. Ligon Collection quite obviously is a mountain × California quail specimen.

Callipepla × *Philortyx Hybrids*

The barred quail and scaled quail exhibit no geographic overlap in ranges, and the barred quail is in natural contact only with the bobwhite and perhaps also with the elegant quail. Since the barred quail has only rarely been maintained in captivity, it is surprising that any hybrids at all have been produced. However, at the Centro de Investigaciones Basicas, Campo Agricola Experimental, Progreso, Guerrero, a variety of Mexican quail species are being raised for study and release. A single wild-caught male barred quail has been present for several years, and has been kept with a group

of scaled quail. In 1969 it mated with a female scaled quail, as a result of which twelve hybrid offspring were reared (plate 111). When I saw the hybrids in June of 1970 all twelve (predominantly females) were still alive, but no eggs had been produced. The birds did not appear to be paired, nor had they exhibited any sexual behavior, according to the station manager, Sr. Alvaro Aragon.

Laboratory Hybridization of Quail

For the past several years I have been attempting to produce a variety of intergeneric and intrageneric hybrids of New World quails, for behavioral studies as well as for the genetic and evolutionary information that such hybridization might be able to provide (Johnsgard, 1970, 1971). Although the methods and some of the results have already been reported, an updated summary of hybrid fertility and hatching success is presented here (table 11). It may be seen that individuals representing eight different hybrid combinations (three of which are intergeneric on the basis of nomenclature used in this book) have hatched from pairing representing ten possible combinations. As was previously reported (Johnsgard, 1970), one of these intergeneric combinations had previously been unreported in the literature, and to my knowledge the crested bobwhite × bobwhite hybrid combination also is previously unreported. Not noted in the table is the recent hatching of two hybrids between the bobwhite and the black-throated bobwhite from twenty-one incubated eggs.

So far, only four hybrid combinations have been produced beyond the first generation. One of these is a backcross resulting from the mating of a male scaled quail with a female Gambel × scaled quail, from which eight offspring were hatched, although none was raised to maturity. The second successful backcross has been one produced by mating a male California quail with a female California × scaled quail hybrid. A total of twenty-two individuals representing this combination have been hatched, most of which were reared to their adult plumage. One F_1 hybrid pair, resulting from a mating of a male bobwhite with a female crested bobwhite × bobwhite has produced fourteen offspring. Attempts to produce F_2 Gambel × scaled quail and F_2 California × scaled quail have thus far failed, although the females of both these crosses lay normal-sized eggs and the males are obviously sexually active. In contrast, only abnormally small eggs have been produced by female hybrids between bobwhite and Gambel quail and between bobwhite and scaled quail. The small eggs laid by these females have been infertile or have usually undergone only limited embryonic development.

Attempts to produce F_2 bobwhite × scaled quail hybrids have proven fruitless, and backcross attempts in both directions have been made. To date only twenty backcross individuals have survived to hatching, and none has lived beyond two weeks after hatching. Interestingly, hybrid females appear to be relatively more fertile than are hybrid males, judging from our limited data. In all three cases where backcross pairing has produced either living offspring or survival until late embryonic stages, the maternal parent was the hybrid and the father was one of the parental species. In cases where the male parent was a hybrid and the female was a pure of one of the parental species, all of the eggs have proven to be infertile or have at most died early in embryonic development.

TABLE 11

FERTILITY AND HATCHABILITY OF HYBRID QUAIL EGGS

	Total Eggs	*Infertile Eggs*	*Embryonic Death*	*Total Hatched*
F_1 hybrid pairings				
Bobwhite x scaled (B x S)	197	92	52	53
Scaled x bobwhite (S x B)	338	303	35	0
Crested bobwhite x bobwhite (CB x B)	107	81	20	6
California x scaled (C x S)	47	21	7	19
Bobwhite x Gambel (B x G)	17	0	4	13
Scaled x Gambel (S x G)	28	17	4	7
Gambel x California (G x C)	13	11	2	0
Gambel x scaled (C x S)	9	6	2	1
Scaled x elegant (S x E)	5	3	1	1
Mountain x California (M x C)	34	27	4	3
	Totals 795	561 (70.6%)	131 (16.5%)	103 (12.9%)
F_2 hybrid pairings				
F_1 BG x F_1 BG	16	6	10	0
F_1 GS x F_1 GS	33	26	7	0
F_1 CS x F_1 CS	266	264	2	0
F_1 BS x F_1 BS	370	370	0	0
F_1 BS x F_1 CS	9	9	0	0
	Totals 694	675 (97.2%)	19 (2.8%)	0
Backcross hybrid pairings				
BB x F_1 CBB	22	5	3	14
F_1 BG x G	28	28	0	0
S x F_1 GS	32	11	13	8
F_1 CG x G	32	19	13	0
F_1 BS x B	146	146	0	0
F_1 BS x S	106	106	0	0
B x F_1 BS	249	165	64	20
S x F_1 BS	108	40	0	0
C x F_1 CS	66	12	32	22
	Totals 789	600 (76%)	125 (15.8%)	64 (8.1%)

Since the hybrids mentioned here involve species having remarkable differences in head patterning and crest condition, it is of interest to consider the inheritance of these traits in the hybrids. On the basis of male hybrid specimens obtained in my laboratory, those I have seen in museums, and one literature description, it has been possible to produce a diagram indicating the male head plumages of eight hybrid combinations occurring among six different species of *Colinus*, *Callipepla*, and *Oreortyx* (figure 11). The diagram illustrates quite clearly the remarkable plasticity in facial patterning and probable visual signal characters (sign stimuli) that can be achieved by the addition or subtraction of feather pigments and the modification of crest shape and length. The genetic basis of both the feather pigmentation and the crest condition is as yet unknown, but it seems probable that these are under fairly simple genetic control. Certainly the variations in crest lengths and head pigmentation that are apparent in adjacent populations of the numerous Central and South American races of *Colinus cristatus* would suggest that this is the case. If so, it would seem that the evolution of distinctive male visual signaling devices under the influence of natural selection might occur quite rapidly and result in quite widely divergent appearances in the heads of fairly closely related species. The differences in the appearance of the head of the scaled quail from the closely related and geographically overlapping Gambel quail might provide a case in point. Here, a combination of differences in crest length, crest color, and throat color provides for a completely different head appearance, in spite of the fact that the colors of the back, flanks, wings, and tail are distinctly similar in these two species.

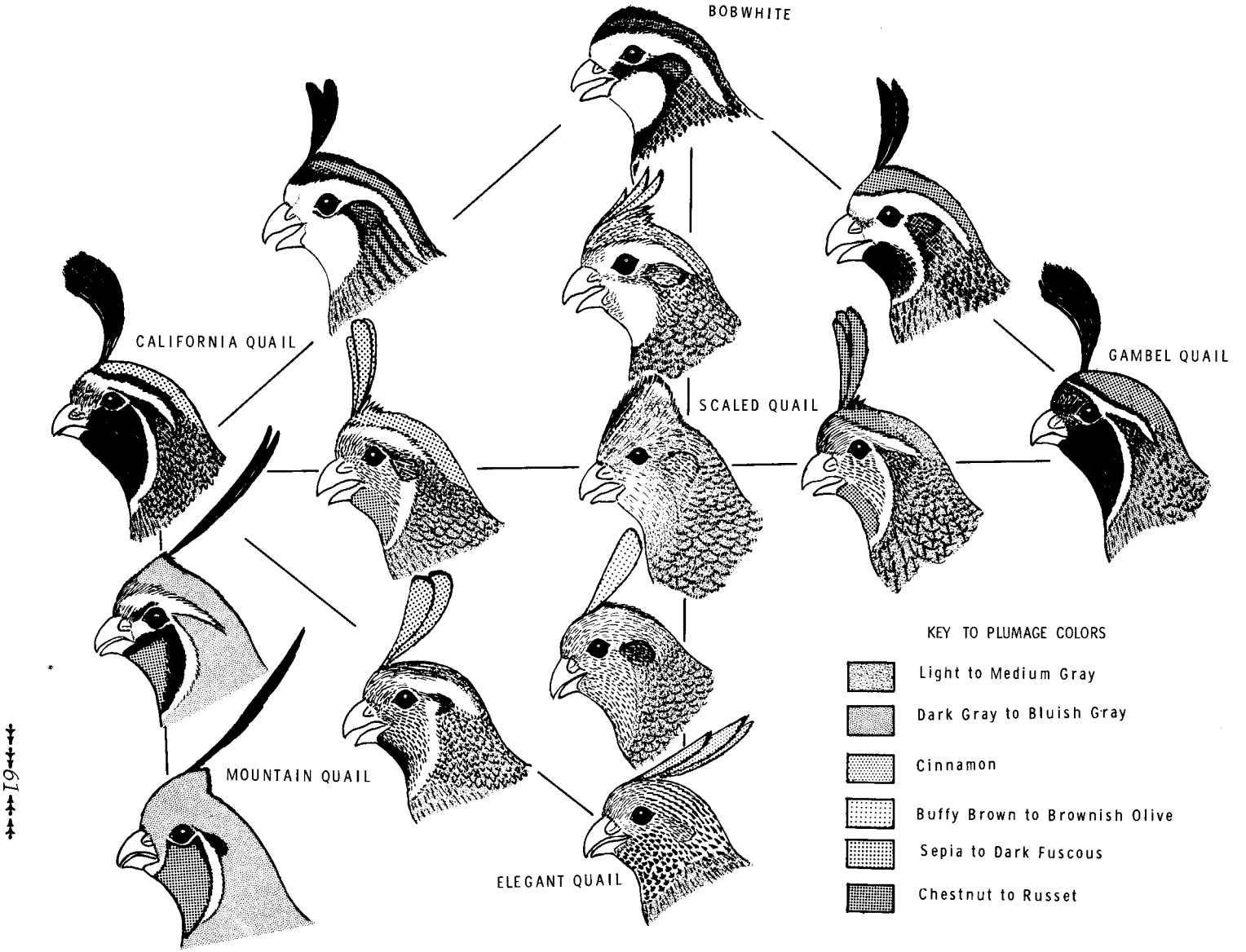

FIGURE 11. Head plumage patterns of hybrid quails, compared with parental species (from Johnsgard, 1971).