

WHITE GEESE INTERMEDIATE BETWEEN ROSS' GEESE AND LESSER SNOW GEESE

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THIS paper describes white geese with morphological characteristics intermediate between the Ross' Goose (*Chen rossii*) and the Lesser Snow Goose (*Chen hyperborea hyperborea*). Although the parentage of these intermediate white geese is unknown, they apparently represent the hybridization of Ross' Geese and Lesser Snow Geese in the wild.

Johnsgard (1960) analyzed the occurrence of intratribal hybridization among Anserini based primarily on hybrids reported by Gray (1958). Ross' Goose is known to hybridize in captivity with both the Blue Goose (*Chen caerulescens*) and Lesser Snow Goose (Sibley, 1938; Gray, 1958: 53). Intergeneric hybrids have been reported from avicultural collections between the Ross' Goose and the domesticated Greylag Goose (*Anser anser*), Emperor Goose (*Philacte canagicus*), and Cackling Goose (*Branta canadensis minima*) by Sibley (1938), and the Red-breasted Goose (*Branta ruficollis*) by Scott (1951: 38). Sibley (1938) also documents the intertribal hybridization of a captive Ross' Goose and Blue-winged Goose (*Cyanochen cyanopterus*). Wild hybrids of Ross' Geese and these species have not been reported.

Scientific nomenclature follows the A.O.U. Check-list (A.O.U., 1957), although taxonomic revisions of the Anatidae suggested by Delacour and Mayr (1945), Delacour (1954), and Johnsgard (1968) have been accepted by an increasing number of waterfowl biologists. Terminology and concepts of hybridization conform with the definitions and descriptions of Mayr (1963) and Short (1969). The term "intermediate" is used to denote the apparent hybrids of Ross' Geese and Lesser Snow Geese.

SOURCE OF INTERMEDIATE WHITE GEESE

Twenty-four intermediate white geese were studied between 1962 and 1968 (Table 1). In addition, information is presented on 18 other intermediates to document further the occurrence and distribution of these geese.

While banding waterfowl at Teo Lake (51° 35' N, 109° 24' W) near Kindersley, Saskatchewan, on 4 October 1961, Dzubin captured a goose with characteristics intermediate between the Ross' and Lesser Snow Geese. This adult female goose was carefully examined but escaped before measurements were taken. Dzubin trapped and measured a second intermediate goose, an immature female, at Teo Lake on 24 October 1962.

Independently, Trauger captured an adult female intermediate goose on 29 December 1962 while cannon-netting geese at Squaw Creek National Wildlife Refuge (40° 05' N, 95° 15' W) near Mound City, Missouri. This goose was presented to the

TABLE 1
SOURCE OF INTERMEDIATE WHITE GEESE EXAMINED BETWEEN 1962 AND 1968

Specimen No.	Location ¹	Date	Age ²	Sex	Present status
1	A	24 October 1962	I	F	Escaped
2	C	29 December 1962	A	F	Specimen No. 479427 U. S. Natl. Mus.
3	C	16 October 1963	I	F	Escaped
4	B	1 October 1964	I	F	Killed in captivity
5	B	1 October 1964	I	F	Specimen No. 1401 Iowa State Univ.
6	B	1 October 1964	I	M	Captivity Iowa
7	A	12 October 1965	A	M	Captivity Saskatchewan
8	C	29 March 1966	A	F	Escaped
9	E	1 July 1966	A	F	Specimen JPR, No. 65-66 ³
10	B	13 October 1966	I	M	Specimen CWS-PMBRC ⁴
11	B	13 October 1966	I	M	Specimen CWS-PMBRC
12	F	6 August 1967	A	M	Specimen JPR, No. 50-67
13	F	6 August 1967	A	M	Specimen JPR, No. 51-67
14	B	27 September 1967	A	M	Specimen CWS-PMBRC
15	D	30 September 1967	I	F	Killed by hunter
16	B	30 September 1967	A	M	Specimen CWS-PMBRC
17	B	30 September 1967	I	M	Specimen CWS-PMBRC
18	A	1 October 1967	A	M	Banded and released
19	A	19 October 1967	SA	F	Specimen CWS-Edmonton
20	A	22 October 1967	I	F	Banded and released
21	A	22 October 1967	I	M	Banded and released
22	G	1 August 1968	A	M	Specimen JPR, No. 44-68
23	A	5 October 1968	SA	F	Specimen CWS-PMBRC
24	A	21 October 1968	I	F	Specimen CWS-PMBRC

¹ A, Teo Lake, Kindersley, Saskatchewan (51° 35' N, 109° 24' W). B, Buffalo Coulee Lake, Coleville, Saskatchewan (51° 46' N, 109° 18' W). C, Squaw Creek National Wildlife Refuge, Mound City, Missouri (40° 05' N, 95° 10' W). D, Forney's Lake Game Management Area, Thurman, Iowa (40° 45' N, 95° 45' W). E, Karrak Lake, District of Keewatin, Northwest Territories (67° 15' N, 100° 15' W). F, Simpson River, District of Keewatin, Northwest Territories (67° 40' N, 100° 27' W). G, Perry River, District of Mackenzie, Northwest Territories (67° 40' N, 102° 15' W).

² I, immature; SA, subadult; A, adult.

³ JPR, J. P. Ryder, Collection.

⁴ CWS-PMBRC, Canadian Wildlife Service, Prairie Migratory Bird Research Centre, Saskatoon, Saskatchewan.

U. S. National Museum (No. 479427) where R. H. Manville identified it as a Ross' Goose \times Lesser Snow Goose hybrid.

In subsequent years, Dzubin obtained data on 15 additional intermediate geese in western Saskatchewan (Table 1). These geese were cannon-netted along with Ross', Lesser Snow, and White-fronted Geese (*Anser albifrons*) at Teo Lake and Buffalo Coulee Lake (51° 46' N, 109° 18' W) near Coleville, Saskatchewan. Nine of these intermediates were preserved as specimens, three were held in captivity, and three were banded and released.

H. H. Burgess provided two additional intermediate geese for study from northwestern Missouri (Table 1). One was trapped at Squaw Creek National Wildlife Refuge in October 1963; the other was found among 131 Lesser Snow and Blue Geese that struck a power line near Craig, Missouri (40° 12' N, 95° 24' W) in March 1966. Although several intermediate geese were seen on Squaw Creek National Wildlife Refuge during migration periods between 1963 and 1968, no additional specimens were obtained. However, L. Bates measured and photographed an immature female intermediate goose a hunter shot on 30 September 1967 at Forney Lake Game Management Area (40° 45' N, 95° 45' W) near Thurman in southwestern Iowa.

During February 1968 refuge personnel trapped two intermediate geese at Sabine National Wildlife Refuge (29° 55' N, 93° 25' W) near Cameron in southwestern Louisiana (J. M. Valentine, Jr., pers. comm.; James, 1968). These geese were banded, photographed, and released. As many as four additional intermediate geese were seen near the banding site at Sabine National Wildlife Refuge by J. J. Lynch and K. McCartney between 23 January and 28 February 1968.

While inspecting flocks of Lesser Snow and Blue Geese for neck-collared individuals, J. P. Prevett (pers. comm.) made two definite sightings of intermediate geese. On 24 October 1968, he saw a family group consisting of an adult intermediate goose, and adult Ross' Goose, and four young at Sand Lake National Wildlife Refuge (45° 45' N, 98° 25' W) near Columbia, South Dakota. He also identified an adult intermediate goose on 20 November 1968 at Plattsmouth Waterfowl Management Area (41° 05' N, 95° 55' W) near Plattsmouth, Nebraska.

Ryder has observed intermediate white geese on the breeding grounds at three locations in the central Arctic (Table 1). He collected an adult female in a nesting colony of Ross' Geese at Karrak Lake, Northwest Territories (67° 15' N, 100° 15' W) in July 1966 and trapped eight adult males while banding geese on the Simpson River, Northwest Territories (67° 40' N, 100° 27' W) in August 1967. Six of these geese were banded and released, two were collected. In 1968 Ryder studied a nesting pair of intermediate geese at Karrak Lake during June and July. This pair was successful in bringing off a brood of three goslings. He also collected another intermediate while banding Ross' Geese on the Perry River, Northwest Territories (67° 40' N, 102° 15' W) in August 1968. Intermediate geese are not restricted to the central arctic during the breeding season. In August 1967 J. P. Prevett and C. D. MacInnes (pers. comm.) reported trapping and banding an adult female intermediate goose accompanied by a brood on the McConnell River delta (60° 50' N, 94° 25' W) near Eskimo Point, Northwest Territories.

DESCRIPTION OF INTERMEDIATE WHITE GEESSE

Measurements were made of 12 adult (including subadult) and 12 immature intermediate white geese following methods described by Palmer (1962: 5) and the Canadian Wildlife Service (1963). These

TABLE 2
COMPARISON OF MEASUREMENTS (mm) AND WEIGHTS (g) OF INTERMEDIATE WHITE GESE WITH LESSER SNOW AND ROSS' GESE

Age and Sex	Culmen (exposed)		Tarsus (total)		Middle toe		Flat wing		Total length		Weight	
	Ross'	Inter. ¹ Snow	Ross'	Inter. Snow	Ross'	Inter. Snow	Ross'	Inter. Snow	Ross'	Inter. Snow	Ross'	Inter. Snow
Adult male												
No.	47	7	32	47	7	32	47	4	32	47	4	32
Min.	39	40	53	80	87	91	371	414	428	604	657	700
Max.	47	48	61	91	92	108	411	419	474	658	678	776
Mean	41.9	45.1	56.2	84.8	89.6	98.4	394.8	415.8	449.0	625.4	668.8	739.7
SE	0.3	1.2	0.4	0.4	0.8	0.7	1.3	1.2	2.0	1.8	4.4	3.7
SD	1.7	3.1	2.2	2.6	2.1	3.7	8.6	2.4	11.4	12.4	8.8	20.7
CV	4.0	6.8	3.9	3.1	2.3	3.7	2.1	0.6	2.5	1.9	1.3	2.8
Adult female												
No.	32	5	36	32	5	36	32	4	36	32	4	36
Min.	37	45	50	74	84	90	362	382	413	571	570	678
Max.	44	50	59	85	90	101	391	404	461	616	662	742
Mean	39.0	46.6	53.5	79.9	86.5	94.7	376.0	393.5	430.2	591.2	626.3	708.4
SE	0.3	0.9	0.4	0.5	1.5	0.5	1.5	4.5	1.7	2.1	19.7	2.9
SD	1.5	2.1	2.2	3.0	3.0	2.7	8.3	9.0	9.9	11.9	39.4	17.4
CV	3.7	4.5	4.1	3.7	3.5	2.8	2.1	2.3	2.3	2.0	6.3	2.4
Immature male												
No.	44	5	36	44	5	36	44	5	36	44	5	36
Min.	36	39	51	71	81	92	350	370	402	561	590	683
Max.	42	48	60	93	96	104	392	414	455	625	658	733
Mean	39.3	44.0	55.9	83.4	88.6	98.1	375.0	392.2	424.6	597.8	631.2	712.6
SE	0.2	1.5	0.4	0.5	2.7	0.5	1.4	6.9	1.6	2.3	11.4	2.3
SD	1.5	3.4	2.4	3.5	6.0	3.0	9.1	15.6	9.9	14.9	25.4	13.8
CV	3.7	7.7	4.2	4.2	6.7	3.0	2.4	4.0	2.3	2.4	4.0	1.9
Immature female												
No.	36	7	35	36	5	35	36	7	35	36	6	35
Min.	34	39	49	72	83	88	347	377	384	546	578	643
Max.	41	46	56	86	87	99	380	402	434	592	635	710
Mean	37.9	42.9	52.6	78.9	85.2	93.5	360.9	386.9	409.0	568.3	623.2	679.7
SE	0.3	0.9	0.3	0.5	0.7	0.5	1.3	3.3	1.9	2.2	9.1	2.4
SD	1.6	2.5	1.9	2.8	1.5	2.8	7.9	8.6	11.4	13.4	22.2	14.3
CV	4.2	5.8	3.6	3.5	1.8	2.9	2.2	2.2	2.7	2.3	3.6	2.1

¹ In spite of small sample sizes, calculations of SD, SE, and CV were made to facilitate comparisons.

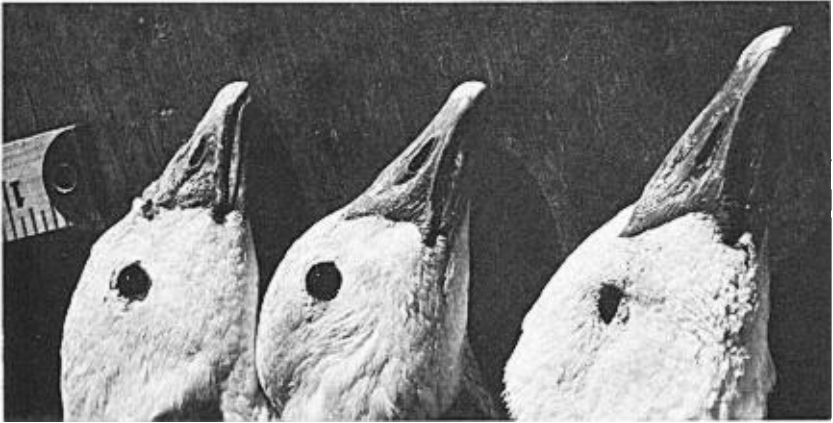


Figure 1. Comparison of heads and bills of adult Ross' (left), Intermediate, and Lesser Snow Geese. Note narrow tomlia, slim mandible, and laterally, slightly rounded fusion of feathers with the upper mandible in the intermediate.

measurements were compared with similar data from 79 adult and 80 immature Ross' Geese, and 68 adult and 71 immature Lesser Snows obtained during the 1965 fall migration in western Saskatchewan. Although considerable overlap was found among mensural characteristics, intermediate geese were generally larger than Ross' Geese and smaller than Lesser Snow Geese for all age and sex categories (Table 2).

Heads and bills.—Heads and bills most strikingly showed the intermediate nature of these geese in comparison with Ross' and Lesser Snow Geese (Figure 1). Heads of intermediate geese are not so massive or angular in shape as those of Lesser Snow Geese nor as diminutive and rounded as in Ross' Geese. Feathers of the lores meet the base of the upper mandible in a slightly rounded arc in intermediate geese, whereas this juncture of feathers and mandible forms a straight line in Ross' Geese and a sharply curved arc in Lesser Snow Geese (Figure 1).

Bills of intermediate geese are markedly shorter than bills of Lesser Snow Geese and are slightly longer than bills of Ross' Geese (Table 2). Culmen measurements of intermediate geese and Ross' Geese overlap, but measurements of the culmen for Lesser Snows and intermediate geese do not. Bills of intermediates are more slender and less massive in shape when compared with Lesser Snows but more elongate than bills of Ross' Geese.

Bill coloration of immature intermediate geese trapped in the fall closely resemble the bill coloration of young Ross' Geese. The sides of the upper mandible are gray with bright pink anterior to the nostril and on the dorsal surface. The lower mandible is generally pinkish-gray. Lesser

Snow Geese normally have gray or black mandibles in autumn. The mandibles of adult intermediates are dark pink with a greenish-gray or bluish-gray area near the base of the upper mandible. This area of pigmentation generally is not as dark nor as extensive as in Ross' Geese and shows no evidence of swelling.

Warty protuberances between the nostrils and base of the upper mandible, characteristic of Ross' Geese, are reduced or absent on the bills of intermediate geese. Lesser Snows lack coloration, swellings, or protuberances on the upper mandible. Mandibles of both immature and adult intermediate geese have conspicuous black tomia, a character absent in Ross' Geese but distinctive of Lesser Snows. The black tomia of intermediates forms a thin (6–8 mm) "smile patch" about half as wide as the broad "grinning patch" of Lesser Snow Geese (Figure 1).

Legs and feet.—Legs and feet of intermediate geese are markedly smaller than those of Lesser Snows and are more delicate as in Ross' Geese. Although tarsal measurements overlap between intermediate geese and Ross' Geese, measurements of the tarsus are consistently larger in intermediates and overlap only slightly with comparable measurements in Lesser Snows (Table 2). Midtoe measurements are relatively larger in relation to tarsal measurements in intermediate geese, overlapping less with Ross' Geese and more with Lesser Snows. Thus, intermediate geese tend to have comparatively shorter legs than Lesser Snows and larger feet than Ross' Geese.

Coloration of legs and feet of adult intermediate geese is deep pink as in adult Ross' Geese rather than red as in adult Lesser Snow Geese. In immature intermediates, leg and foot coloration also closely resembles Ross' Goose immatures. In October legs are dark gray with light tan on webs and along toes in intermediates immatures whereas this coloration of legs and feet in Lesser Snow immatures develops during January.

Bodies and wings.—Intermediate geese are smaller and slimmer than Lesser Snows but larger than Ross' Geese. These differences in body size and shape are reflected in total length measurements and weights (Table 2). Maximum measurements of total length in Ross' Geese overlap with minimum measurements for intermediate geese, but total length measurements in Lesser Snow Geese and intermediate geese do not overlap. Total length measurements are particularly influenced by the relative length of the neck in intermediates. Intermediate geese have longer necks than Ross' Geese but shorter necks than Lesser Snow Geese in relation to overall body size.

Measurements of flattened wing show wingspread of intermediate geese greater than in Ross' Geese but considerably less than in Lesser Snows (Table 2). Although flat wing measurements overlap in immature

intermediates and Lesser Snows, they do not in adults. Flat wing measurements in both adult and immature intermediate and Ross' Geese overlap.

Weights.—Although body weight provides the poorest criterion for distinguishing intermediate geese from Lesser Snow and Ross' Geese, weights reflect this bird's intermediate size (Table 2). Weights of intermediate geese average less than Lesser Snow Geese and more than Ross' Geese in spite of extreme variation in weight related to differences in seasonal status, i.e. breeding, molting, migrating, and wintering.

Plumages.—Immature intermediate white geese exhibit considerable variation in plumage coloration. Specimens examined had plumages ranging from the typical plumage of immature Lesser Snows to the typical plumage of immature Ross' Geese. In general, immature intermediates have more white feathering than Lesser Snows and more gray feathering than Ross' Geese of the same age. Plumages of adult intermediates are identical to plumages of adult Lesser Snow and Ross' Geese. Ferrous staining often observed in Lesser Snow Geese is absent from plumages of intermediate geese as in Ross' Geese.

ORIGIN OF INTERMEDIATE WHITE GEESE

The occurrence of white geese with morphological characteristics intermediate between the Ross' Goose and Lesser Snow Goose suggests either the hybridization of these species in the wild or the existence of a heretofore undescribed subspecies of white goose. Two recent observations of interbreeding involving Ross' and Lesser Snow Geese support the hypothesis that the intermediate geese are hybrids. Ryder observed a female Ross' Goose mated with a male Lesser Snow Goose at Karrak Lake, Northwest Territories, in 1967. During June this pair established a nest with two eggs on the largest nesting island. One egg hatched and a deep yellow-colored gosling was seen with the pair in early July. In late June 1968, J. P. Prevelt (pers. comm.) found a nest with two eggs attended by a female Lesser Snow Goose and a male Ross' Goose on the McConnell River delta near Eskimo Point, Northwest Territories; both eggs hatched in early July. Hence fertile matings of Ross' Geese and Lesser Snow Geese have occurred in the wild. White geese with intermediate characteristics most likely represent hybrid offspring of these species.

BREAKDOWN OF ISOLATING MECHANISMS

An apparent breakdown of isolating mechanisms between the Lesser Snow and the Ross' Goose has resulted in the hybridization of these species in the wild. Undoubtedly, several factors have contributed to the loss of natural barriers preventing interbreeding, but recent changes in

TABLE 3
TRENDS IN WINTERING POPULATIONS OF LESSER SNOW AND ROSS' GEESE
IN NORTH AMERICA¹

Winter	Lesser Snow Geese	Ross' Geese
1956-57	641,000	7,930
1957-58	617,000	12,800
1958-59	600,600	15,600
1959-60	657,200	18,000
1960-61	726,400	23,050
1961-62	732,200	27,920
1962-63	857,300	25,250
1963-64	830,200	32,450
1964-65	826,300	31,880
1965-66	752,400	30,400
1966-67	966,400	31,400

¹ After Dzubin (1965) and Lynch (1967, 1968).

the distribution and abundance of Ross' Geese and Lesser Snow Geese seem particularly important.

Dzubin (1965: 525) and Ryder (1967) have recently reviewed the population status of the Ross' Goose. During the past 20 years this species has apparently increased from an estimated 2,000 in 1949 (Hanson et al., 1956: 55) to more than 30,000 in 1967 (Lynch, 1967: 19). Although MacInnes (1964) suggested that at least part of this increment was due to an increase in effort expended to study these birds and an expansion of the wintering areas censused by waterfowl biologists, the increase in the Ross' Goose population has paralleled ($r = +0.815$) an increase in the number of Lesser Snow Geese (Table 3). These population increases have occurred during a period of climatic amelioration in arctic Canada (Hare, 1955; Cooch, 1961; 1963) and may reflect a series of extremely favorable breeding seasons. Severe weather, particularly late seasons, is a major factor governing the productivity of arctic nesting geese (Barry, 1962, 1964), including Ross' Geese (Hanson et al., 1956: 53; Ryder, 1964; 1967: 45), and Lesser Snow and Blue Geese (Cooch, 1961; 1964; Uspenski, 1965).

Concomitant with the increase in continental populations of Ross' Goose, apparent changes have occurred in this species distribution. Although the Ross' Goose and the Lesser Snow Goose were apparently isolated geographically during the Pleistocene (Ploeger, 1968: 97), these species are now broadly sympatric throughout the Canadian Arctic (Barry, 1964). Ross' Goose has been considered a relict species (Amadon,

1953; Johansen, 1956: 98) restricted in its distribution to a narrow migratory route between nesting colonies in the Perry River region of the central Canadian Arctic and wintering grounds in the interior valleys of California (see Delacour, 1954: 134; Van Tyne and Berger, 1959: 191). Recently Ross' Geese have been seen nesting in colonies of Lesser Snow and Blue Geese in the eastern Arctic on Southampton Island and at the McConnell River, Northwest Territories (Cooch, 1954; Barry and Eisenhart, 1958; MacInnes and Cooch, 1963), and in the western Arctic on Banks Island, Northwest Territories (Manning et al., 1956; Barry, 1960). Whether these reports of Ross' Geese from areas other than the Perry River region represent extensions of the distributional range of this species or reflect increased activity by waterfowl biologists is unknown, but Sutton (1932), Manning (1942), and Bray (1943) did not report Ross' Geese in the eastern Arctic, and the Eskimos of Southampton Island have no name for this species (Cooch, 1954). Furthermore, Cooch (pers. comm.) states that moderate-sized breeding colonies of 50-100 Ross' Geese now exist at several locations in the eastern Arctic. He believes that these colonies are either new or, if Ross' Geese were present in the past, their numbers were so small as to be insignificant.

In addition, changes have apparently occurred in the distribution of Ross' Geese during migration and on wintering areas. Dzubin (1965) documented the transposition of the major migratory pathway of this species from central Alberta to western Saskatchewan. This eastward shift in the Ross' Goose migration route after 1960 was preceded by an eastward movement of Lesser Snow Geese about 1955. Recently Trauger (MS) summarized published (Buller, 1955; Smart, 1960; MacInnes and Cooch, 1963; Moyle, 1964; Sweet and Robertson, 1966; and others) and unpublished records of Ross' Geese outside this species' traditional range east of the Rocky Mountains. Since 1960, Ross' Geese have been reported with increasing frequency in the Mississippi and Central Flyways. The upshot of these events has been increased interspecific contact between the Ross' Goose and the Lesser Snow Goose.

Because courtship, pair formation, and copulation in the Ross' Goose apparently take place on the wintering grounds and during the spring migration (Ryder, 1967: 21), recent changes in the distribution and abundance of this species have provided increased opportunities for interbreeding with the Lesser Snow. Trauger (MS) estimates that 200 to 400 Ross' Geese annually winter throughout the Mississippi and Central Flyways, particularly with large flocks of Lesser Snow and Blue Geese in Louisiana, Texas, and New Mexico. These Ross' Geese are isolated from the main wintering concentrations of this species in central Cali-

fornia. Thus the relative scarcity of conspecific mates increases the probability of Ross' Geese mating with Lesser Snow Geese.

Certain factors are known to facilitate the breakdown of isolating mechanisms between closely related species. One important factor is the rarity of conspecific mates when individuals of a species occur beyond the principal range of the species or in areas without an adequate number of suitable mates of the same species (Mayr, 1963: 127-128). In the absence of conspecific individuals, the instinctive mating drive overcomes the inhibitory effect of incorrect species recognition, and individuals of different species form mixed pairs (Sibley, 1961). This appears to be one of the mechanisms involved in the hybridization of Ross' Geese and Lesser Snow Geese. As courtship displays are similar among all the true geese (Delacour and Mayr, 1945: 9; Delacour, 1954: 94; Johnsgard, 1965: 25), there would be few behavioral barriers preventing pair formation in these closely related species. Although the incidence of these interspecies matings is not known, it does occur. In addition to the two observations of Ross' Geese mated with Lesser Snow Geese on the breeding grounds, Refuge Manager R. W. Rigby (pers. comm.) photographed a Ross' apparently mated with a Lesser Snow at Bosque del Apache National Wildlife Refuge near San Antonio, New Mexico.

The unusually late spring of 1967 provided insight to another possible mechanism facilitating the hybridization of Lesser Snow and Ross' Geese. Inclement weather delayed the arrival and nest initiation of both species at Karrak Lake, Northwest Territories. When the snow melted exposing the nesting habitat, Ryder noted considerable interaction between these species as nests were established. Later he found 16 nests containing eggs of both Ross' Geese and Lesser Snow Geese while studying 265 Ross' and Lesser Snow Goose nests during June on the largest nesting island. In early July, Trauger and J. B. Gollop found four additional mixed clutches on another island while determining clutch sizes in 155 Ross' and Lesser Snow Goose nests. With the exception of one nest, the incubating female of these mixed clutches was a Lesser Snow. Apparently Ross' Geese were displaced by Lesser Snows from nests established in preferred habitat. Ryder (1969) estimated more than twice as many Ross' than Lesser Snow Geese at Karrak Lake. Dump nesting by both species also may have occurred.

At present Ross' Geese nest in association with Lesser Snow Geese in at least 18 colonies in the central Arctic (Ryder, 1969) and in 4 colonies in the eastern and western Arctic (Barry, 1964; Cooch, pers. comm.). The incidence of mixed clutches of Ross' and Lesser Snow Goose eggs is unknown in other nesting colonies. It is also not certain

if mixed clutches occur only in years when late seasons delay nesting in both species and provoke acute interspecific competition for preferred nesting sites. Perhaps a few mixed clutches are formed each year.

In context with the behavioral characteristics of the Anserini (Delacour and Mayr, 1945: 8-9; Delacour, 1954: 51, Johnsgard, 1965: 24-25), the occurrence of mixed clutches of Lesser Snow and Ross' Goose eggs has important implications as a possible mechanism contributing to the hybridization of these species. It is possible that goslings of Lesser Snow Geese or Ross' Geese hatched in nests of the opposite species become imprinted to the wrong species-specific characteristics. These morphological features and behavior patterns would be reinforced by the strong family bonds typical of this group, as families migrate and winter as a unit. In geese the young apparently remain with the parents until the beginning of a new breeding season.

Although detailed comparative studies of the ecological and behavioral differences between the Ross' and Lesser Snow Geese have not been undertaken, evidence suggests that few barriers to interbreeding exist other than imprinting to morphological and behavioral characteristics of the parents. Because plumage patterns are similar in both species, the shape of the heads and bills appear to provide the most significant species-specific characteristics in the Ross' Goose and the Lesser Snow Goose. The shape and coloration of the bill may be particularly important characteristics for species recognition in these geese. Johnsgard (1965) notes that hybridization is most likely to occur if the reproductive behavior is nearly identical in two species. Courtship displays in geese are simple and subtle and vary little among the species (Johnsgard, 1963). Thus a Ross' Goose hatched in a Lesser Snow Goose nest could reach sexual maturity with little association with species-specific characteristics of its own species. The selection of a Lesser Snow as a mate and the production of hybrid offspring would be the ultimate natural consequence of mixed clutches whether competition for nesting habitat or dump nesting was the cause.

Interspecific brood adoptions (Wintle, 1968) and promiscuous copulations (Smith, 1968) observed in other waterfowl species are recognized as other possible mechanisms that could lead to the production of hybrid offspring of Ross' and Lesser Snow Geese, but these phenomena are normally intraspecific rather than interspecific when they occur in the wild. The shortage of suitable mates on the wintering grounds and the occurrence of mixed clutches on the breeding grounds appear to be the most important factors contributing to the breakdown of isolating mechanisms and the subsequent hybridization of Ross' and Lesser Snow Geese.

TABLE 4
RELATIVE ABUNDANCE OF INTERMEDIATE WHITE GEESE

Location	Year	Number			
		Inter- mediate Geese	Lesser Snow Geese	Blue Geese	Ross' Geese
Saskatchewan	1961	1	412		256
Saskatchewan	1962	1	227	1	762
Missouri	1962	1	342	348	
Missouri	1963 ¹	1	772	370	
Saskatchewan	1964	3	932		793
Saskatchewan	1965	1	197		218
Missouri	1966	1	47	84	
Saskatchewan	1966	2	35		92
Northwest Territories	1967	8	10	4	927
Saskatchewan	1967	7	1,436	1	1,202
Iowa	1967	1	243	196	
Louisiana	1968	2	202	655	
Northwest Territories	1968	1	186	7	551
Saskatchewan	1968	2	1,448		670
TOTAL		32	6,489	1,666	5,471

¹No intermediates trapped in Saskatchewan in 1963, although 263 Lesser Snow and 333 Ross' Geese handled.

SIGNIFICANCE OF INTERMEDIATE WHITE GEESE

To appraise the significance of the intermediate white geese, a quantitative index of their relative abundance was needed. As intermediates were trapped along with Ross' Geese, Lesser Snow Geese, and Blue Geese for banding, the total capture of these geese provides data for estimating the total number of intermediate geese in the Lesser Snow and Ross' Goose populations (Table 4). Geese were captured with a cannon-net trap in Saskatchewan, Missouri, and Louisiana and in a corral drive trap in the Northwest Territories. The 1966 Missouri data are based on geese found killed or injured in the power line incident, and the 1967 Iowa data are based on geese checked through a controlled public hunting area.

A total of 32 intermediate geese was found in a sample of 6,489 Lesser Snows and 5,471 Ross' Geese between 1961 and 1968 (Table 4). These data suggest a ratio of one intermediate goose to 203 Lesser Snows or one intermediate goose to 171 Ross' Geese. To estimate the total number of intermediates in the continental populations of Lesser Snow and Ross' Geese, the mean population of each species was determined

for the 1961-68 period. Mean populations for these species were calculated from data presented in Table 3 and by Lynch (1968), but populations for Ross' Geese in 1967 and 1968 and Lesser Snow Geese in 1968 were unavailable. Continental wintering populations averaged 807,600 for the Lesser Snow Goose and 29,880 for the Ross' Goose during this period. Based on the apparent incidence of intermediate geese, estimates ranged from 175 intermediates using the Ross' Goose population to 3,978 intermediates using the Lesser Snow population.

The validity of these estimates depends on the following two assumptions: (1) The number of Lesser Snow and Ross' Geese in the sample is representative of the total populations of these species, and (2) the total number of intermediate geese in the sample is representative of the actual number of intermediates occurring in Lesser Snow and Ross' Goose populations. Because the proportion of Ross' Geese in relation to Lesser Snow Geese in the sample is greater than the relative proportion of these species in their continental wintering populations, the first assumption is not satisfied. Therefore it is believed that the estimated number of intermediate geese is low using the Ross' Goose data and high using the Lesser Snow Goose data.

When Ryder spent the 1965-66 winter studying Ross' Geese on the California wintering grounds he saw no intermediate geese, but he alerted waterfowl biologists to the existence of intermediates and solicited their assistance in obtaining specimens. Since then no intermediate geese have been identified in California where thousands of geese are checked in hunter's bags on state public hunting areas (F. M. Kozlik, pers. comm.). Theoretically hybrids should be rarest where the parent species are abundant and commonest where one species is rare (Johnsgard, 1967). Therefore intermediate geese apparently are associated with geese of the Mississippi and Central Flyways, although this does not preclude the possibility of intermediate geese being observed in the Pacific Flyway in the future.

Hence the Lesser Snow Goose population of the Mississippi and Central Flyways between 1961 and 1967 was thought to provide a better basis for estimating the number of intermediate geese. During this period, the Gulf population of Lesser Snow Geese has ranged from 191,200 to 373,300 and has comprised 26 percent to 45 percent of the continental population of this species (Lynch, 1968). The mean population of 288,400 Lesser Snow Geese was used to estimate the number of intermediate geese in these flyways. At the apparent rate of one intermediate goose to 200 Lesser Snows, an average of 1,442 intermediates has occurred in the Mississippi and Central Flyways each year between 1961 and 1968. This represents 0.5 percent of the Lesser Snow Goose

population in these flyways and less than 0.2 percent of the continental population. Yet if 1,442 is a valid estimate, the intermediate goose population is 4.8 percent of the Ross' Goose population, suggesting a fairly high rate of hybridization.

Although the rate of hybridization appears to be increasing (Table 4), whether the increase in the number of intermediates is real or apparent is not known. This trend may merely reflect a larger number of observers familiar with intermediate geese and a greater effort made to identify them. Considerable evidence suggests that the hybridization of the Lesser Snow and Ross' Geese is a relatively recent event in view of the recent changes in the populations and distributions of these species. Nevertheless this does not rule out the possibility that these species crossed in the past but the hybrids were not recognized. Recent emphasis on banding waterfowl and the development of trapping techniques, particularly the cannon-net trap, have allowed waterfowl biologists to capture and handle large numbers of geese. Doubtless these factors contributed to the discovery of the Lesser Snow \times Ross' Goose hybrids.

Although someone familiar with the characteristics of intermediate geese could make an accurate identification of these birds in the field, recent variability among intermediate geese will make this more difficult. Apparently, this variability is due to the presence of F_2 and F_3 generation hybrids and backcrosses in flocks of Lesser Snow and Ross' Geese. According to Mayr (1963), first-generation (F_1) hybrids are generally intermediate between the parental species and tend to be uniform in most characteristics, while F_2 hybrids generally exhibit increased variability. Phillips (1915, 1921) found that many recombinant individuals closely approached parental characteristics in F_2 and backcross generations. This wide variability suggests that introgressive hybridization is occurring on a broad scale between the Ross' and the Lesser Snow Geese, although Mayr (1963) contends that only a small fraction of hybrids backcross with either of the parent species. As early as 1966 Dzubin suspected that one of the intermediate geese captured in western Saskatchewan was an F_2 hybrid or an intermediate goose \times Ross' Goose backcross. In 1967 white geese exhibiting a whole spectrum of intermediate characteristics appeared to be emerging. During October Dzubin examined at least three specimens with characters departing markedly from typical intermediate geese and approaching either Ross' Geese or Lesser Snows. In November Trauger captured an aberrant white goose in northwest Missouri that closely approached the Lesser Snow Goose in mensural and morphological characteristics but had several features typical of intermediate geese. This goose, the apparent offspring of a

Lesser Snow \times intermediate backcross, was also examined by H. H. Burgess and J. P. Prevett. In 1968 Dzubin caught eight geese that were the apparent progeny of F_2 or F_3 generation hybrids or backcrosses with the parent species.

Direct evidence of intermediate geese backcrossing with the parent species was obtained on the breeding grounds. In 1966 Ryder found a female intermediate goose mated with a male Ross' Goose at Karrak Lake. She laid three eggs. When D. F. Parmelee and G. M. Sutton visited the colony on 16 June, they confirmed Ryder's identification and photographed the unusual pair. On 1 July the eggs hatched and both the intermediate goose and the Ross' Goose mate were collected (JPR No. 65-66). The goslings weighed about 90 g at hatching whereas typical Ross' goslings weigh about 65 g (Ryder, 1967). In addition, J. P. Prevett (pers. comm.) saw a definite family group consisting of an intermediate goose-Ross' Goose pair and four goslings on 24 October 1968 at Sand Lake National Wildlife Refuge near Columbia, South Dakota. The young were smaller and more advanced in molt than Lesser Snow Geese.

Thus hybridization and introgression between Ross' Geese and Lesser Snow Geese appear to be occurring on a broad scale at several locations in the Canadian Arctic. The hybrids and backcrosses appear to be fully fertile between each other and the parent species. Johnsgard (1960) concludes that evidence of hybrid sterility is infrequent among waterfowl. Delacour and Mayr (1945: 9) state that hybrids from crosses between species of *Anser* (including *Chen*) usually are fertile, whereas intergeneric hybrids from crosses between *Anser* and *Branta* are sterile. According to Sibley (1961), hybridization proves genetic compatibility of the interbreeding gene pools and a close phylogenetic relationship. The hybridization of Lesser Snow and Ross' Geese brings into question Ploeger's (1968: 97) statement that "though resembling each other closely, they do not interbreed, not even in mixed colonies and, therefore, they have apparently passed the species limit." The evolutionary significance and taxonomic implications of avian hybridization have been thoroughly discussed by Sibley (1959, 1961), Mayr (1963), and Short (1969).

If the present trend of hybridization and introgression continues, several valid reasons suggest that Ross' Goose, one of the rarest North American geese, may be in serious jeopardy as a species. Hybridization may pose a potential threat to the Ross' Goose because of genetic swamping by the Lesser Snow Goose analogous to the situation postulated by Johnsgard (1967) for the Black Duck (*Anas rubripes*) and Mallard (*Anas platyrhynchos*). Because of its much smaller gene pool, Black Ducks are theoretically vulnerable to eventual swamping through hybridization and introgression with Mallards. Likewise Ross' Goose has an extremely

small gene pool in comparison with the Lesser Snow Goose. The ratio of the continental populations of Black Ducks to Mallards is 1:6 (Johnsgard, 1967), whereas the ratio of Ross' Geese to Lesser Snow Geese is 1:27 (Table 4). Hence the Black Duck is nearly five times more abundant in relation to the Mallard than Ross' Goose is to the Lesser Snow. Although the rate of hybridization in Black Ducks and Mallards has been analyzed in greater detail (Johnsgard, 1961: 35, 1967), the apparent rate of hybridization in Ross' Geese and Lesser Snow Geese may be more than twice this rate.

A comparative study of the behavioral and ecological isolating mechanisms of the Lesser Snow Goose and the Ross' Goose seems highly desirable, because genetic barriers to interbreeding apparently are lacking. There is a need to define more precisely the habitat requirements and preferences of these species where they are sympatric in order to determine if the degree of competition for food, nesting sites, and other requisites is having a deleterious effect on either species and is contributing to hybridization. There is also a need to determine further the distribution and abundance of intermediate white geese to follow changes in the rate of hybridization of Lesser Snow and Ross' Geese. This appears to be the only practical way of determining if the hybrids have behavioral or ecological advantages over the parent species that would be of selective importance. Field workers, especially those banding or handling samples of Lesser Snow, Blue, and Ross' Geese, are encouraged to record the number of intermediate geese in relation to the other species as shown in Table 4. These data will provide a quantitative measure of the relative abundance of intermediate white geese to appraise the significance of Lesser Snow and Ross' Goose hybridization in the future. The degree of biological success of hybrids depends upon the extent to which natural selection acts against them (Sibley, 1961). There is no evidence that the hybrids of Lesser Snow Geese and Ross' Geese are selected against in obtaining mates or are inferior in producing young or adapting to the environment. Regardless of the overall genetic significance of hybridization to the Ross' Goose or the Lesser Snow Goose, more contact of these species on breeding and wintering areas and along migratory routes will probably result in the production of more intermediate white geese.

The intermediate white geese described in this paper have been recognized as the hybrids of Lesser Snow Geese and Ross' Geese by the Canadian Wildlife Service and United States Fish and Wildlife Service. Recently, the A.O.U. Number 170.3 was assigned to Ross' \times Lesser Snow Goose hybrids by the Migratory Bird Populations Station for bird banding purposes.

ACKNOWLEDGMENTS

Many individuals in several state, provincial, and federal organizations aided in various aspects of this study. We are especially grateful for the valuable contributions made by the following: Harold H. Burgess, Harvey W. Miller, John J. Lynch, Jacob M. Valentine, Jr., Richard W. Rigby, Glen A. Sherwood, Harvey K. Nelson, United States Fish and Wildlife Service; George Schildman and John Sweet, Nebraska Game and Parks Commission; J. Paul Prevett and Charles D. MacInnes, Western Ontario University; F. Graham Cooch, J. Bernard Gollop, Dennis G. Raveling, Canadian Wildlife Service; Loren C. Bates and Paul A. Vohs, Jr., Iowa State University; Frank M. Kozlik, California Department of Fish and Game; Richard H. Manville, George E. Watson, and Richard C. Banks, United States National Museum. We are indebted to Milton W. Weller, Iowa State University, for helpful comments on the manuscript. Field work by Dzubin and Ryder was done under the auspices of the Canadian Wildlife Service; Trauger was employed by the United States Fish and Wildlife Service.

SUMMARY

White geese with characteristics intermediate between Lesser Snow Geese and Ross' Geese were studied between 1961 and 1968. Although the parentage of these intermediate geese was unknown, they apparently represented the first wild hybrids reported for these species.

The 42 intermediate white geese examined by various individuals were obtained in all seasons: 17 were trapped in Saskatchewan during autumn, 12 migrating and wintering birds were captured or observed in Louisiana, Missouri, Iowa, Nebraska, and South Dakota from autumn through spring, and 13 were collected or studied on the breeding grounds of the central and eastern Canadian Arctic in summer.

We measured 24 intermediates for comparison with Lesser Snow and Ross' Geese. In spite of considerable variation, mensural characteristics of these geese are intermediate for all ages and sexes. Heads and bills provide the most obvious evidence suggesting that the intermediate geese are hybrids of Lesser Snow and Ross' Geese. Plumages of intermediates are identical to Lesser Snow and Ross' Geese in adults but are variable in immatures.

Recent changes in the distribution and abundance of Lesser Snow Geese and Ross' Geese have increased interspecific contacts throughout the annual cycle. The occurrence of Ross' Geese outside the traditional wintering range has possibly contributed to the breakdown of isolating mechanisms caused by a shortage of conspecific mates in large concentrations of Lesser Snow and Blue Geese in the Mississippi and Central Flyways. Interspecies pairs have been observed on breeding and wintering grounds. In addition, competition for nesting sites in large colonies where Lesser Snow and Ross' Geese are sympatric has resulted in mixed clutches, particularly in late springs. Young hatched in these nests

may become imprinted to the wrong species-specific characteristics facilitating hybridization.

Based on the apparent incidence of intermediate white geese in samples of Lesser Snow and Ross' Geese, an estimated 1,400 hybrids may have been produced annually in recent years, and a hybrid complex appears to be forming between the two species. Intermediate white geese are known to be fully fertile with each other and the parent species. Because of its relatively small gene pool, the rare Ross' Goose may be vulnerable to eventual genetic swamping by the Lesser Snow Goose.

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