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Cranes of the World: Whooping Crane (*Grus americana*)

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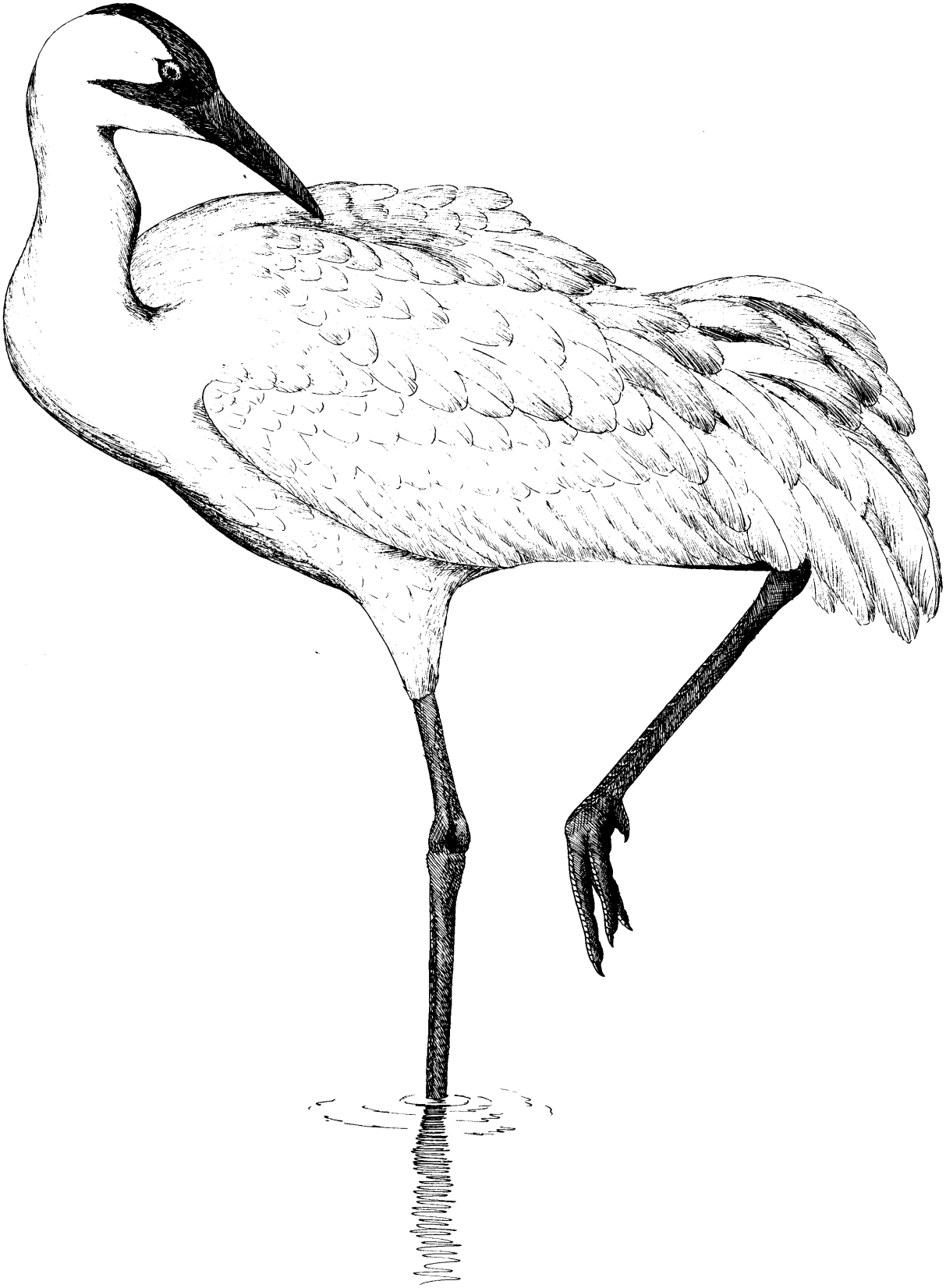


Whooping Crane

Grus americana (Linnaeus) 1758

Other Vernacular Names. Whooper; Big white crane; Grue de Amerique, Grue blanche Americaine (French); Schreikranich, Trompeterkranich (German); Amerikanishiy krikpivy zhuravl (Russian); Grulla griteria, Grulla blanca (Spanish).

Range. Breeds in Wood Buffalo National Park, Northwest Territories. Migatory, wintering at Aransas National Wildlife Refuge, coastal Texas. Formerly much more widespread, breeding south to North Dakota, Minnesota, Iowa, and Illinois, and reported from as far west as Utah, east to Cape May New Jersey, and south to coastal Louisiana. Birds hatched from eggs recently transported to Grays Lake, southeastern Idaho, have been reared by greater sandhill cranes and now winter with them in the Rio Grande area of south-central New Mexico.

Subspecies. None recognized.

Measurements. Wing, males 550-630 mm (average of 15, 601.7 mm); females 535-610 mm (average of 7, 597.9 mm). Exposed culmen, males 129-147 mm (average of 15, 138.5 mm); females 117-148 mm (average of 7, 136.7 mm). Tarsus, males 265-301 mm (average of 15, 276.5 mm); females 260-295 mm (average of 7, 281.4 mm) (Ridgway, 1941). Eggs, average 98.4 × 62.4 mm) (87-108 × 50.2-76.5 mm) (Walkinshaw, 1973).

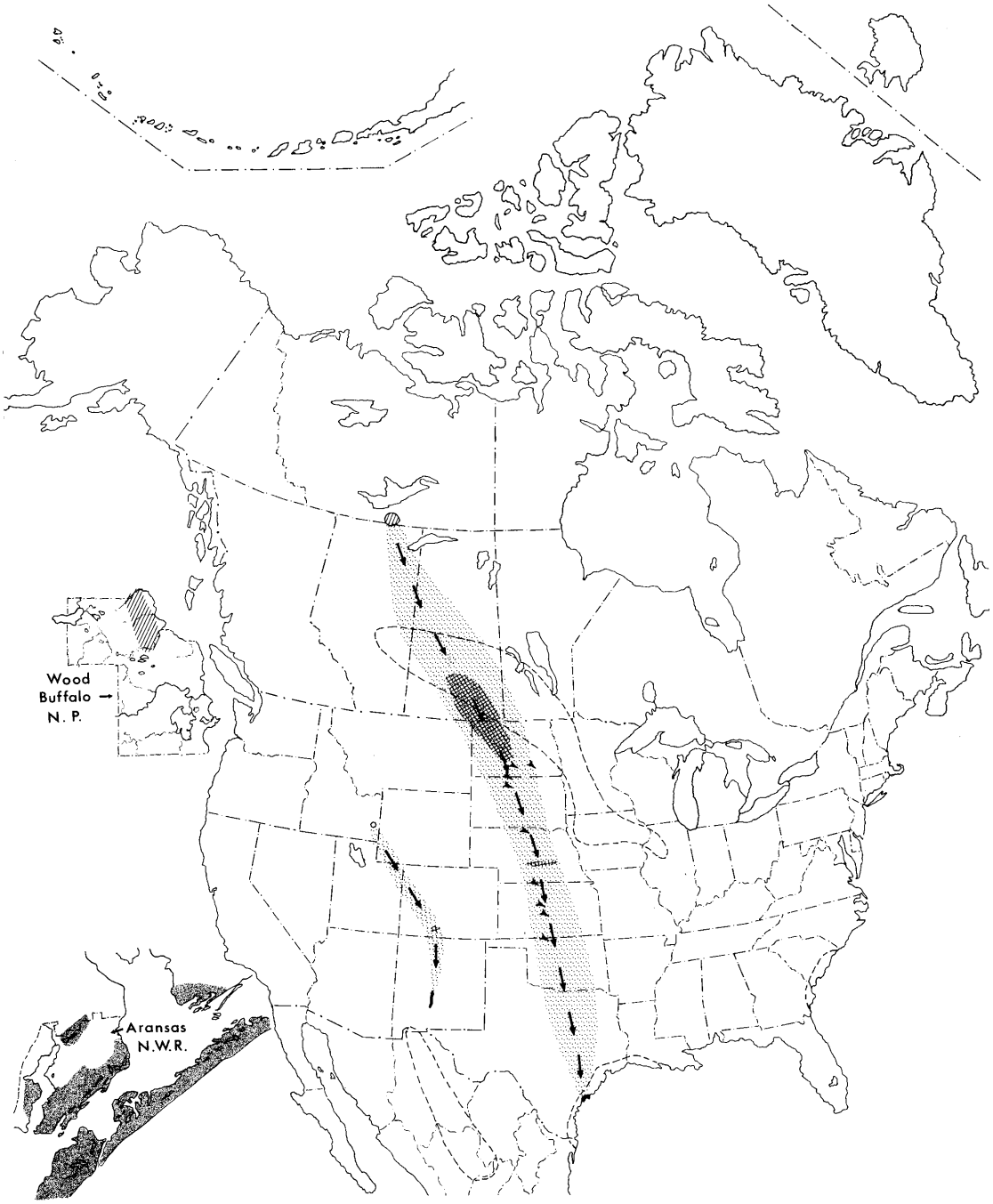
Weights. Six immatures (250 days old) weighed 5,700 to 6,700 grams (Stephenson, 1971). Adults range from 15 lb. 12 oz. to 17 lb. 5 oz. (7,142-7,851 grams) (Roberts, 1932). Erickson (1976) reports the average adult male weight as 7,300 grams, and that of adult females as 6,400 grams. The estimated egg weight is 212 grams.

Description

Adults of both sexes have the crown and anterior portion of the occiput covered with warty, carmine reddish skin that is sparsely covered by black hairlike feathers, especially on the crown. The lores and malar region, including a narrow strip extending down the throat, are also naked, carmine, and similarly bristled. There is an elongated postoccipital patch of blackish feathers, but the rest of the body and the wings are pure white except for the primaries, their greater coverts, and the alula, which are slate black. The bill is wax yellow, tipped with dull greenish or yellowish, the iris is yellow, and the legs and toes are black.

Juveniles have entirely feathered heads, and the feathers on the areas that become bare are short and rather dusky. The rest of the plumage, excepting the primaries, their greater upper coverts, and the alula, is whitish, heavily washed, mottled, and blotched with cinnamon or brownish. The upperparts of the body and the wings are heavily mixed with white and cinnamon buff feathers, with the cinnamon ones more numerous on the scapulars, interscapulars, and back. The primaries are dull blackish, the alula and greater upper coverts are dull blackish tinged with buffy, and the bill is as in the adults, but darker (Ridgway, 1941). The development of the juvenile plumage requires about 100 days, and the molt to the adult or all-white plumage is completed at 450 days in hand-reared birds (Stephenson, 1971). Fledging occurs at about 90 days, and by the second autumn young birds are not easily distinguished from adult-plumaged birds (Erickson, 1976).

Downy chicks are generally dull cinnamon to brownish on the upperparts, becoming deeper brown to russet on the rump, paler and grayer on the neck, and still paler behind the wings. The underparts are pale dull grayish buffy or dull brownish white, tipped or suffused with pale cinnamon. The bill is pale buffy brown with a flesh color basally and a small whitish spot on the upper mandible, and the legs and toes are light



Breeding (hatched) and wintering (inked) ranges of the whooping crane, together with major migratory routes (arrows), primary migratory staging areas (cross-hatching), regular migratory stopover points (arrowheads), and total current migratory corridors (stippling). Probable historic breeding and wintering areas are shown by broken lines, and Gray's Lake National Wildlife Refuge and Aransas National Wildlife Refuge, which are intensively used by whooping cranes, are shown in insets.

brownish (Ridgway, 1941). The downy stage lasts about six weeks (Stephenson, 1971).

Identification

In the field, this is the only North American crane that is pure white, except for black primaries, and it is the largest crane in North America. Its calls are loud and penetrating, and when calling in unison both sexes tend to droop their primaries somewhat, but males do so more strongly.

In the hand, this extremely large crane (wings at least 550 mm.) is readily identified by its white plumage with black legs and primaries. Even juveniles are much whiter than are juvenile sandhill cranes. The trachea in the whooping crane is much more extensively coiled within the sternum than is that of the sandhill crane.

DISTRIBUTION AND HABITATS

Historical Breeding Range

According to Allen (1952), the whooping crane's historical summering range consisted of four separate regions of known use. These included two separate nesting areas, a large area in western Canada and the north-central United States and a small area in Louisiana, and two summering areas used by nonbreeding birds, one area in the northern United States (primarily North Dakota) and the other in the Gulf Coast. The major nesting area in the north included portions of seven states and provinces, as well as the Mackenzie District of Canada's Northwest Territories. Records obtained between 1748 and 1922 indicate that seven nesting sites were known from Saskatchewan, five from Manitoba, four each from Alberta and Ontario, and two from Mackenzie. In the northern United States twelve nesting sites were reported from Iowa, three from Minnesota, two from North Dakota, and one from Illinois. The last known nesting of this migratory population south of Canada occurred in Minnesota in 1889, and the last Canadian record prior to the discovery of the breeding area in Wood Buffalo National Park in 1955 was one at Muddy Lake, Saskatchewan, in 1922. There was also a resident breeding colony in the marshes above White Lake in southwestern Louisiana. Although specific information is lacking, there was certainly a fairly extensive colony in the area that centered in the *Panicum* marshes of White Lake and extended as far west as Mallard Bay, the northeastern arm of Grand Lake. The colony evidently declined rapidly after 1900, and there is no exact information on its size until it was studied in the late 1930s. In 1938, only 11 birds were present in this colony (table 29). No nesting is known to have occurred in Louisiana after the late 1930s, and the population was totally eliminated by 1950.

A tabulation of 74 historical occurrences of the birds in Canada between 1748 and 1922 indicated that 47 percent were in aspen parklands, 15 percent were in transitional (plains to parklands) communities, 13 percent were in northern coniferous forest types, and the remaining 25 percent were in a variety of community types. Fourteen of the 18 Canadian nesting sites were in aspen or transitional communities, and all of the northern U.S. nesting sites and summer occurrence records were in prairie habitats (Allen, 1952).

Allen believed that the Iowa area may have represented the optimum breeding habitat of the species, namely tallgrass prairie marshes. However, there is little real information on the distribution of whooping cranes in northern prairie areas, for these areas were abandoned by the birds for nesting soon after white settlement. Indeed, all of the Iowa nesting records are for the period 1868-1894, during the major homesteading era. During that same period the whooping crane was apparently still abundant on the similar tallgrass prairies of Louisiana, in the parishes of Calcasieu, Jeff Davis, Allen, Evangeline, and Acadia. In all, there may have been close to two million acres of tallgrass prairie in southwestern Louisiana before the advent of rice culture, and clearly this area could have supported a potentially large whooping crane population. It was not until the late 1920s, when the U.S. Army Engineers extended the Intracoastal Waterway to Grand Lake, that the *Panicum* marshes in the White Lake area became easily accessible to humans and the center of the whooping crane's Louisiana habitat thus became threatened. In 1940 the population was reduced from 13 to only 6 individuals, effectively destroying that population and making the fate of the species dependent on the highly vulnerable migratory population, which was then known to winter largely if not entirely in the Aransas area of coastal Texas and to breed somewhere in northwestern Canada.

Current Breeding Range

The discovery of the whooping crane's northern breeding grounds in 1955 represents one of the most famous detective stories in American ornithological history, and has been fully recounted by Allen (1956), the man most responsible for its ultimate success. With the observation of a small group of whooping cranes by a mammalogist doing a survey in Wood Buffalo National Park in June of 1954, the stage was set for Allen's survey of the area in 1955, and the sighting of several pairs with young. Rather remarkably, the birds were nesting in an area already designated as a national park, in the middle of a wilderness area covering about

17,300 square miles. The actual region where the birds were found to be nesting was a pothole area of about 500 to 600 square miles, between the extreme headwaters of the Nyarling, Klewi, and Sass rivers, and the Little Buffalo River. This is an area of mostly small ponds and small lakes, varying from about an acre to up to 50 or 60 acres in area, nearly all extremely shallow and separated from one another by low ridges that support dense thickets of dwarf birch, willows, black spruce, and tamaracks. Many of the ponds have border growths of bullrushes (*Scirpus validus*) and cattails (*Typha*), which occasionally cover entire bays and arms of the larger lakes. Additionally, sedges (*Carex*), spike rush (*Eleocharis*), musk grass (*Chara*), bent-grass (*Calamogrostis*), arrow grass (*Trilochin*), and other marsh plants are present. In general, the area lies at the northern edge of the Boreal Forest region in the Hay River Forest Section, and just west of the limits of the Canadian Shield. Because of glacial action, a high proportion of the surface drift material is calcareous, with associated leaching of the limestone soils (Kuyt, 1981a).

Nesting associates of the whooping cranes in these ponds include the sora (*Porzana carolina*), the red-winged blackbird (*Agelaius phoeniceus*), the arctic loon (*Gavia arctica*), and various ducks. Mammals include the red fox (*Vulpes vulpes*), moose (*Alces americana*), black bear (*Ursus americanus*), and wood bison (*Bison bison*). Lynx (*Lynx canadensis*) and wolves (*Canis lupus*) also occur in the general region (Allen, 1956).

The water conditions of the Wood Buffalo nesting area are rather variable in pH, and the cranes apparently use only those areas with water of pH of 7.6 to 8.3, whereas the water in adjacent potholes that are not used is approximately 7.2 to 7.3. Additionally, only those potholes are used that are shallow enough to all for feeding by wading. The dominant vegetation in the potholes occupied by the cranes is bulrush, which also forms a major component of their nests. Cattails and sedges, although common in the area, are associated with deeper sloughs that are usually not used by the birds (Novakowski, 1966). However, Kuyt (1981a) reported that all these plants are used as nesting materials.

Historical Wintering Range

Allen (1952) believed that wintering of the whooping crane occurred in five major habitat types. The first of these consisted of coastal lagoons and maritime beaches that extended from the Brazos River to the Willacy County line, in Texas. The second, and perhaps the most important, consisted of interior tallgrass prairies of southwestern Louisiana; these prairies also extended to eastern Texas. Sea-rim and brackish marshes, extending from southwestern Louisiana west to the Brazos River, Texas, constituted the third habitat type. The fourth consisted of fresh swales and prairie marshes of southwestern Louisiana, which are characterized by intermittent ponds and areas of permanent fresh water, which may have been used more by nesting than by wintering birds. The last and most widespread habitat was the interior grassland plateaus of Texas and north-central Mexico. These upland grasslands are still the major wintering areas of sandhill cranes, and probably whooping cranes intermingled with these smaller cranes to a limited extent, judging from available records.

There are also scattered historical records of migrant or wintering birds extending as far east as the Atlantic Coast, which may have represented a wintering area for birds breeding in the prairie areas of Iowa and Illinois, and as far west as Great Salt Lake. However, by the early 1950s Allen (1952) was able to state with certainty that the species then wintered only on the Aransas National Wildlife Refuge of Texas and on nearby Matagorda and St. Joseph Islands.

Current Wintering Range

Apart from a recent development of limited wintering in the Rio Grande area of central New Mexico, the wintering areas used by whooping cranes are exactly the same at the present time as they were when Allen (1952) summarized the species' status. That is, the Aransas National Wildlife Refuge of coastal Texas is still the wintering area of the entire breeding population of whooping cranes (Labuda and Butts, 1979). Regular wintering still occurs only on Aransas, Matagorda Island, St. Joseph Island, and portions of the Lamar Peninsula and an area on the eastern side of San Antonio Bay called Welder Point. Altogether, about 20,000 acres of salt flats on the refuge and these adjacent islands comprise the species' principal wintering grounds (Derrickson, 1980).

Since 1950, intensive studies on habitat use in the refuge have been carried out, and four areas have been found to be of major value to cranes during that period. Sundown Bay, covering about 372 hectares and averaging less than a meter in depth, has accounted for about 45 and 53 percent of the adult and juvenile use-days between 1950 and 1978. The Dunham Bay Area, of 1,502 hectares, has accounted for 14.3 and 11.4 percent of the adult and juvenile use-days during the same period. South Matagorda Island averaged 13.2 and 11.8 percent of adult and juvenile use, and an area composed of Mustang Lake, Redfish Slough, Mustang Slough, and surrounding tidal flats and encompassing 697 hectares has accounted for 12.3 and 22.6 percent use by adults and juveniles respectively. A large number of other areas have been used to a minor degree.

Generally, all of these areas may be characterized as having a flat, estuarine topography, with salt flats that

vary under differing tidal conditions from dry sandy flats to pools of salt water up to a meter in depth. Characteristic plants include such salt-adapted forms as *Distichlis, Monanthorchloe, Spartina, Borrichia, Salicornia,* and *Lycium* (Labuda and Butts, 1979).

The reasons for the highly localized distribution of the birds in Aransas are still unknown, but it is unlikely that major differences in local food supplies account for these patterns. Labuda and Butts (1979) suggested that perhaps site preferences are associated with traditional use patterns. All of the most heavily used areas are close to the heavily used Gulf Intracoastal Waterway, indicating that human use is not a significant factor in determining crane distribution, at least under conditions of protection from disturbance.

Breeding Habitat Requirements and Densities

Allen (1956) noted that 60 percent of the total whooping crane population known to exist in 1956 was found on a single survey flight within an area of some 12 square miles, but he did not attempt to judge the basis for this extreme degree of population localization. He judged that four successful pairs nested in the Sass River area that year, and at least two additional families were probably present in the Klewi River area, with additional unsuccessful or nonbreeding adults also present in the same general area.

Kuyt (1976b) reported that pairs return annually to the same general vicinity, and in the Sass River area there are six nesting sites to which the birds have returned almost annually since at least as far back as 1966. By mapping circles around all of the nests built by a single pair over their years of known occupancy, Kuyt judged that the radius of nesting territories varied from 0.6 to 1.3 kilometers, with an average of 0.9 kilometer. Only rarely has he found active nests of adjoining pairs closer than 1.3 kilometers apart. Thus, in spite of a tendency for clustering of nests into the same general area, there is also a definite tendency toward dispersion within that area.

Because of the inaccessibility of the area, and the danger that human disturbance might affect reproductive success, there are few detailed studies on the flora and fauna of the area. Annual precipitation in the nesting area averages only 13 inches, but higher than normal rainfall early in the season causes delayed nesting, nest flooding, and lowered success. When the weather is unusually dry the nesting proceeds normally, but adults and young have to travel farther from the nest site to feed. However, there are enough potholes of varying depths in the general area to assure foraging sources regardless of these weather conditions. Areas around the nests tend to dry up each summer, and may remain dry until the following spring. This might explain why nest sites tend to be abandoned and not used in the following year. Kuyt (1976b) observed birds nesting in the same marsh or on the same island in subsequent years, but never on the exact nesting mound. Novakowski (1966) stated that nests are rarely used more than four years.

Novakowski investigated food supplies in the nesting area, and questioned whether local variations in these were responsible for nesting locations. He was unable to confirm Allen's (1956) view that the fat and protein content of the mud at the bottom of the ponds was unusually high and thus would provide unusual food value for the bird. The major insect and crustacean life of the ponds likely to be important foods for the cranes are mostly naiads of dragon-flies, larvae of caddisflies, mayflies, and chironomids, and some amphipods (*Hyalella*). However, the occurrence of all of these forms is sporadic, and may account for the tendency of individual families to forage in so many different potholes during a single summer. Although numerous, small mollusks such as snails (*Physa, Stagnicola*) and pill clams (*Pisidium*) probably provide little organic matter for food. Terrestrial food supplies, such as berries, are probably also very secondary as food sources for young cranes.

It is clear that there are no specific aspects of the habitat that clearly make this small region different from all others, or that can be selected out as critical habitat components for nesting. The general isolation of the area, and the more local isolation as provided by the numerous small potholes visually isolated from others by intervening woods and scrub, may provide the spatial separation from one another required by these highly territorial birds. Further, a low incidence of human disturbance is also apparently needed. Food supplies are obviously not unusually high, and the length of the breeding season is marginal at best, considering the long periods required for incubation and fledging of the young. It seems likely, in fact, that Wood Buffalo National Park actually represents only marginally acceptable breeding habitat, the birds having long been evicted from more favorable and more productive habitats farther to the south.

Breeding densities are difficult to judge with any degree of accuracy, because of the problems of estimating territory and home-range sizes for the species. Kuyt (1981a) reported that 18 whooping crane territories averaged about 710 hectares, but it is clear from his maps (e.g. 1976b, 1981a) that substantial areas of apparently unused territory often exist between adjoining nesting territories.

Wintering Habitats and Requirements

Allen's (1952) early studies on Aransas Refuge brought out the fact that winter territoriality is an important aspect of the whooping crane's biology, and that about

400 acres of salt flats, including water areas, are needed for each family or pair of birds. He believed that killifishes (*Fundulus*) and decapod crustaceans, especially blue crabs (*Callinectes sapidus*), probably represent the key food forms for whooping cranes. He also believed that the most important mortality factors on the wintering grounds were probably illegal shooting and periodic failures of the natural food supply. Disturbance by cattle was considered to be a negligible factor in the crane's welfare.

More recent studies by Blankinship (1976) indicate that blue crabs and several genera of clams (*Tagellus, Ensis, Rangia, Phacoides, Barnea*) are the preferred and most important food items of wintering whooping cranes, and that water levels influence the particular species that are consumed. He estimated an average territorial size for 10 territories of 176 hectares (as compared with Allen's estimate of 400 acres, or 162 hectares, for 14 territories), but also found that some pairs and family groups shared territories in some areas. He observed considerable variation in the degree of territorial defense and interactions between pairs and families, and in one case found an area of about 77 hectares being shared between a family and a neighboring pair. He believed that the most important threat to whooping cranes on their wintering grounds is the possibility of an oil and chemical spill from barges in the Intracoastal Waterway. He noted that during times of low crab populations, clams seem to offer an important alternative food supply and that cranes are very efficient at capturing both crabs and clams. Besides blue crabs and clams, cranes have been observed feeding on fiddler crabs (*Uca*), mud shrimp (*Callianassa*), white shrimp (*Penaeus*), eels, snakes (*Natrix, Thamnophis*), and crayfish (*Cambarus*), as well as on acorns and the fruit of the salt-flat cranberry (*Lycium*). Various of these foods have been examined for chemical contaminants and these have all been found to be quite low.

FOODS AND FORAGING BEHAVIOR

Foods of Adults

The early studies of Allen (1952) summarized what was known at that time about the foods of the whooping crane. Using early published and unpublished records, he concluded that the animal foods of the whooping crane included crayfish, blue crabs, aquatic insects, and freshwater minnows. Plant foods included marsh onions (*Crinum*), prairie lily (*Nothoscordum*), roots of three-square (*Scirpus olneyi*) and *Spartina,* and also such crops as sweet potatoes and sprouting corn. Later observations indicated that shellfish and fish also are consumed, but it was not until the detailed studies of Allen and Francis Uhler at Aransas that any real information on feeding behavior and foods began to emerge. By observing foraging birds, collecting droppings, and inspecting areas where the cranes had been feeding, Allen was able to establish that at least 28 types of animal materials and 17 kinds of plants are consumed on the wintering grounds. The seven major foods were determined to be a polychaete worm (*Laeonereis*), pistol shrimp (*Cragnon*), mud shrimp (*Callianassa*), blue crabs (*Callinectes sapidus*), crayfish (*Cambarus hedgpethi*), short razor clams (*Tagellus gibbus*), and green razor clams (*Solen*). Of these, blue crabs, mud shrimps, and other decapods are taken first and by preference, as they are abundant and tend to be easily obtained. Fish, insects, and reptiles are apparently chance prey, as are probably frogs and birds, at least at Aransas. However, on migration the birds evidently fed on the egg masses of frogs and toads, on various insects, and perhaps on a variety of freshwater fishes.

Blankinship's (1976) recent studies at Aransas indicate that adult cranes are very efficient at capturing both crabs and clams, in spite of the latter's burrowing abilities. A female was observed to capture 32 clams in 30 minutes, and similar rates were observed on various occasions. Clams and smaller blue crabs are swallowed whole, while large crabs are carried to shore, where the claws are broken off and the body then swallowed, followed by the claws. Clams at least 10 centimeters long and 4 centimeters in diameter are also swallowed whole.

Foods of Young

Little is known of the food of juveniles on the breeding grounds, but it presumably consists of insects and aquatic invertebrates. One crane that was captured on the breeding grounds in 1964 excreted berries in its feces, suggesting that older juveniles may use berries for a supplemental food source to these animal materials (Novakowski, 1966).

On the wintering ground the young birds feed within their parents' territories, and are regularly fed by them. Usually the young bird remains within a few yards of its mother and utters a series of soft but penetrating calls, especially when the female has captured a food item and the juvenile begins begging. About half of the food caught by the female is passed on to the young, at least during fall and winter months. As spring approaches the young birds show more independence, and sometimes move up to 90 meters away from her, periodically returning to her. Males occasionally also feed the young, but this task is seemingly done primarily by the female. Males have also been observed to bite a begging juvenile. One crane, evicted by his mother's new mate, was observed to capture and

consume nine blue crabs in only ten minutes, suggesting a considerable degree of foraging independence (Blankinship, 1976).

Foraging Behavior

On the wintering areas, daily activity is divided between active foraging and defense of the foraging territory. The adult male is the defender of the territory, as well as a general guardian. Females and young remain together throughout much of the daylight hours in their foraging activities. The birds generally also drink the brackish water in their own foraging ponds.

When foraging, the birds wade in water 5 to 10 inches deep, lowering their heads at intervals, They evidently probe in the holes of clams and burrowing crustaceans such as mud shrimps, presumably usually capturing these animals at the mouths of their burrows, rather than digging them out. However, most of the clams taken are burrowing species, and thus the long bill must be used as a digging tool on occasion.

MIGRATIONS AND MOVEMENTS

Seasonal Movements

Allen (1952) analyzed the migrations of this species in great detail, and Derrickson (1980) supplemented these early records with more recent ones. The material in table 2 summarizes the timing of the spring and fall migrations by state and province, and also provides information on average flock sizes for these two time periods.

In general, the migration follows a narrow and direct corridor between Wood Buffalo National Park and Aransas National Wildlife Refuge. The corridor is widest in the Canadian provinces and North Dakota, and generally narrowest in the area from the Platte Valley of Nebraska southward. Nebraska provides the largest number of historical records of migrating cranes, primarily because the Platte River was apparently their most important spring and fall staging area. Like the sandhill cranes using the same general area, the whooping crane also roosted on the river bars at night and came to buffalo wallows early in the morning, where they fed on various aquatic life. The birds also foraged on the prairie uplands, often turning over cattle chips and feeding on the beetles below them. An analysis of the migrations of whooping cranes through Nebraska was provided by Swenk (1933), which up until the establishment of the Aransas refuge was the major source of information on whooping crane populations. Swenk's acceptance of many unverified records proved to be a near disaster for the cranes, whose status by the 1930s was much more precarious than Swenk estimated (Johnsgard, 1982), but nevertheless a good deal of useful information was assembled by Swenk. A more recent summary of whooping crane migrations in Nebraska was provided by Johnsgard and Redfield (1978).

Derrickson (1980) has summarized the general migratory picture for this species. According to him, spring departure from Aransas usually falls between April 1 and April 15, with the last birds leaving by May 1, but with occasional stragglers remaining until mid-May, and rarely staying all summer. Spring departure from Aransas may extend over a period of as long as 44 days, or as short a period as 13 days. Allen (1952) estimated the spring migration to require from 9 to 23 days, averaging about 15-16 days. The first birds generally arrive on the Wood Buffalo National Park breeding grounds in late April.

The southward migration from Wood Buffalo falls between September 12 and September 26, and normally all the birds have arrived at Aransas by mid-November. Nonbreeding birds evidently migrate earlier or faster than do breeders, since the earliest arrivals rarely have any immatures with them. Some stragglers arrive as late as the latter part of December (Derrickson, 1980). The normal fall migration, from late September to early November, is a more protected movement than is the spring migration.

Daily Movements

Daily movements are so far rather little studied, but by using radio-telemetric methods biologists were able to track one whooping crane family all the way from Wood Buffalo National Park to Aransas in 1981. The family left the park on October 4 and flew 175 miles to the Ft. McMurray area of Alberta, where they remained for five days. On October 9 the birds flew 270 miles to Reward, Saskatchewan, and there they spent 11 days. On October 20, as snow was falling, the birds flew 175 miles to Swift Current, Saskatchewan. On the next day they flew 150 miles to Plentywood, Montana, and 470 miles the day thereafter to Valentine, Nebraska. On October 23 they flew about 125 miles to Kearney, Nebraska, and on October 24 some 190 miles to Rush Center, Kansas. On October 25 they covered 120 miles, to Waynoka, Oklahoma, and on the next day they flew 140 miles to Lawton, Oklahoma. On October 27 the birds flew an additional 30 miles to the Red River, near Byers, Texas. They remained along the Red River until November 1, when they flew 230 miles to Rosebud, Texas. The next day they flew 178 miles to Tivoli, Texas, only 18 miles from Aransas. The next morning they flew on to Aransas, completing a 2,271 mile journey (*American Birds* 36:196, 1982).

GENERAL BIOLOGY

Sociality

Information on average flock sizes during spring and fall migration periods is presented in table 2, where it may be seen that whooping cranes tend to migrate in very small groups. Part of this is of course a reflection of the overall rarity of the species, but there is little evidence of large flocks even during historical times. In the fall as well as in the spring, single birds, pairs with or without young, and other small groups are the typical social units. The largest group reported in Derrickson's (1980) summary of confirmed sightings, which updated Allen's earlier report, is of a group of 12 birds observed during March in Oklahoma. The next largest unit is of 9 birds, observed during April in Nebraska, and a group of the same size observed in North Dakota in November.

Daily Activities

Like the other cranes, the whooping crane is diurnal, and while on migration it roosts in shallow water at night. In Nebraska, whooping cranes traditionally have used the same areas of the Platte River as do the sandhill cranes, and spend the daylight hours foraging in the same manner, but apparently covering a good deal more ground. According to early observers, they also apparently left the Platte Valley in the middle of the day, rising and circling on air currents under favorable weather conditions (Allen, 1952).

Besides foraging and roosting, some time is spent on migration and wintering areas in such social interactions as fighting and dancing. Dancing occurs throughout the time that the birds are in the Aransas area, but the greatest amount of activity is observed just after fall arrival and again prior to departure in the spring (Blankinship, 1976).

Interspecific Interactions

There is relatively little information on whooping crane predators, but presumably predation on adult birds is extremely rare, because of their large size. However, one cross-fostered juvenile bird was observed to be attacked and killed by a golden eagle (*Aquila chrysaetos*) during its first fall migration south between Idaho and New Mexico.

As noted earlier, potential predators in the breeding grounds include lynx, black bear, and wolves, but it is unlikely that any of the species pose regular serious threats to young cranes or crane eggs. Kuyt (1981a) mentioned that one young crane was killed by a wolf about a week before it had attained fledging. He also noted (1981b) an instance of an egg having apparently been taken by a black bear. Most evidence indicates that it is the juvenile segment of the population that is most susceptible to mortality, especially during their first spring migration, when they become isolated from their parents and must face long migration routes, food changes, and imperfectly known obstacles (Novakowski, 1966). Mortality rates appear to be very high in the first year of life, at least as compared to that of adults (Johnsgard, 1982), but probably many of the postfledging losses can be attributed to accidents, illegal hunting mortality, and similar factors independent of predation.

The sandhill crane is theoretically a competitor of the whooping crane, but besides being much smaller it is clearly adapted to a much more vegetarian and land-based form of foraging. Thus, at least at the present time, there does not seem to be a significant degree of competitive interaction between these two species.

A considerable number of threats to the wintering habitat at Aransas exist, including the possibility of oil spills, chemical contamination of foods, disturbance by humans, accidental kills by waterfowl hunters, and possible housing developments along St. Charles Bay. All of these human-caused interactions might pose serious problems for whooping cranes in the future.

BREEDING BIOLOGY

Age of Maturity and Time of Breeding

Derrickson (1980) noted that plumage and behavioral evidence suggest that whooping cranes probably become sexually mature when from four to six years old. Males raised in captivity have produced viable semen when between three and four years old, and one female laid eggs in her fifth year. Apparent pair-bonding behavior has been observed in two- and three-year-old birds (Bishop and Blankinship, 1981).

Historical whooping crane records (table 14) indicate that about two-thirds of the available egg dates are for May, and nearly all of the remainder are for June. Recent observations in Wood Buffalo National Park indicate that eggs are normally laid in late April or early May, and hatching occurs a month later at the end of May or in early June (Derrickson, 1980). Old observations from the White Lake marsh area of Louisiana also indicate that most eggs there were found in May or early June, although newly hatched young were also reported in April and well-grown young in May, suggesting a considerably earlier onset of the nesting season there than in Canada. In a nesting effort by semicaptive birds at Aransas in 1949 the birds apparently laid their eggs on April 29 and May 1 (Allen, 1952).

Pair Formation and Courtship

Allen's (1952) early accounts of whooping crane courtship are still among the most detailed available.

He observed "solo" dancing by a male as early as mid-December, and dancing by a pair in late January. He noted that dancing became more frequent as the spring migratory departure approached, and that it could be set off, for example, by the pair encountering a group of ducks. Blankinship (1976) also observed that dancing is common while the birds are at Aransas, but that it is not limited to a courtship role, and sometimes occurred as part of antagonistic behavior between males of two pairs. Interestingly, Blankinship observed that in January of 1973 one of the parents (probably a male) of a family was lost to unknown cause. The remaining bird and its offspring stayed in the same area without obvious change in behavior, but only three weeks later the surviving bird took a new mate. This was evidently done rather rapidly, and Blankinship made no mention of the process other than that the new male would not tolerate the juvenile and repeatedly drove it away. Thus, pair bonds can evidently be formed fairly rapidly in whooping cranes, in spite of the permanent pair-bonding typical of all cranes. Maroldo (1980) also provides an interesting history of the famous whooping crane Crip, the male that was involved in the 1950 nesting attempt at Aransas, and which had first been observed as a cripple at Aransas in the winter of 1945 or 1946. Crip also was the male of the pair that nested in the mid-1950s at the Audubon Park Zoo, in New Orleans (Conway, 1957). During his lifetime of at least 35 years (he was of unknown age but in adult plumage when first noticed), Crip had a total of five different mates, three of which were provided him under captive conditions.

After his first wild mate was shot in March of 1948, he was observed with a new mate within a month, indicating that mate replacement under wild conditions can occur fairly rapidly.

The unison call ceremony of the whooping crane places it in the same behavioral category as that of the Japanese, Eurasian, and hooded cranes (Archibald, 1975, 1976). The female's voice resembles that of the hooded crane; she usually utters one long call, followed by a short call, for each male call, but sometimes also utters two or three short calls for each male call. The female does not usually lower her wrists during the unison call ceremony, but the male strongly lowers his, exposing the black primary feathers. The curved tertial feathers are held upward, forming a distinct plume, in both sexes.

Copulatory behavior in the whooping crane is apparently still undescribed, but is probably very similar to that of the Japanese crane and Eurasian crane, which are both well studied in this regard.

Territoriality and Early Nesting Behavior

Nesting studies at Wood Buffalo National Park have been carried out since 1966, and especially since 1970. Kuyt (1981a) has summarized much of the resulting information on territoriality and nest use. He noted that of 192 nest sites studied, at no time have the birds used the same nest in successive years, although they often nested in the same marsh. Territorial defense occurs in these areas, but the breeding range is lightly populated, and there are contacts with only a few other birds each year. Since the birds are both very long-lived and have a high fidelity to old territories, there is probably only a small amount of territorial interacting each year. Kuyt noted that resident birds attacked and chased off both single and paired cranes. He believed that the territorial bond is sufficiently strong for a bird to return to its territory even in the event of the death of its mate. Thus territories are likely to be reused for many years, and may become vacant only in the event that both adults die during the same year. The composite nesting areas in the Sass River and Klewi River vicinity range from 1.3 to 11.2 square kilometers, averaging (in 15 cases) 3.9 square kilometers each. Two territories in the Nyarling River area averaged 34.8 square kilometers, and one in Alberta only 0.4 square kilometer. The grand average from all areas is 7.2 square kilometers. These generally large areas include some habitats not used for nesting, although much of the area becomes used by the pairs or families during foraging or other daily activities. The present low density of the breeding population probably is responsible for the large breeding territories and the extensive areas between active territories which cranes rarely used, according to Kuyt.

Most historical records of crane nests indicate that they are located along lake margins or among rushes or sedges in marshes, with the water anywhere from 8 to 10 inches to as much as about 18 inches deep. The nest studied by Allen (1952) at Aransas was constructed in cattails, in water apparently initially about a foot deep. However, falling water levels eventually made this level much less. The nests often are between 2 and 5 feet in diameter, and range in height from about 8 to 18 inches above the surrounding water level. Nesting has also been reported on muskrat houses and on damp prairie sites.

Egg-laying and Incubation

Judging from various accounts, it is likely that the eggs are normally laid two days apart, and that in most cases two eggs are laid. Kuyt (1981b) reported that of 203 clutches observed between 1966 and 1980, 90.6 percent of them contained two eggs, 7.9 percent had a single egg, and 1.5 percent had three eggs. He also reported two apparent cases of renesting in wild birds. One nest with a single egg was found abandoned on May 1, 1976, but a new nest about a kilometer away in the same territory was found on May 6 with two eggs. In 1980, a

nest with two eggs was found abandoned on May 14, but on June 3 a new nest was found 700 meters away from the abandoned one.

Both sexes incubate, and Allen (1952) provided detailed observations on incubation behavior and nest-relief activities. He noted that the male spent more time on the nest than did the female, and that there was an average of 7.6 nest exchanges per day. Toward the end of the incubation period the female began to spend more time on the eggs and to relieve the male more frequently. Walkinshaw (1973), studying the same birds for seven days, made similar observations. He found that the female did more nighttime incubation than did the male, but that the male did 52.9 percent of the daytime incubation. During the entire seven-day period the eggs were incubated 92.7 percent of the time. Conway (1957) watched the same pair some years later when they nested in the Audubon Park Zoo, and found that on that occasion the male did most of the nighttime incubation and the female undertook most of the daytime responsibility.

Whichever bird does the incubating, the other one serves as a "guard." In particular, Allen found the male to be intolerant of intruders such as herons, egrets, and spoonbills, particularly the herons and egrets. Vultures and deer were also sometimes challenged by the cranes. Walkinshaw observed cranes chasing herons, egrets, pelicans, ducks, and even swallows. Historical accounts by egg collectors indicate that injury-feigning, with wings drooping and spread and the head lowered, is a common response to human intrusion near the nest.

The incubation period is probably 33 to 34 days under wild conditions, but has been found to be 30 to 31 days at the Patuxent Wildlife Research Center. Conway (1957) reported that the second chick hatched three days after the first one, and the second-hatched bird did not feed until some 30 hours after hatching.

Hatching and Postbreeding Biology

Conway (1957) reported that the newly hatched chicks at the New Orleans Zoo were fed earthworms, dragonflies, and grasshoppers by their parents, and that the young birds were offered food almost constantly. Rusty, a chick hatched at Aransas Refuge in 1950, was quite active within 24 hours after hatching and by the fourth day was being brooded more than 100 yards from the nest.

During the first 20 days after hatching, the families generally remain within 1.8 kilometers of the nesting site, with daily movements averaging about 0.8 kilometer (Derrickson, 1980). The young birds fledge when they are about 80 to 90 days old. Until that time they are vulnerable to large predators such as wolves, and Kuyt (1981b) reported at least one case and perhaps two of unfledged young being killed by wolves.

Kuyt's (1981b) data suggest that chick and juvenile losses tend to occur throughout the summer, rather than being concentrated during the first two weeks after hatching. He suggested that relatively dry conditions during recent summers in the breeding grounds may have made the older young more vulnerable to large predators than is the case when water supplies are adequate.

Whooping crane juveniles continue to be fed by their parents, especially the female, for an extended time during their first fall and winter of life, and probably do not become truly independent until they are gradually abandoned by their parents the following spring. However, the young birds often do follow their parents northward in the spring, and it is likely that they are not forcefully separated from them until their arrival on the breeding grounds.

RECRUITMENT RATES, POPULATION STATUS, AND CONSERVATION

A great deal of information is now available on recruitment rates in the whooping crane, owing to the opportunities for a complete yearly census of the entire wintering population at Aransas Refuge (table 29). Absolute mortality rates as well as natality rates and rates of population increase can also be easily calculated (Johnsgard, 1982; also table 8). It is apparent that since 1938 the age ratios, and thus gross recruitment rates, have declined considerably, but there has also been a decline in mortality rates, presumably reflecting a higher level of protection from poaching and other losses caused by humans. However, the actual annual rates of population increase are currently at an all-time low (Johnsgard, 1982), and in recent years the Canadian and American conservation agencies have made innovative efforts in trying to protect the whooping crane population by cross-fostering efforts with greater sandhill cranes. These efforts, discussed more fully in chapter 9, are not yet far enough along to predict with certainty their success or failure. So far, none of the cross-fostered birds have successfully paired and bred. However, they have drawn a good deal of attention to the plight of the whooping crane, and have virtually made it the universal symbol of wildlife conservation in North America. It can only be sincerely hoped that such efforts will succeed in preserving the most spectacular of all wild birds in North America for future generations to see and admire.

EVOLUTIONARY RELATIONSHIPS

There can be little doubt that the nearest living relative of the whooping crane is the Japanese crane, as is indicated by their behavior (Archibald, 1975, 1976) and also by their anatomy (Wood, 1979). The two might well be regarded as a superspecies, judging from their great morphological and behavioral similarities.