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January 1983

Cranes of the World: Wattled Crane (*Buggeranus carunculatus*)

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Wattled Crane

Bugeranus carunculatus (Gmelin) 1789

Other Vernacular Names. Great African wattled crane; Grue caroncule (French); Glockenkranich, Klunkerkranich (German); Hooka Zuru (Japanese); Asbrikanskiy Sorodavachaty (Russian); Mothlathomo (Sotho, Sesuto); Grulla zarzo (Spanish); Makalanga (Zambian).

Range. Resident in eastern and southern Africa, from Ethiopia in the north southward discontinuously through southern Tanzania (apparently absent from Kenya and northern Tanzania) and Mozambique to the Transvaal and Natal, and westward to southern Angola and Namibia (South West Africa), in the latter area breeding locally only. Now extirpated from Cape Province and Orange Free State, and probably declining elsewhere (West, 1976).

Subspecies. None recognized.

Measurements. Wing (chord), males 613-717 mm (average of 7, 669.7 mm); females 619-687 mm (average of 7, 634.1 mm). Exposed culmen, males 150-185 mm (average of 7, 174.0 mm); females 124-183 mm (average of 7, 161.4 mm). Tarsus, males 298-342 mm (average of 7, 321.6 mm); females 232-330 mm (average of 7, 309.8 mm). Eggs, average 101.9 mm × 65.3 mm (91.0-116.5 × 59.3-71.5 mm) (Walkinshaw, 1973).

Weights. An adult male and female at the International Crane Foundation weighed 8,966 and 8,285 grams (G. Archibald, pers. comm.). The estimated egg weight is 240 grams. Weights of 21 infertile eggs ranged from 199 to 258 grams (Conway and Hamer, 1977). One fresh egg weighed 265.3 grams (Walkinshaw, 1973). Sugita and Suzuki (1980) provide growth curves for three chicks to 135 days of age, when they averaged over 5,000 grams.

Description

Adults of both sexes are similar, but the bare skin of the

male is darker red than that of the female. In both sexes this bare area is covered by small, rounded excrescences. The feathered portion of the head is dark slaty gray above the eyes and on the crown, but is otherwise white, including the wattles, which are almost fully feathered and hang down from the region of the upper throat. The mantle, breast, primaries, secondaries, tail coverts, and tail are black, and the remainder of the back and wings are ashy gray. The breast and neck are white, continuous with the head. The inner secondaries are elongated, reaching beyond the tail. The iris is dark orange to reddish, the bill is light reddish brown, and the legs and toes are black or dark gray.

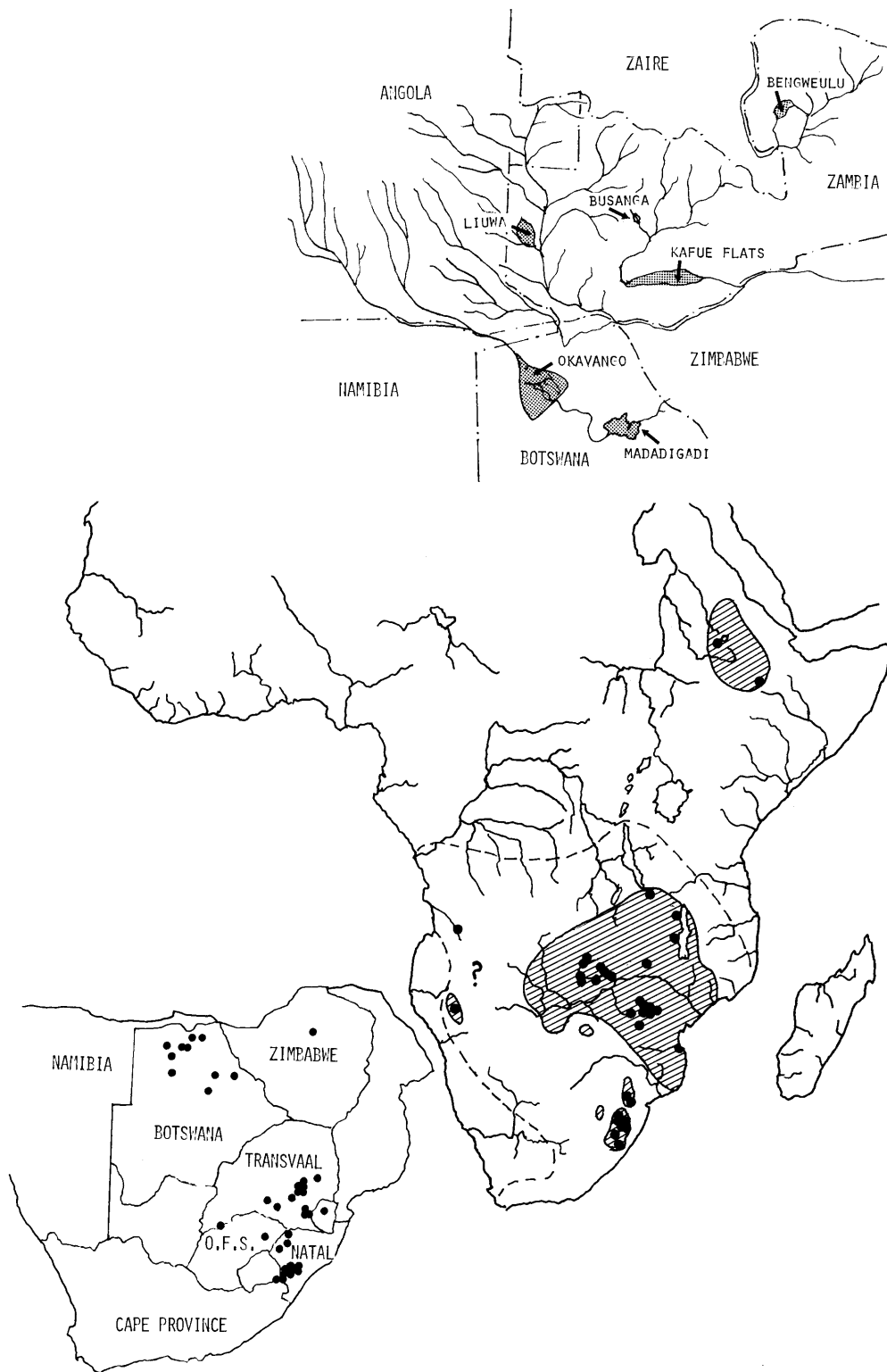
Juveniles lack the bare skin on the face, and have less prominent wattles. The body plumage is more tawny and less contrasting than that of the adult.

Immatures in their first winter resemble adults but lack black crowns and are not so black on the back and underparts.

Downy chicks are pale buff on the head and neck, becoming dark brown on the lower neck, back, the back of the wings, and the thighs. The iris is brown, the bill is horn-colored, and the legs and feet are bluish black. The wattles are slightly evident and covered with pale buff down (Walkinshaw, 1973).

Identification

In the field, this is the only African crane that has an all-white neck, contrasting with a blackish crown, breast, and back. Like the blue crane, it has long and pointed secondaries that nearly reach the ground, but the blue crane lacks a wattle or red on the face. The wattled crane's calls are higher in pitch than those of any other cranes except the Siberian crane, and are usually begun from a coiled-neck posture, followed by vertical neck-stretching.



Distribution of the wattled crane in Africa, including known current distribution (hatching), probable maximum historical range (broken line), and breeding records (after Snow, 1978). Insets show 1980 sightings (after Day, 1980), and the locations of major breeding areas in upper Zambezi Basin (after Konrad, 1981).

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In the hand, the pendent wattle immediately identifies this species. This trait is present even in downy young chicks. Internally, the trachea does not penetrate the sternum, but merely indents the keel with a vertical loop.

DISTRIBUTION AND HABITATS

Historical Range

There can be little doubt that the range of this species has retracted considerably in the current century, but even today its distribution is rather poorly known. The wattled crane is a bird of local and discontinuous distribution (Snow, 1978) and is largely limited to rather inaccessible wetlands. The northern population seems to have always been confined to the Ethiopian uplands, although there is an apparently undocumented occurrence in Somalia. Records from Ethiopia are fairly numerous and range in elevation from 7,000 feet (2,134 meters) to 12,000 feet (3,990 meters). The most northerly of these records is from the vicinity of Asmera, in Eritrea, and the most southerly from northern Sidamo Province (Snow, 1978; Walkinshaw, 1973). Breeding records exist for Dangila, Gojam (Gwejam) Province, in 1928, and for Adkoba, in Bale Province, in 1963 (Walkinshaw, 1973).

The other population of wattled cranes is separated by an equatorial gap of more than 1,000 kilometers from the northern birds; there are no records for either Uganda or Kenya. In Zaire there are but few records, including an old coastal record from Banana. There are also specimen records from Kasai Occidental, from Nieuwdorp in the upper Katanga drainage, from Kinda in the Lulua District, Elisabethville, and from Lalambwe and also 65 kilometers north of the Mwati River. No breeding records exist for Zaire.

To the south of Zaire, in Angola, one breeding record (1934) exists, for Andula, in the Bie District. At least in the late 1800s it was common in the interior of Benguela, and more recently (Traylor, 1963) was widespread in the southern interior, north to Cuanza Sul and southern Lunda.

In northern Namibia (Ovamboland) there are several old records, and the species had probably long existed in the flats and intermittent rivers that flow north and east into Angola and Botswana. However, the only available breeding records are fairly recent ones, from Ovambo (West, 1976).

In Botswana, (previously Bechuanaland Protectorate) the species has probably always been confined to the northern areas (Ngamiland); nonbreeding records extend south to the vicinities of Lake Dow (Xau) and Lake Ngami (Snow, 1978).

Probably the greatest changes in historical ranges

have occurred in South Africa. The species was once widespread from the Eastern Cape to as far south as Somerset West and Caledon in the Western Cape. However, Snow (1978) does not show any breeding records for anywhere west of the border area separating Cape Province from Natal. Walkinshaw (1973) likewise provides no breeding records for the Cape Province, but there is a possible breeding record for the Cape Town area from the 1800s (West, 1963). However, breeding is historically well-documented for Natal, Orange Free State (at Harrismith), and for the Transvaal (Belfast and the Vaal River).

The species is seen in Lesotho during migration, and in Swaziland its historic occurrence is undocumented. However, in Natal the species has apparently long been relatively common, especially among the vleis that lie directly below the low berg regions, at elevations of 1,524 to 1,829 meters. Breeding records exist for as early as 1895 for the Newcastle area, while other early records exist for the Mooi River area, Hidcot, and Nottingham Road. More recent Natal breeding records from the 1960s exist for the Dartmoor Forestry Reserve, Greytown, Himeville (Underberg), the Hlatikulu River area, and Howick, Sarsdon Hill (Walkinshaw, 1964).

In Mozambique, breeding has been documented for the mouth of the Sabi River, near Lourenco Marques. This seems to be the only sea-level breeding record for the species.

In Zimbabwe (previously Southern Rhodesia), a rather large number of breeding records exist (Walkinshaw, 1973), but in Tanzania there are but a few nonbreeding records (Burungi and Hhehe). The northernmost record from eastern Africa seems to be from the vicinity of Iringa, in southern Tanzania (Snow, 1978).

In Zambia (previously Northern Rhodesia), the species has apparently always been fairly common, and there are many breeding records (Benson et al., 1971; Walkinshaw, 1973). It is especially frequent in the west, but is scarce in the northeast and the Luangwa Valley, and evidently absent from the middle Zambezi. Breeding records there extend throughout the year, with a peak between May and July.

Current Range

The present status of the wattled crane in Ethiopia is totally unknown, but current political conditions there make it unlikely that the species is prospering.

The species' status in Zaire is scarcely better known, but Konrad (1981) suggested that the southeastern corner of this nation may support some birds, especially in the Upemba Basin region.

In Angola, the situation is likewise poorly studied, but Konrad (1981) believes that a significant population may still exist in the tributaries of the Zambezi River in the east, in the wetlands bordering Namibia in the

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south, and in the central highland and associated basins.

In Namibia, wattled cranes now occur only in the extreme northern grasslands and are probably decreasing as a result of human population pressures (West, 1977).

In South Africa the wattled crane has now been extirpated from Cape Province (West, 1976; Konrad, 1981). In Orange Free State the situation is scarcely better; West reported "no reliable records," and Konrad stated that only two pairs are known to exist there.

In Natal the species is said to be fairly widespread in areas above 1,282 meters, and is most common above 1,648 meters (West, 1963). However, Day (1980) estimated that only about 40 pairs are now known in all of Natal. In the Transvaal the wattled crane is declining, and perhaps the area supports no more than about 25 pairs (Konrad, 1981); about 18 pairs are in the Belfast area, and 3 other pairs occur south of Belfast between Lake Chrissie and Amsterdam (Day, 1980; Tarboton, in press).

In Swaziland the species is now considered to be extirpated (Konrad, 1981), although as recently as the 1970s a few pairs were believed to be resident in the western part of the country (West, 1976).

In Mozambique, the situation is uncertain. In the lower areas, the cranes appear to be nomadic, occurring during the summer and early autumn in Gorongosa, the Banhine, and the Delta grasslands. There are also records from various high-altitude grasslands, and there may be a migration of birds between these grassland types. Probably breeding birds are most likely to occur in the mountainous border country of Zimbabwe and Mozambique from Inyanga south to Chipinga (West, 1976).

In Malawi, there are resident wattled cranes on the highland plateaus, but these areas are being affected by afforestation of the plateau grasslands and by human population densities (West, 1976). This population may now be endangered (Konrad, 1981).

In Botswana, the primary wattled crane habitats are found in the Okavango Delta and the Magadigadi wetlands. The Okavango area, a permanent wetland with associated savannas within a 13,000 square kilometer area, supports several nesting pairs and perhaps as many as a thousand birds during February, in the nonbreeding period. Magadigadi likewise has large numbers (from several hundred to as many as 2,000) of cranes between January and May; these birds are believed to come from the Kafue Flats area of Zambia during high-water periods there, and many molt during this period.

In Zambia, the most important present wattled crane habitats are in the upper Zambezi and the nearby Kafue River, while the Bangweulu area of the Chambezi and Luapula rivers provides a secondary area of significance. On the upper Zambesi, the Liuwa floodplain is a

3,500 square kilometer area that attracts both nesting and nonbreeding cranes. In one November census, 145 wattled cranes were observed, and 58 percent of them were paired. The area is included in the Liuwa Plain National Park. To the east, the Kafue Flats area, a floodplain of some 6,000 square kilometers along the Kafue River, supports Africa's largest single population of wattled cranes, including about 300 breeding pairs and up to 3,000 birds during the peak season. Breeding here peaks in June and July, when from 3 to 40 percent of the paired birds attempt to nest, depending on the amount of flooding. During the rainy season, which begins in November, many cranes leave the area during years of high rainfall, evidently moving to the Magadigadi flats of northern Botswana. In Zambia, near the Kafue Flats, is a small permanent wetland, Busanga, encompassing about 400 square kilometers. This also is a wattled crane nesting area; it is part of Kafue National Park, and is thus protected (Konrad, 1981).

Lastly, the Bangweulu wetlands is a 20,000 square kilometer area composed of a lake and its associated wetlands, and supporting a still unknown number of resident wattled cranes. Konrad (1981) observed 20 cranes there in his 1978-79 census, half of which were paired.

Habitat Requirements and Densities

This is a relatively specialized species of crane, and depends on the presence of shallow wetlands and associated vegetation for its sedge-based vegetarian diet. Foraging is done primarily by probing in a soft substrate, and thus an abundance of aquatic plants that grow in shallow water and can be pulled or dug out, to obtain their roots or tubers, are critical components of the habitat. The birds are also highly territorial during the breeding season, defending an area greater than a square kilometer, which means that breeding densities will always be relatively low. Konrad (1981) estimated that the 6,000 square kilometer area of Kafue Flats might support some 300 breeding pairs, or a breeding range of 20 square kilometers per breeding pair. The other areas he surveyed had appreciably lower estimated breeding densities.

Nonbreeding Range and Habitats

There is little information on the nonbreeding range of this species, although it is clear that in some areas a degree of migration does occur. The most notable example of this is the use of the Magadigadi area of northern Botswana as a wet-season concentration and molting area, but not for breeding. Probably nonbreeding habitats differ little from breeding ones, since the mode of feeding is seemingly the same throughout the year, and thus the environmental conditions probably

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differ rather little, save for the specific habitat needs associated with nesting sites and other breeding-season activities.

FOODS AND FORAGING BEHAVIOR

According to Walkinshaw (1973), this is primarily a vegetarian and insect-eating species, but at times extends its prey-catching to frogs and snakes. It typically digs in the soil, for plant tubers, insects, and the like. At times it will also eat grain and grass seeds as well, but not to the extent of the other two African cranes.

Konrad's (1981) study of foraging behavior is especially valuable. He noted that the better part of each day is spent in foraging, primarily by digging in a wet substrate. Water lilies (*Nymphaea*) and the underground parts of *Cyperus* and *Eleocharis* sedges are the most commonly consumed foods.

When a food source is located, the bird begins a vigorous probing with its bill, sometimes digging so strongly that the whole body moves with the effort. Most of the digging is done in areas covered by shallow water, and apparently the food is largely found by tactile means. Digging in upland areas is confined to soft soils, such as rain-moistened ones. Of nearly 750 feeding habitat sites observed, 86.5 percent were in shallow water, 10.6 were in uplands, and 2.8 percent were in deep water, where the bird had to submerge its entire head to obtain food. Of nearly 800 feeding activities records, 98.4 percent were by digging, one percent by pecking, and there was a single observation of a crane picking up a snail. Stripping of grass has also been observed in this species (Douthwaite, 1974).

Foods taken by chicks have not yet been studied but presumably are very similar to the predominantly invertebrate foods consumed by other young cranes.

MIGRATIONS AND MOVEMENTS

Although very little is known of the migrations of this species, it is apparent that considerable seasonal movements do occur. These may be opportunistic ones, depending on local water conditions, rather than regular ones associated with seasonal temperature variations, but nonetheless are important to understand in terms of conservation of the species. Thus, the largest single known breeding population, that of the Kafue Flats, apparently regularly moves to Magadigadi during the rainy season. During a normal year, less than 1,000 are present at Magadigadi during high flood, but as the water subsides the population increases and may reach a total of 3,000 birds (Douthwaite, 1974). In different years the total may vary from a few hundred to

2,000 birds, suggesting that this is indeed an opportunistic movement rather than a fixed migratory pattern. There are perhaps also some migratory-like movements between the high and low plateau areas of Mozambique (West, 1976).

Daily movements of this species are still unstudied, although it is reported that the birds are relatively sedentary while on their small wetland nesting territories (Konrad, 1981).

GENERAL BIOLOGY

Sociality

Outside of the breeding season, these birds are moderately gregarious, and at times the flock size may be considerable. West (1963) provides some tabular data on flocks in Natal, indicating flock sizes of up to 89 birds. Of 63 flock counts, 40 percent were up to 10 birds, 19 percent 11 to 20, 6 percent 21 to 30, 5 percent 31 to 40, and 9.5 percent each in the 40s, 50s, and 60s or higher. Konrad (1981) observed nonbreeding birds in groups of from 3 to 43 individuals.

Daily Activities

According to Konrad (1981) most of the daylight activities are foraging activities. Perhaps the specialized foraging behavior of this species requires that a larger part of its available time be spent in such activities. No specific information is yet available on roosting behavior of the wattled crane.

Interspecific Interactions

Wattled cranes exhibit occasional contacts with crowned cranes, but their habitat needs are considerably different. Thus, Konrad (1981) noted that in the Liuwa area of the Zambezi Basin the crowned cranes were six times more abundant than wattled cranes. This greater abundance was associated with their more upland habitats and greater areas of undisturbed breeding habitat during the rainy season. Crowned cranes typically feed in upland habitats and forage by grazing, pecking, or seed-head-stripping rather than digging.

In nearly all the wetlands studied by Konrad, lechwe antelope (*Kobus lechwe*) were present in association with wattled cranes. The lechwe and wattled cranes feed on the same plants, with the lechwe consuming the emergent and submerged portions and the cranes eating the tubers and rhizomes, according to Konrad.

Spur-winged geese are also close associates of the wattled crane, but often frequent somewhat deeper waters (Konrad, 1981). They feed on the shoots and seed heads of grasses, the soft parts of aquatic plants such as water lilies, and to a small extent on animal materials.

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Thus their foraging niche overlaps somewhat with that of the wattled crane.

No information on important predators of the wattled crane is available, but the large size of adults probably places them out of the reach of most predators. West (1963) mentioned the jackal (*Canis mesomelas*) as a probable predator of one chick, and noted that humans are also an important source of mortality to young birds.

BREEDING BIOLOGY

Age of Maturity and Time of Breeding

In Natal, nesting occurs throughout the year (Cyrus and Robson, 1980). In Zambia also wattled cranes breed throughout the year but with a distinct peak around June (Konrad, 1981). Records from elsewhere indicate breeding in Ethiopia from May to August, in Malawi from May to July and also in October, and in the Transvaal during August (West, 1963).

Although the actual age of maturity in wild wattled cranes is unknown, Konrad (1981) suggests that they mature in their third or fourth year, and at that time form a life-long pair bond. A pair of wattled cranes at the Flamingo Gardens, in England, bred initially when both were eight years old (unpublished survey of Joe Blossom).

Evidently juveniles remain with their parents for their entire first year, since West (1963) observed a yearling with its parents in late April, and by May 19 the pair were again already incubating.

Pair Formation and Courtship

Courtship displays of the wattled crane are still only poorly described. West (1963) described dancing by a breeding pair during late April, just prior to nest-building. Although both birds participated, one danced in a more restrained fashion. During dancing they assumed a weird heraldic attitude, with the wings held high, the beak open, and the legs often lifted from the ground. West did not describe any associated calling, and considered breeding birds to be remarkably silent.

According to Archibald (1975, 1976), the wattled crane's unison call differs from all other species except for the Siberian crane. The female begins the display by quickly lowering her head to the shoulders, then instantly extends the coiled neck to the vertical while holding the head about 30 degrees in front of the vertical. This posture is maintained through the rest of the display, which lasts for from three to seven seconds. The male joins in the display very soon after the female begins her preliminary movements, and his head movements and initial vocalization closely resemble those of the female initially. However, whereas the female utters

a series of evenly spaced short calls after her introductory call, the male produces a long and partly broken call, followed by a series of short calls, and ends with another long call. As the final call is uttered he raises his humeri about 20 degrees above the back. The calls of the wattled crane are higher in pitch than those of any other crane except for the Siberian crane.

Copulatory behavior in the wattled crane is still undescribed.

Territoriality and Early Nesting Behavior

According to West (1963), the birds become territorial prior to nest-building; in one case the breeding area was initially occupied in mid-April, the nest site was fixed by late April, and hatching occurred on June 28. The territory seemed to be as large as the birds could see from the nesting vicinity, and was maintained through the rearing period of the chick. The area used exceeded 200 acres (0.8 km²) all of which was defended and fed over. Even after the chick was able to fly the birds returned to the breeding territory for some lengths of time, and thus it was not totally abandoned, even when the birds were sometimes absent for days or weeks at a time.

West (1963) reported that in 1956 he first saw a pair of cranes at a nest site on April 29, with one of them crouching and apparently stacking bits of grass. They were not seen at the nesting site again until May 15. The nest was not actually visited by West until May 30, and hatching occurred on June 28, indicating that egg-laying and incubation must have begun about the end of May. This would suggest an approximate three-week interval between the initial observed nest-site activity and egg-laying. In large wetland areas the exact timing of nest initiation is probably dependent on local hydrologic factors such as the amount of inflow from local precipitation, the timing of floodwaters from more distant upper basins, and the rate of local outflow. This kind of nest-initiation strategy takes maximum advantage of the large areas of shallow floodplain that "bloom" with new sedge growth after a dormant period during high floods (Konrad, 1981).

The nests are typically built in open grass and sedge marshes that are bordered by drier flat to sloping grassy meadows, with vegetation from knee- to shoulder-high, and water up to a meter in depth. Most nests are large piles of grasses, tossed into a crude heap and gradually packed down. Some are placed on natural mounds, knobs, or old nests of spur-winged geese, while others are built entirely by the cranes themselves. One nest was found on the top of a large submerged rock in the middle of a stream. When the nest is built in a marsh, the area immediately around the nest is stripped of plants for a distance of up to four meters from the nest. The nest itself is often from about 120 to 180 centimeters wide at the water level, and may be in water up to at least 61 centimeters deep (Walkinshaw, 1973).

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Egg-laying and Incubation

It is clear that the average clutch size of this species is the smallest of all of the world's cranes (see table 16). Konrad (1981) reported an average clutch of only 1.6 eggs among 95 nests, and suggested that the probability of many of these being incomplete clutches is quite small, since the second egg is laid within 18 hours of the first. It is further possible that many pairs do not attempt to breed every year, but instead breed opportunistically whenever conditions permit. Such breeding occurs in large upland areas when floodwaters recede, increasing the areas of available floodplain for foraging and nesting. In smaller wetland areas nesting occurs when rains provide enough water to provide habitats in the wetland edges and in nearby upland areas.

According to West (1963), during the first week of incubation both birds remained close to the nest and never left the eggs untended. After the end of the first week, the nonincubating member of the pair spent an increasing amount of time away from the nest vicinity, feeding in fields up to a quarter of a mile away from the nest, often in dry cover dominated by tall *Hyparrhenia filipendula*. From about the eighteenth day onward, both birds occasionally were found off the nest simultaneously. However, at the time of hatching, both birds attended the nest once again.

Walkinshaw (1973) noted that during a two-day study, the male incubated at night, while the daylight activities were shared by both birds. The average period of daytime incubation was 157 minutes for the male and 238 minutes for the female. There were four changeover periods during the day, and, in total, the male incubated 35 percent of the daytime hours and the female 59.5 percent of the time, leaving the nest unattended for about 5 percent of the time. The nonincubating bird fed as far as a kilometer away from the nest, and usually walked away to feed.

Incubation periods for this species have been variously reported as 36 days (Crandall, 1945), 38 or 40 days (West, 1963), and 33 days (Sugita and Suzuki, 1980). In any case, this appears to be the longest average incubation period of any crane, and indeed the total breeding season is also one of the longest of all cranes.

Hatching and Postbreeding Biology

Observations by West (1963) are the only available ones for this phase of the reproductive cycle. In 1956, he observed a nest that hatched the first of two eggs on June 28. When West approached the nest the newly hatched chick left the nest and moved about ten feet away. With its parents, the chick slowly retreated from the area. Once in tall vegetation, the two adult birds began to "paddle a circle," lifting their feet high and plunging their beaks into the water. This evidently was done for obtaining food to feed the chick. During the

next three weeks the chick was kept close to the nest, and each night the birds would return to roost, with one parent sleeping on the nest with the chick, and the other in the marsh nearby. As the chick grew older, only a single parent tended it as they fed.

In another nest, which hatched in late October of 1955, the parents' behavior was quite different, and both parent birds spread their wings and screeched when approached. In both 1956 and 1957 this display was seen little, if at all, suggesting to West that the birds had become conditioned to this kind of disturbance.

In 1956, when the chick was 80 days old, the parents hid it in tall grass when they went into a nearby maize field to feed. Hiding the chick seems to be typical of the species, and occurs from the moment of leaving the nest until the chick fledges. Hiding the chick usually occurs at the first sign of danger, usually when the intruder is still some hundreds of yards away. However, very young chicks can often be found by their "chirruping" calls, although older ones lie very quietly.

During three different years, West found that fledging occurred at periods of about 103 days, 131 days, and less than 148 days. This is the longest known fledging period of any crane, and places the species at a considerable disadvantage with regard to predators (Konrad, 1981).

In addition to a low initial clutch size, there seems to be little probability of the cranes raising two young even when two-egg clutches are present. Walkinshaw observed twelve groups of two birds, six of three, and three of four, suggesting to him that both young are sometimes raised. However, Konrad (1981) stated that no wattled crane pair has ever been recorded with two chicks. He further noted that only some 10 to 25 percent of the paired birds are successful in raising a chick to fledging; the average of all wetland populations he studied was 13 percent. Further, fledged chicks represented only 4.2 percent of the total populations of these wetlands, and ranged from 3.6 to 9.5 percent. This is the smallest recruitment rate that has yet been reported for wild crane populations. Konrad attributed this to the low initial clutch size, irregularity of breeding attempts, and vulnerability of the young to predation during the unusually long fledging period.

As noted earlier, young birds apparently remain with their parents an entire year, or to the beginning of the next nesting cycle. Rather large numbers of nonbreeding birds often associate in groups of from 3 to about 30 birds, and Konrad (1981) reported a total of 31.5 percent nonbreeding and nonpaired birds among the flocks he surveyed in southern Africa. This is, in fact, a rather low percentage of apparent nonbreeders by comparison with the whooping crane, for example, and may indicate an earlier average age of pairing in the wattled crane than in the whooping crane.

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RECRUITMENT RATES, POPULATION STATUS, AND CONSERVATION

As noted earlier, the best estimate of recruitment rate now available is Konrad's (1981) figure of 4.2 percent young among a total of 784 birds. This figure includes 33 young associated with 254 pairs, suggesting that the rate of pair success in wattled cranes is approximately 13 percent. This is appreciably lower than the 45 percent of young whooping cranes relative to the number of known breeding pairs in the 1968 to 1979 whooping crane population (Kuyt, 1981a), and suggests a less efficient degree of nesting and fledging success for the wattled cranes.

There are still no accurate figures for the total population of wattled cranes, but the largest single population unit, in the Kafue Flats area of Zambia, supports about 300 breeding pairs and a maximum total of 3,000 birds at peak populations. Probably most or all of the up to several thousand wattled cranes that sometimes assemble at Magadigadi, in Botswana, are the same birds, and thus cannot be added to the population estimate (Konrad, 1981). If one assumes that these general areas of the upper Zambezi, Okavango, and Luapula rivers support no more than 4,000 wattled cranes in total, then it is apparent that the species' overall African population is probably in the vicinity of 5,000 to 10,000 birds. Some of these probably occur in areas such as the still unstudied Upemba wetland area of nearby southern Zaire, and other breeding populations will likely be found in the Linyanti-Chobe River floodplain area of the Namibia-Botswana border (Konrad, 1981). Yet others probably exist in eastern Angola, in addition to the known northern population of Ethiopia and the remnant groups in Malawi, Mozambique, Namibia, and South Africa. The key to the survival of the species clearly lies in the upper

Zambezi drainage, and it is extremely unfortunate that the most important of these areas are threatened by various development projects. The damming of the Kafue River about the Kafue Flats to regulate flooding will reduce the floodplain area and stop much of the seasonal flooding on which the wattled crane depends for nesting. The two dams already completed in this project have apparently already had significant effects on breeding success in this area, according to Konrad (1981). Other development projects include the possible damming of the Luapula River, which would convert the Bengweulu basin into a reservoir and destroy its wetland ecology. There are also plans for wetland reclamation in the Okavango, in conjunction with tsetse fly control programs of the Botswana government (Konrad, 1981). All of these possibilities pose serious threats to the future of the wattled crane, which is certainly the most vulnerable of the African cranes.

EVOLUTIONARY RELATIONSHIPS

This species has most frequently been maintained in a monotypic genus (e.g., Sharpe, 1894; Peters, 1934; and Archibald, 1975), presumably largely on the basis of its unique wattle and its distinctive adult plumage pattern. However, Wood (1979) found that in its skeletal characteristics the wattled crane clustered with the Siberian crane, although this clustering did not hold in his analysis of external characteristics. Nonetheless, he suggested that "the two may in the future be considered congeneric," and recent studies of the behavior of the Siberian crane by Archibald (1976) suggested to him that the Siberian crane has closer phyletic relationships with the wattled crane than to the species of *Grus*, with which it traditionally has been allied.