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Cranes of the World: Crowned Crane (*Balearica pauonina*)

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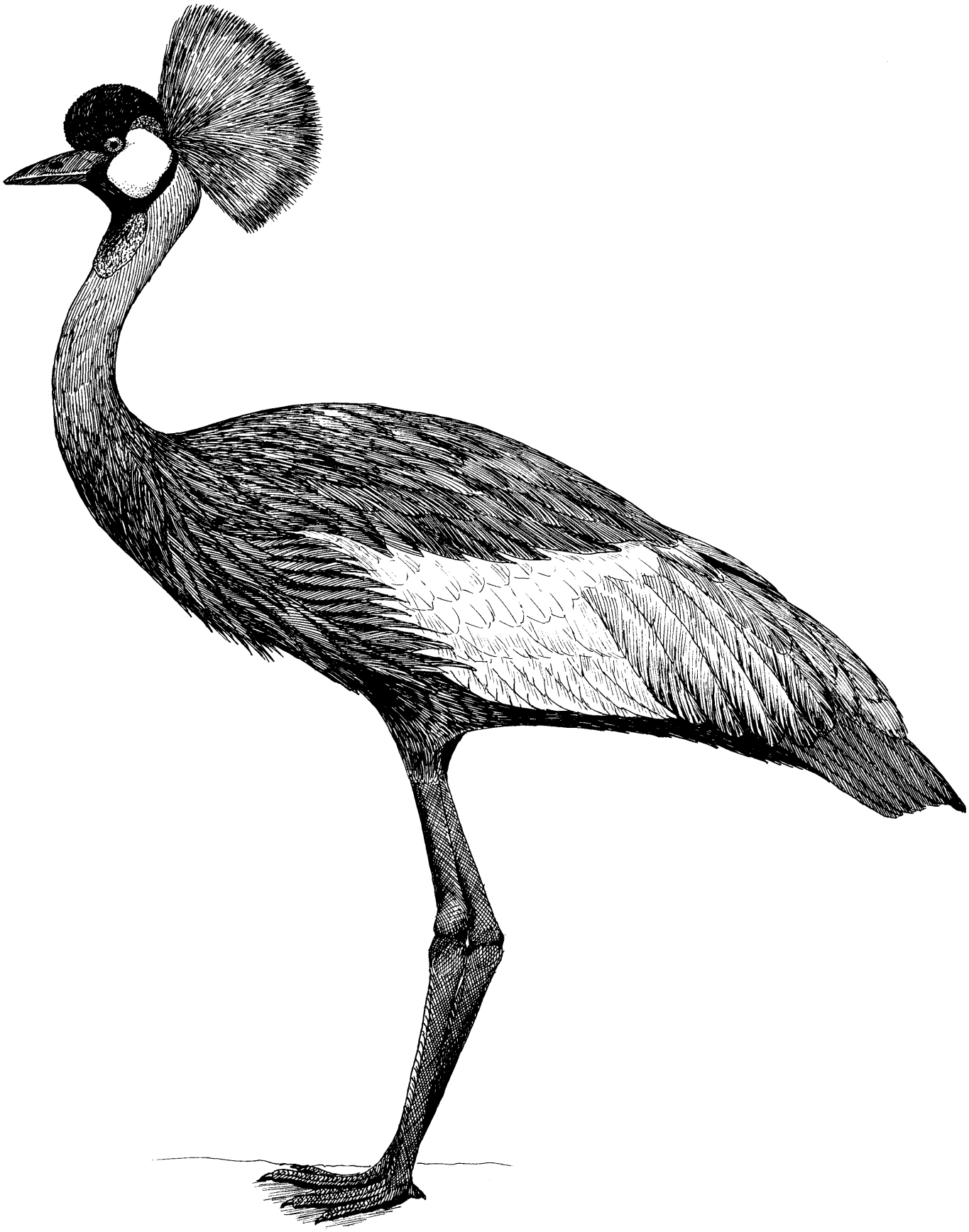


Crowned Crane

Balearica pavonina (Linnaeus) 1758

Other Vernacular Names. Blue-necked or gray crowned crane (*regulorum* and *gibbericeps*), Black-necked or dark crowned crane (*pavonina* and *ceciliae*); Ma-hem (Afrikaan); Grue couronnee, Grue ronnee du Cap (French); Konigskranich (German); Minima kanmuri-zuru (Japanese); Makoka zhuravl (Russian); Grulla corona (Spanish); I-hem (Xhosa); U-Nohemu (Zulu).

Range. Resident in open country over most of Africa south of the Sahara, excepting the Congo Basin and the driest portions of southwestern Africa.

Subspecies or Semispecies.

B.p. pavonina: West African Crowned Crane. Resident north of the Congo Basin from Senegal east to Lake Chad, and south to Sierra Leone, Nigeria, and northern Cameroon.

B.p. ceciliae: Sudan Crowned Crane. Resident in the Nile Valley from Malakal south to Nimule and east to Lake Rudolf and the Ethiopian lakes.

B.(p.) gibbericeps: East African Crowned Crane. Resident in eastern Africa from extreme eastern Zaire, Uganda, and Kenya to central Tanzania. Sometimes considered (with *regulorum*) a separate species.

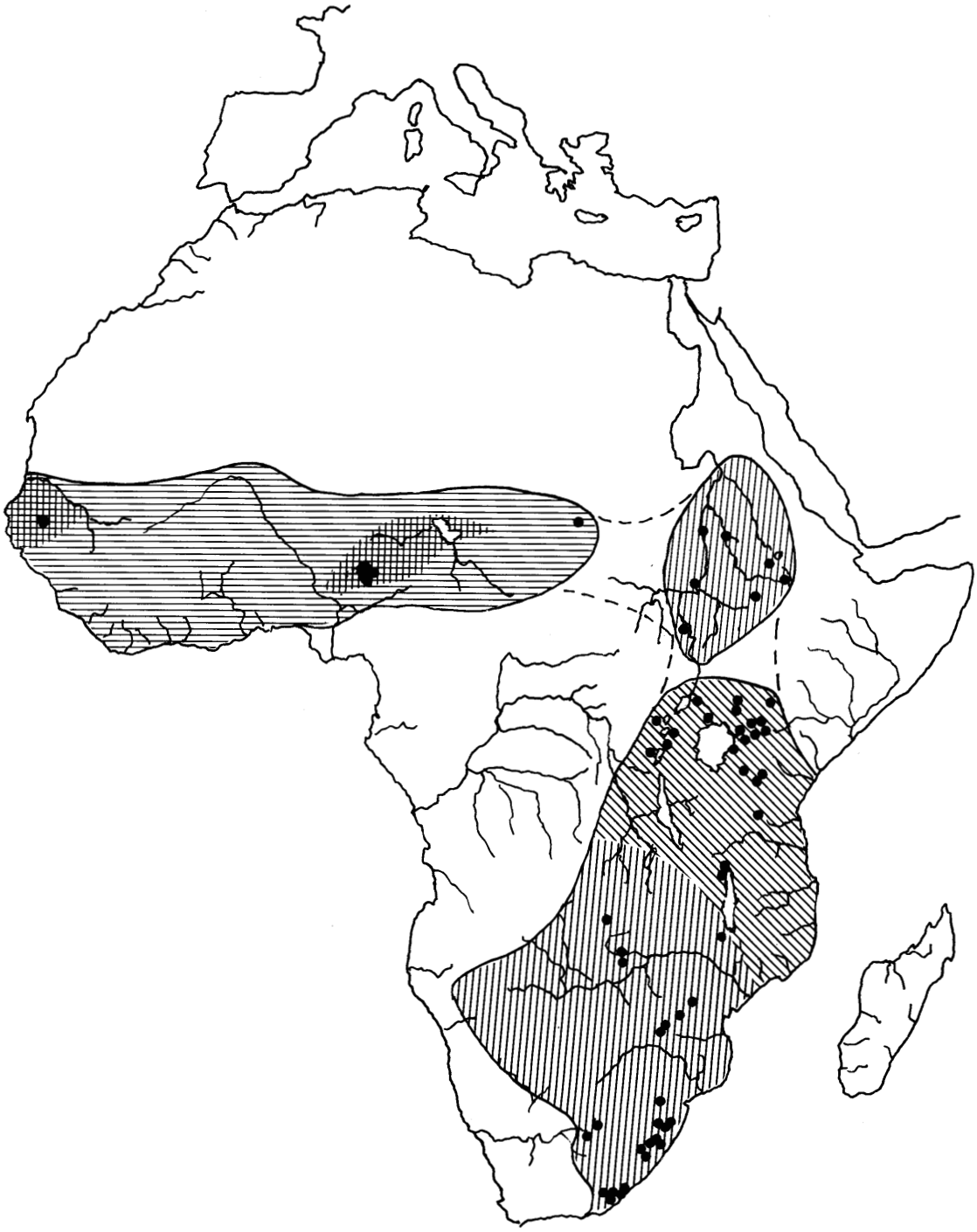
B.(p.) regulorum: South African Crowned Crane. Resident in southern Africa from Mozambique southward to about Port Elizabeth, South Africa. Sometimes considered (with *gibbericeps*) a separate species, here considered a semispecies.

Measurements. Wing, both sexes of *ceciliae* average 496.7 mm (range 470-565 mm), of *pavonina* average 547.5 mm (range 506-585mm), of *gibbericeps* 559.4 mm (range 458-615 mm) and of *regulorum* 565.2 mm (range 523-642 mm). Exposed culmen, both sexes of *ceciliae* average 56.1 mm (range 49-62 mm), of *pavonina* 56.5 mm (range 53-64 mm), of *gibbericeps* 59.4 mm (range 52-71 mm) and of *regulorum* 61.9 mm (range 57-68 mm). Tarsus, both sexes of *ceciliae* average 188 mm (range 172-205 mm), of *pavonina* 196 mm (range 190-203 mm), of *gibbericeps* 201.1 mm (range 170-207 mm), and of *regulorum* 207.1 mm (range 170-234 mm). Females generally average from 85 to 95 percent of male measurements, but rarely exceed male measurements. Eggs, average (in *pavonina*) 85.5 × 57.5 mm (82.3-89.5 × 55.8-58.9 mm); in *regulorum* 75.4 × 55.2 mm (70.4-78.4 × 52.0-58.8 mm) (Walkinshaw, 1973).

Weights. Walkinshaw (1973) lists a male and female of *ceciliae* as 3,628.8 grams each. Pomeroy (1980a) shows weights for four adults of *gibbericeps* ranging between 3 and 4 kilograms. Estimated egg weights are from 122 grams (*regulorum*) to 156 grams (*pavonina*).

Description

Adult males and females are alike. Those of *pavonina* and *ceciliae* are generally darker than the two southern forms, and have smaller red chin wattles. In these two northern forms the bare cheek patches are white above, and a much larger lower portion is pinkish to reddish, while in the southern forms the cheek patches are almost entirely white, with a small upper portion bright red. A large, straw yellow crown covers the top of the head (paler in the southern forms), with each feather in the crest black-tipped and ringed with whitish or brownish. There are black velvety feathers around the bare cheek patches, which are bounded below with reddish skin areas of varying size, becoming large wattles in the southern forms. The neck feathers are pearl gray (southern forms) to slate gray (northern forms), becoming elongated and pointed toward the base of the neck and grading into body feathers of the same color. The primaries are black, as are the outermost one or two secondaries; the next two or three secondaries have black inner webs and chestnut on the



Distribution of the South African (vertical hatching), East African (diagonal hatching), Sudan (vertical hatching), and West African (horizontal hatching) crowned cranes. Cross-hatching indicates areas of greatest abundance, and inked circles indicate breeding records (mainly after Snow, 1978).

exposed webs. The innermost secondaries are broad, long, and plume-like. The tail is black, and the upper and lower wing coverts are white, with the inner greater coverts becoming straw-colored and plume-like. The iris is grayish white to pale blue, the bill is black, and the legs and toes are black.

Juveniles are generally grayish, the upperpart feathers being edged with rufous, and those of the underparts with sandy buff. The crown and nape are brown, the face is feathered and buffy, and the crest is spiky and golden buff. The wing coverts are white, with buff tips or with varying amounts of gray and buff. The iris is brown, the legs and toes are pink initially, gradually changing to horn and finally to black. The throat wattle (which appears at about four months) is initially pink. The adult plumage is attained at about 12 months, but adult eye color and full development of the throat wattle and facial color may not occur for about another year (Pomeroy, 1980a).

Downy chicks (of *regulorum*) are pale buff, with the head pale ivory to light buff, and the back and dorsal stripe umber, and with dark flank spots, dark shoulders, and a dark caudal spot. The underparts are very pale buff, and the chest is a darker buff. The bill is gray, with a flesh color at the base of the lower mandible, and the base of the bill is light horn color. The iris is dark brown, the legs are flesh color, and the soles of the toes are pale yellow (Walkinshaw, 1973).

Identification

In the field, the distinctive white upper and under wing coverts, which contrast with darker brown or black flight feathers, allow this species to be identified at any distance. The yellow crown is also diagnostic. The calls are honking and hollow-sounding, of generally low pitch and with considerable harmonic development.

In the hand, the presence of a "crown" is diagnostic. The races *pavonina* and *ceciliae* typically have reddish on the lower part of the cheek patch (extending about halfway up in *pavonina* and more than halfway in *ceciliae*), and both have very small bare wattles. the races *regulorum* and *gibbericeps* typically have larger red throat wattles, and cheek patches that are mostly white with a small reddish area near the top. All these features appear to be somewhat variable. In *gibbericeps* the bare area typically extends upward well above the eyes into the velvety black forehead, forming a rounded knoblike process. The trachea does not penetrate the sternum; it passes directly back to the bronchial bifurcation without looping downward.

DISTRIBUTION AND HABITATS

Historical and Current Ranges

The historical ranges of the four populations of crowned cranes have been reviewed by Walkinshaw (1964, 1973), from which it would appear that no major range retractions have occurred in recent times. The form *ceciliae* once ranged north to Khartoum, where the type specimen was taken, but it rarely if ever occurs there now. Of the four populations, it is probable that the West African form *pavonina* may be the most vulnerable, in spite of its apparently broad distribution. Only two actual breeding records were indicated throughout the range of this subspecies by Snow (1978), and most records of breeding seem to be from Nigeria, where it is now becoming rare (Parker, 1971). The smallest apparent range is that of the Sudan race *ceciliae*, which was also the last subspecies to be described. This form occurs in the western provinces of Ethiopia only locally (Urban and Walkinshaw, 1967), and is otherwise largely restricted to the Upper Nile of Sudan, with the southernmost record apparently from extreme northern Uganda at Dufile, near Nimule. Cranes from northern Uganda reportedly often show intergradation between *ceciliae* and *gibbericeps*, although specimens from the critical areas seem to be lacking (Walkinshaw, 1964). *Ceciliae* has also been collected in extreme northern Kenya, at the northeastern end of Lake Rudolf (Owre, 1966). Except for these records, the crowned cranes of Uganda and Kenya all appear to be of the East African form *gibbericeps* (Pomeroy, 1980a). In Uganda, crowned cranes are most common in southeastern areas, where swamps are frequent, and are generally less numerous in the formerly forested areas of south central Uganda. This subspecies is likewise apparently most common in the southwestern portions of Kenya, east of Lake Victoria, becoming scarce in the drier areas to the north (Donald Young, pers. comm.). It also has been regularly reported in the Rift Valley lakes from Lake Albert southward through Lake Edward, Lake Bunyoni, and Lake Kivu, with nonbreeding records extending to about the south end of Lake Tanganyika. *Gibbericeps* is also the form ranging into Tanzania and Malawi, and extending southward an uncertain distance, where it evidently intergrades with *regulorum*. There are specimens attributed to the latter race from as far north as Zambia, Zimbabwe, and the Zambezi River (Walkinshaw, 1964). In Zambia the subspecies is fairly widespread, but is scarce in the Northern Province and is most common in the Kafue Basin and Luanga Valley (Benson et al., 1971). Breeding records from the South African crowned crane *regulorum* are largely limited to Zambia and South Africa, although nonbreeding records extend

west all the way to the Cunene River of extreme southern Angola (Snow, 1978).

Habitat Requirements and Densities

Crowned cranes are associated with open country, especially grasslands near water, and they are apparently largely sedentary (Snow, 1978). The birds forage primarily in grasslands, but also require swamps for breeding, and wherever available they use large trees for roosting. However, where necessary, they will also use smaller trees for roosting, or may even roost in shallow water (Pomeroy, 1980b). In some areas they have been able to exploit croplands, where they sometimes do damage to crops such as groundnuts and soybeans. They may also destroy cotton seedlings by uprooting them while searching for insects. In areas where the rainfall is less than 700-800 mm per year the birds are sparse (Pomeroy, 1980b).

On their breeding grounds in Natal, South Africa, crowned cranes nest in marshes that have such associated grass genera as *Pennisetum, Andropogon, Arundo,* and *Miscanthidium,* and such sedges as *Carex, Cyperus, Scirpus, Pycreus,* and *Ascolepis*. Other typical genera are *Disa* (Orchidaceae), *Chironia* (Gentianaceae), and *Dierama* (Iridaceae). In Zambia, some of the grasses associated with breeding areas are *Panicum, Sporobolis, Chloris, Hyporrhinia, Setaria, Brachiaria, Digitaria,* and *Echinochloa*. A variety of herons, egrets, storks, ibis, ducks, and other marsh-breeding birds were also reported to be typical nesting associates by Walkinshaw (1964). He noted that both blue cranes and wattled cranes were found nesting in the same South African marshes; the blue crane occupied a different niche, and the wattled cranes tended to nest during a different season. In Zambia, however, there is a substantial overlap in the nesting periods of crowned and wattled cranes, with crowned cranes nesting mainly between December and March and wattled cranes primarily from March to October (Benson et al., 1971).

In South Africa, nesting habitats consist of open marshes having a few centimeters of standing water and knee-high to shoulder-high stands of sedges and grasses. According to Walkinshaw, the preferred South African breeding biotype consists of the shorelines of lakes or large marshes grown up to reeds, rushes, sedges, and papyrus, where the cover is extremely dense and tall enough to effectively hide the birds. These areas may be rather deep, with some floating islands of vegetation, or they may be fairly small and shallow. In the West African form the bird nests not only in such marshes but also in flooded fields of rice, atcha, or yams, and nesting may even occur on dry land, although always very close to water (Walkinshaw, 1973). In the Sudan race, typical breeding biotypes seem to be rather large and grassy marshes, from a few centimeters to a meter in depth, and with knee-high to hip-high vegetation dominated by *Cyperus, Eleocharis, Scirpus, Setaria, Cynodon,* and various legumes and rosaceous plants (Urban and Walkinshaw, 1967). In Uganda, the nesting habitat of the East African race consists of grassy swamps (Pomeroy, 1980b).

Population densities are not yet well verified in this species. Pomeroy (1980b) suggested that in southern Uganda large areas may support at least one crane per square kilometer, suggesting a total Ugandan population in the tens of thousands. Burke (1965) judged the population in the Kisii District of western Kenya to be about 1.14 birds per square mile (0.4 per square kilometer). Walkinshaw (1981a) found 7 pairs and 34 nonbreeders in an area of 21 square miles in Nigeria, or 2.28 birds per square mile.

FOODS AND FORAGING BEHAVIOR

Foods of Adults

Crowned cranes are relatively diverse in their foraging activities, and consume not only a diversity of vegetable materials but also such animal life as lizards, grasshoppers, other insects, millipedes, and earthworms. In Kenya they have been observed feeding on armyworms (*Spodoptera* spp.) and cutworms (noctuid moths), and in the Sudan on crickets (Pomeroy, 1980b). Walkinshaw (1973) reported that the West African form has been reported to eat crabs (*Potamon* sp.).

Vegetable material consumed by crowned cranes includes the seed heads of sedges (*Cyperus* spp.) and such grasses as *Cynodon* spp., and evidently long grasses growing around swamps that are in the process of seeding are preferred foods. The birds also have been observed pecking at old cobs of maize, and seem to prefer knocking seeds off heads of millet and maize cobs rather than picking up loose seeds. The birds often forage in croplands, especially of such types as soybeans and groundnuts, or consume the flowers and pods of bean plants. Damage to crops is sometimes indirect, as when the birds trample cotton crops while displaying, or dig up seedlings, apparently in search of insects (Pomeroy, 1980b).

Foraging Behavior

Several observers have commented on the tendency of crowned cranes to stamp their feet while walking through grassy vegetation, apparently to disturb and thus expose insects (Walkinshaw, 1964; Pomeroy, 1980b). These birds have also been seen walking among feeding cattle, much in the manner of cattle egrets (*Bubulcus ibis*), presumably catching the insects disturbed by the moving cattle. The birds are also attracted to freshly plowed fields, and they tend to feed in short grass rather than in long grassy cover, again presumably for the easily captured insect life. They are sometimes attracted

to rubbish dumps, where insects are associated with waste food (Pomeroy, 1980b).

MIGRATIONS AND MOVEMENTS

No specific migrations have been documented in this species, although during the nonbreeding season the birds flock, and may then gather at favorable locations well away from nesting areas. Thus, during the nonbreeding season, large flocks of the West African race have been reported in the northern portion of Cameroon, and in the vicinity of Lake Chad, northeastern Nigeria, apparently dispersing to breed elsewhere during the rainy season (Walkinshaw, 1973). In Uganda the population appears to be essentially sedentary, and the birds seem to make only local movements (Pomeroy, 1980b). There is no good information suggesting significant movements from the other East African or South African populations.

GENERAL BIOLOGY

Sociality

In Uganda, a certain amount of breeding activity occurs throughout the entire year, although breeding is at a low point during September and October, and has distinct peaks at about November to February, and again from May to July, during relatively drier periods. Thus, the most common group size of cranes in Uganda is of paired birds (about 57 percent of 118 groups counted), while single birds are the next most common social unit (17 percent); most of the remaining birds were seen in groups of from 3 to 20 birds, with only a few observations of groups ranging from 51 to 150 birds (Pomeroy, 1980b).

Studies by Walkinshaw (1964) in Zambia (Northern Rhodesia) and in South Africa during December and January, during the breeding period, indicated that 59 percent of the birds were then in pairs, while the flocked birds were of nonbreeding individuals. In Natal, he observed twelve single birds, nineteen groups of 2, two groups of 3, one of 19, and two of 28 birds. Among the breeding birds, Walkinshaw noted that the mate of the incubating bird always roosted in the marsh near the nest, even if nearby trees were available.

According to Walkinshaw, crowned cranes that are successful in raising young retain their family group structure for as long as 9 or 10 months, after which the adults drive away the young and prepare to nest again. When the family breaks up, the young birds tend to join together in flocks, and spend much of their time feeding in fields. Some of the foods consumed by such groups of young birds are the seeds of grasses, sedges, and grains (Walkinshaw, 1964).

Daily Activities

Unlike other cranes, crowned cranes normally roost in trees. They exhibit a preference for open trees such as mvule (*Chlorphora*), which has high, bare lower branches that provide an excellent view, or the tops of leafless trees. The birds leave their roosts at dawn, or variably later during wet or misty mornings, and do not return until just before nightfall. During the daylight hours they feed from 50 to 75 percent of the time, being least active during the middle of the day. On especially hot days they may move into shade or pant visibly. Even within large flocks, the birds can be seen to move about in pairs, suggesting a prolonged pair bond. Within such flocks, displays are not infrequent, and mutual preening, especially of the neck feathers, has also been observed. Sometimes displays are stimulated by minor disturbances, and occasionally the entire flock may become involved in this activity. Such activities are more frequent as evening approaches, but rarely last more than a few minutes, and are typically interspersed with foraging behavior (Pomeroy, 1980b).

Interspecific Interactions

Crowned cranes are locally sympatric with wattled cranes and blue cranes. They are smaller than and subordinate to wattled cranes (Walkinshaw, 1964), and probably occur on rather wetter and more heavily vegetated habitats than are typically used by blue cranes. The bill shape of crowned cranes is quite different from the bills of wattled or blue cranes, suggesting quite different foraging niches.

When nesting, the birds are able to expel other crowned cranes, blue cranes, and spur-winged geese quite easily, and have been observed to cause a steer to retreat from their nesting site (Walkinshaw, 1973).

BREEDING BIOLOGY

Age of Maturity and Time of Breeding

The period of sexual immaturity in crowned cranes is still uncertain but full adult eye color and coloration of the bare face and neck areas are not attained until the birds are 20 to 24 months old (Pomeroy, 1980a). Steel (1977) reported that hand-raised East African cranes that he reared in 1967 did not attempt to breed until 1974.

The period of nesting in crowned cranes seems to be remarkably variable in different parts of Africa. The West African race breeds in Gambia in September and October, egg records in Nigeria are during the rainy season from July to early September, and there is a southern Mauritania breeding record for October (Mackworth-Pread and Grant, 1970; Walkinshaw, 1973). In the Sudan race, breeding records include nest-building in August, eggs in September and early

October, downy young in late October and November, and 6-week old young in February (Walkinshaw, 1973). Breeding records in Uganda extend throughout the year for the East African race, but there are peaks in the breeding activity associated with drier periods (Pomeroy, 1980b). According to Brown and Britton (1980), crowned cranes generally breed in the rainy season in most areas of East Africa, but in the wettest portions the dry period seems to be preferred. In Zambia the breeding records for *regulorum* extend from December to April, with the largest numbers occurring in December and February (Benson et al., 1971). This corresponds to the rainy season in Zambia. Breeding during the rainy season is also typical of Malawi (Nyasaland) and the Rhodesias (Zambia and Zimbabwe), with nearly half of the breeding records from January (Benson, 1960). In South Africa the breeding season is also associated with the rainy period, probably from mid-October to May 22, but probably peaking between December and February (Walkinshaw, 1973).

Pair Formation and Courtship

Courtship in this species is still only very poorly understood. One of the first good descriptions of display was that of Serle (1939), who described the "nuptial dance" of *pavonina* as follows:

> The birds would be walking sedately side by side when the performance began, which was heralded by both birds simultaneously bobbing the whole body up and down. Then they leapt forwards together, still side by side, and at each forward leap the wings were flapped. After a few leaps this prelude to the dance would conclude in a short forward run. Sometimes, when they appeared less excited, they would leap without opening their wings. Presently they would leap in opposite directions till they were some thirty yards apart, when they would turn and bound towards each other with great leaps and, when they had met, dance round each other in circles, all these movements being carried out with delightful grace and buoyancy. Towards the end of the performance one bird would get tired and, when the other came flapping towards it, only responded by dipping its head and indulging in a few demure hops without flapping its wings. When the dance was concluded they remained immobile for a while and then flew off to perch on a tree near the fadama.

A similar description was provided by Walkinshaw (1964) for crowned cranes in general:

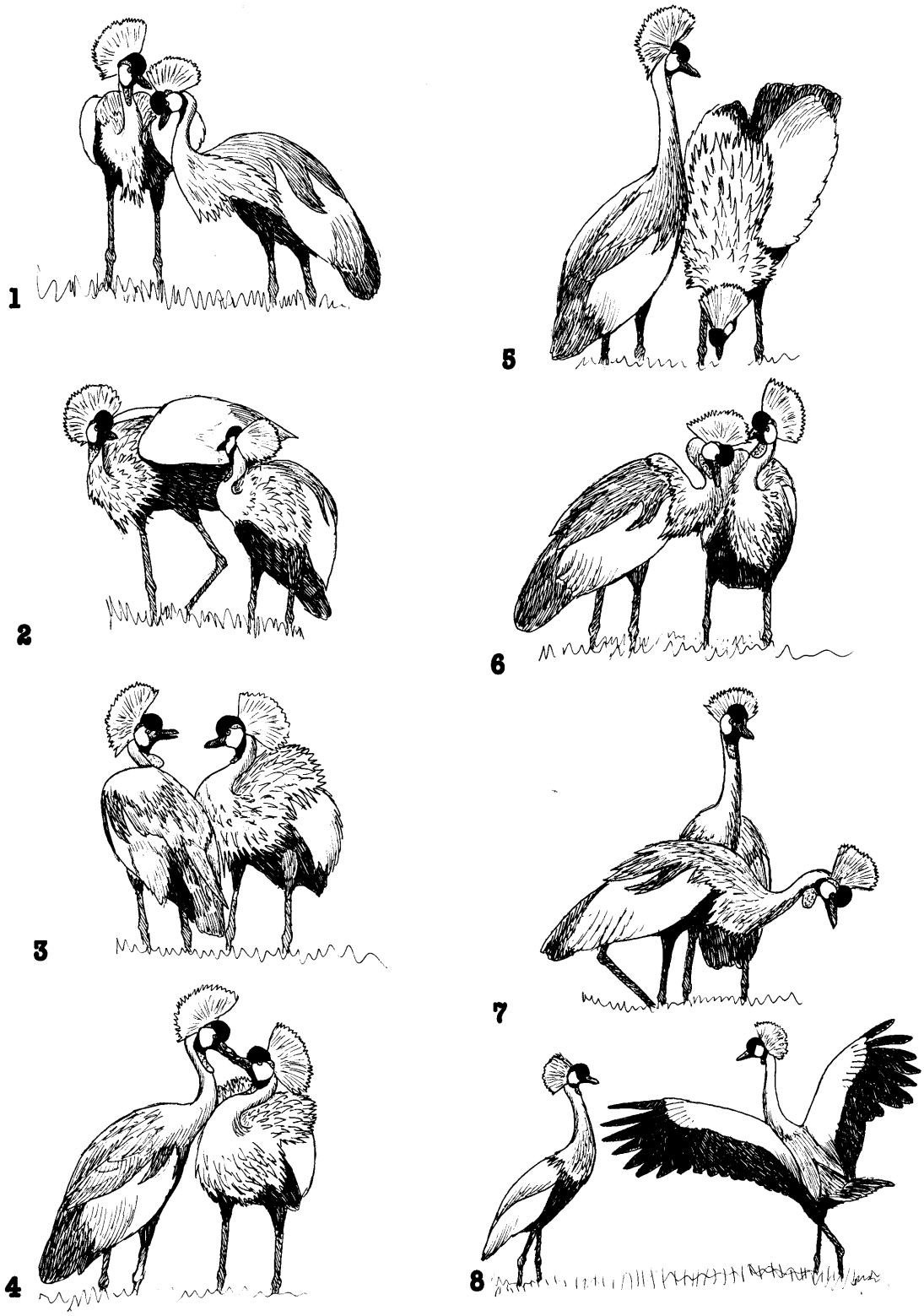
> Both male and female participate, but usually the male is the aggressor. Crowned cranes begin their dance differently than do other cranes that I have observed. Without moving their body, they bob their heads up and down four to ten times. Sometimes this is all they do, but often they begin to bow. Then, spreading their wings, they jump 6 to 8 feet into the air with legs drooping motionless beneath them. Sometimes between hops they pick up objects from the ground and toss them into the air. Sometimes they call, sometimes not. The dancing crane often goes completely around his mate doing all this and sometimes both birds dance opposite each other. Sometimes one does the dancing, again the other.

The sequence of drawings showing display in a pair of wild East African crowned cranes (figure 13) is based on a series of 35 mm transparencies taken in Kenya by Donald Young, and well illustrates the strong bowing component (with strongly ruffled neck feathers), as well as an apparent touching of the beaks at one point.

Copulatory behavior in the crowned crane is only incompletely described, but Walkinshaw (1973) observed a pair of West African cranes mating. The female suddenly raised her head forward and upward, and stood quietly in that position for about a minute. The male, standing some ten feet away, approached quickly, mounted her as she squatted slightly, and as they copulated he stood on her back with his wings slightly waving. Afterwards they began feeding. This description would suggest that copulatory behavior in *Balearica* is very much like that of *Grus*.

Adult vocalizations of the West African ("Nigerian"), East African ("Kenyan"), and South African ("Southern") crowned cranes were studied by Archibald (1975, 1976). He observed rather marked differences between the West African form and the other two populations studied, as well as marked differences between *Balearica* and typical gruine cranes. Thus, the guard call of *Balearica* is a hollow-sounding, honklike vocalization that is relatively low in pitch and rich in harmonic development. However, although the guard call of the West African races is a monosyllabic honk, that of the other forms studied is a disyllabic *ka-wonk*, with the second syllable higher in pitch. Further, in the unison display, guard calls predominated in the West African form, while "booming" dominated in the East African race. In both types, the gular sac is inflated during calling, but it is larger in the eastern and southern populations, and the calls are correspondingly lower in pitch.

Crowned cranes begin their unison display in varied ways. The pair may be standing close together or not, and either sex may begin or end the call sequence. The display is of variable length, and may last more than a minute. The birds stand in the same place throughout the display, and do not move their wings. The display is usually begun with a series of guard calls, during which the red gular sac is inflated and the head is slowly turned from side to side as the mandibles remained



13. Sequence of bowing (1-7) and dancing (8) behavior in the East African crowned crane, based on a series of photographs taken by Donald Young.

closed. The neck is held erect and the beak horizontal. Then, a series of booming calls is uttered, with the neck lowered, the beak elevated to about 45 degrees, and the head held at shoulder level. Guard calls may also be uttered during or following the booming sequence. During the display, the calls phase in and out of synchrony, since each bird calls at a fixed rate that is independent of that of its mate (Archibald, 1975, 1976).

Territoriality and Early Nesting Behavior

According to Walkinshaw (1973), territories of the West African crowned crane varied from 86 to 388 hectares (212-958 acres). The size was evidently smallest where cranes had territories adjoining those of other pairs, although typically each pair lacked close neighbors. The territories included both a nesting territory and a feeding area, and the birds paid little attention toward defending the latter. In fact, both cranes and other birds were allowed to forage in the feeding territory without disturbance. Feeding usually occurred from a half a mile to a mile from the nest site, and the birds would either walk or fly to their foraging grounds from the nesting site.

On the other hand, all birds, such as other crowned cranes, ducks, spur-winged geese, bustards, and owls, were quickly chased from the nesting territory. On two occasions a breeding pair of crowned cranes landed near the nest of another pair. In this case, both members of each pair approached until they were only a few meters apart, and the male of each pair assumed a display posture with its neck and head arched in a curve, the bill pointed downward, and stood almost motionless for ten to thirty minutes. Both males performed "false" preening during this period, but no actual fighting ensued. After a period of preening by all four birds, they gradually moved back into their respective territories.

During actual attack, the cranes spread their wings and approach with arched neck and lowered head, the two members of the pair usually approaching side by side. Fighting is done by jumping, wing-flapping, kicking, and stabbing with the beak. If humans, cattle, or snakes should approach the nest, distraction display is typical. This includes dancing on the part of one or both birds. Head-bobbing is done frequently, and the birds will sometimes spread their wings, run around the intruder, or jump up and down. At times they will also pick up objects from the ground and toss them into the air (Walkinshaw, 1964).

According to Walkinshaw (1973), crowned cranes can readily drive blue cranes out of their territories, or even spur-winged geese, but are distinctly fearful of wattled cranes and avoid approaching them very closely. However, he observed a pair frighten away a steer that approached the nest too closely.

The usual location of nests in crowned cranes is in standing water, or at least very near it, although on rare occasions the birds have been known to nest in trees (Steyn and Ellman-Brown, 1974).

Walkinshaw's (1973) accounts of the South African and East African crowned cranes indicate that nest construction is relatively simple. Both members of a pair begin pulling up marsh vegetation and trampling it down around the nest site, so that a circular area 5 to 15 meters in diameter is flattened. In the middle of this the birds toss grass and sedges into a haphazard pile, occasionally trampling it or sitting on it to flatten it and make a depression in the middle. Six nests of the South African race that Walkinshaw measured were from about 50 to 86 centimeters in diameter. The rim averaged about 12 centimeters. Of eight West African crane nests that he studied, seven were on dry land, but all were within 3 meters of water, and one was placed in water 2 feet deep. Six were placed among farm crops, and all were within 100 meters of higher and drier land where the birds fed. These nests averaged larger than did the South African nests, and ranged from nearly 70 to 140 centimeters across. The one that was built in deep water was raised so that the top was 33 centimeters above water. Nest materials are apparently not carried to the nest. If they are obtained out of reach of the nest, they are simply thrown toward the nest with a slight sideways action. If the material lands away from the nest, it may again be picked up later and tossed onto the nest. Scratching with the feet is a second although minor method of accumulating materials on the nest (Walkinshaw, 1973). In the case of the tree-nesting crowned crane described by Steyn and Ellman-Brown (1974), the nest was about 6 meters above ground, and was a relatively small and flat platform of twigs that had evidently been snipped from the tree.

Egg-laying and Incubation

The rate of egg-laying is evidently somewhat less than 1 egg per day. Steel (1977) noted that a pair of captive crowned cranes produced 3 eggs in 4 days in one year, and 4 eggs in 6 days in another year. On the latter occasion a replacement clutch of 4 eggs was laid after the loss of the original clutch. Walkinshaw (1973) found a nest in Nigeria in which 3 eggs were laid in a 5-day period, while all 3 eggs in a South African nest were laid during a 1-week period. Similarly, Wyndham (1940) reported that 3 eggs were laid in a 7-day period.

It is doubtful that significant differences in clutch sizes exist in the various forms of crowned cranes. Walkinshaw (1973) reported average clutch sizes of the South African crane as 2.67 eggs (34 clutches) for South Africa and 2.35 eggs (17 clutches) for Zambia and Rhodesia (Zimbabwe), while Pomeroy (1980b) noted that the average clutch size in Kenya and Uganda for the East African race was 2.56 eggs (41 nests). Pomeroy

noted, however, that the clutch seems to vary with altitude; 12 nests from areas of generally below 1,500 meters averaged 2.17 eggs, while 29 nests from highland areas above 1,500 meters averaged 2.72 eggs. Records of 17 West African crane nests provided by Walkinshaw (1973) indicate an average clutch of 2.47 eggs.

Incubation begins with the first egg, with the birds changing incubation duties periodically. Walkinshaw, (1973) estimated that in a nest he studied in Nigeria the eggs were incubated 81.4 percent of the daylight hours in a 2-day period, although one or the other adult was present at the nest for 96.47 percent of this period. The smaller bird, presumably the female, incubated at night, while the other bird roosted up to a mile away in a tree. In a South African crane nest that he studied, the female incubated during 3 of 4 nights, while in another nest the eggs were incubated 90.5 percent of the time in a 2-day period, the male contributing slightly over half the total. Although the first and last eggs of a nest may be laid nearly a week apart, hatching of the entire clutch usually occurs within about a 24-hour period, suggesting that the early stages of incubation prior to clutch completion may not be very intense. Thus, while the incubation period of the first-laid egg may be about 31 days, the last-laid egg typically hatches 28 or 29 days after it is laid (Walkinshaw, 1973).

Hatching and Postbreeding Biology

Like other crane chicks, those of crowned cranes remain near their nest for the first day or so, but by the second day after hatching are prone to wander off with their parents in search of food. However, they remain near the general nesting area, and may return at night for brooding. Unlike the families of wattled and blue cranes, the young of crowned cranes are not led out into the nearby plains or veldt, and instead tend to remain in heavy cover (Walkinshaw, 1973).

A description of the development of the young has been provided by Pomeroy (1980a). He observed that the rate of growth of the tarsus and the increase in wing length were relatively rapid, while the weight increase as well as the growth rate of the bill, tail, and crest were relatively slow and only approach adult dimensions at 12 to 20 months of age. Pomeroy estimated that fledging occurred at about 100 days of age, and Walkinshaw (1973) stated that hand-reared West African cranes may not fly until they are 4 months old. However, Steel (1977) estimated that hand-reared East African birds were virtually fledged at 8 weeks of age, and Archibald and Viess (1979) reported fledging in hand-reared birds at only 63 days after hatching. Clearly, these wide divergences in estimated fledging times must indicate an unknown source of considerable variation, perhaps in the amounts of food available to the young cranes.

Walkinshaw (1973) noted that in all of three South African nests he studied the young cranes were fed pieces of crabs (*Potamon* sp.) when about 24 hours old. The chicks seem to feed less on insects and more on grass seeds than do other crane chicks, and they also do not dig as much as do the longer-billed species of cranes.

RECRUITMENT RATES, POPULATION STATUS, AND CONSERVATION

Unfortunately, there are no good estimates of numbers for any of the races of this species. Pomeroy (1980b) judged that the Uganda population alone was probably in the tens of thousands, and might well be increasing. He judged that, for those nesting efforts producing young that survived beyond three months after hatching, the number of young per pair averaged 1.3. He noted that young birds make up a small proportion of the total birds seen, and the overall recruitment rate might be no greater than that estimated by Miller, Hochbaum, and Botkin (1972) for the sandhill crane (2-8 percent annually), in spite of the considerably larger average clutch size of the crowned crane. Parker (1971) reported that in Nigeria the crowned crane merits a conservation priority. Urban (1981) believed the Sudan race to be secure.

EVOLUTIONARY RELATIONSHIPS

The general evidence on the distinctive position of *Balearica* in the family Gruidae has already been offered in the chapter on classification and evolution, and so little needs to be added here. Wood (1979) reported that *Balearica* was anatomically divergent from all other species of extant cranes in six to ten analyses that he performed. In the remaining four analyses it was more similar to *Anthropoides* or *Bugeranus* than to *Grus*. The additional similarities of *Balearica* to such fossil genera as *Paleogrus* and *Probalearica* (Brodkorb, 1967; Cracraft, 1973) would suggest that *Balearica* is of a more generalized type than are these other modern genera, and should be listed first in taxonomic sequence.