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Cranes of the World: 3. Vocalizations

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Vocalizations

3 Of all avian sounds, few have the power to catch the human imagination and thrill the senses as much as does the bugling of a flock of distant cranes. Leopold (1949) referred to the progressively louder sounds of an approaching flock of sandhill cranes as “a tinkling of little bells,” the “baying of some sweet-throated hound,” and finally as “a pandemonium of trumpets, rattles, croaks and cries.” The Greeks called it “iangling,” and most recent writers have compared the calls of typical *Grus* cranes to trumpets or bugles. In doing so, they have inadvertently drawn attention to the similarity of the calls to the sounds generated by musical instruments, and it is important to investigate the similarities and dissimilarities between the vocalizations of cranes and the sounds generated from man-made musical instruments.

Crane Vocabularies

The vocal repertoires of nonpasserine birds seem generally to be fairly limited, and rather infrequently exceed about fifteen distinctly different signals, or call types (Thorpe, 1961). In contrast to the songs of at least some passerine birds, the calls of cranes seem to represent innately acquired signal systems that are not subject to experiential modifications nor are they evidently dependent upon gradual acquisition of significance through associative learning during an individual's lifetime (Archibald, 1975). Rather, they are stereotyped vocal performances, instinctively performed and responded to, and, as such, they play an extremely important role in the integration of the complex social behavior patterns of cranes, which primarily rely on vision and hearing for evaluating their social and physical environments.

Based on his studies of blue, sandhill, Eurasian, and Japanese cranes, Archibald (1975) has provided a complete inventory of grune vocalizations, and a less complete survey of crowned crane calls (table 4). The

following summary of crane vocabularies is derived from his observations.

Cranes begin to vocalize at the time of hatching, uttering high-pitched peeping calls that subsequently persist for most of the first year of life. The first two types of calls uttered by hatching and newly hatched chicks are the contact call and the stress call. The contact call is a low-amplitude, purring call that indicates the chick's well-being and its proximity to its parents. It is uttered almost constantly during foraging or while being brooded. Separation from the adults, chilling, hunger, or other similar stressful conditions elicit the stress call, a loud, unbroken call likely to attract the attention of the adults.

A food-begging call is usually uttered within the first 24 hours after hatching, and is a plaintive peeping note that stimulates feeding of the young by its parents. It occurs with diminishing frequency until the young bird is about a year old, or well after actual feeding by the parents has terminated.

At about the time of fledging, the flight-intention call is first uttered. This is a brief, high-frequency unbroken call that is uttered as the bird stands erect and faces into the wind. At about this time the alarm call also appears. It is a lower-pitched, more broken, and rapidly uttered call that is given in response to a frightening stimulus.

For most of the first year of life, these five calls constitute the young crane's vocabulary, but in times of extreme threat the guard call may occasionally be heard. The guard call is often uttered during the collective threat of parents and chick toward other crane families, but at times it may also be directed toward somewhat frightening stimuli, such as a distant dog. It is a loud, single-syllable call.

At the age of about 8 or 9 months (Eurasian crane) or 10 to 11 months (blue, sandhill, and Japanese cranes), the chick begins to lose its peeping voice and to acquire the lower, more guttural voice of the adult. The contact

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TABLE 4

List of Call Types of *Balearica* and *Grus* Cranes*

<i>Call Type</i>	<i>Age When Uttered</i>	<i>Balearica</i>	<i>Grus</i>
Contact Call	Throughout life	Present	Present
Food-begging Call	Chicks only	Present	Present
Stress Call	Mainly in chicks	Present	Present
Flight-intention Call	From fledging onward	Absent	Present
Alarm Call	From fledging onward	?	Present
Guard Call	After voice change	Present	Present
Location Call	After voice change	Present	Present
Unison Call	After 24 months	Present	Present
Precopulation Call	After 24 months	Present	Present
Click Call	As adults	Present	Absent
Quack Call	As adults	Present	Absent
Booming Call	As adults	Present	Absent
Grunt Call	As adults	Present	Absent
Nesting Call	When nesting	Absent	Present
Total chick calls		3	3
Total adult calls		8	8
Total calls		11	10

*Based primarily on descriptions of Archibald (1975, and pers. comm.).

call then becomes more low-pitched, and is used subsequently as a signal between "familiar" birds. At this time the food-begging call disappears, and the stress call becomes only rarely uttered. The flight-intention, alarm, and guard calls all become much louder.

After the voice change, a few major new calls appear. One, the location call, resembles the guard call but is more plaintive, and is used to vocally locate other cranes after visual separation. A second new call is the precopulatory call. This consists of a series of purr-like notes uttered with the crane in a distinctive posture.

Perhaps the most significant new call to emerge with vocal maturity is the unison call. This is typically not uttered by cranes until their second or third year of life, when they begin to pair. Unlike the single-noted guard call, the unison call is a complex and extended series of temporally coordinated calls uttered by a pair with the birds standing in a specific posture and in a specific spatial relationship to one another.

While nest-building, paired cranes emit a low, moaning nesting call, often while arranging nesting materials, or while the female is sitting on the nest in preparation to laying an egg.

Although the crowned cranes exhibit many of these same calls, they also have some unique calls that do not appear to be shared with any of the more typical gruine cranes, according to Archibald. Chicks of *Balearica* utter a contact call similar to that of *Grus*, but it is of

lower frequency and more broken. A call possibly comparable to the stress call of *Grus* has been heard in crowned crane chicks, and food-begging calls are also present in these chicks (G. Archibald, pers. comm.). Yearling crowned cranes have been heard uttering guard calls, and the unique "booming call" has been observed in birds as young as 17 months old. In this call the gular sac is inflated and apparently serves as an adjunct resonator as a low-pitched call is produced. A unique "quack call" also occurs in crowned cranes, and is apparently used for mate location. Likewise, a distinctive "click call" is uttered when investigating a novel object. The unison call of *Balearica* usually consists of a guard call duet followed by a boom duet.

Interspecific Differences in the Unison Call

Archibald (1975, 1976) has provided an excellent comparison of the unison calls of all crane species except the black-necked crane, and unless otherwise indicated the following discussion is based on his summary.

In all cranes, the unison call is uttered with the crane in an erect, alert posture, with folded wings. In the crowned cranes, the pair members may or may not be standing close together, and either sex can begin the call. Additionally, the display is of varied length, and may last for more than a minute. The wings are not moved during the sequence, and the birds remain

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standing at a single place throughout. Typically, crowned cranes begin the display as a series of guard calls, which sometimes occur during the later booming sequence or may follow it. In the West African form (*pavonina*) the guard calls are monosyllabic honks, but in the eastern and South African forms (*gibbericeps* and *regulorum*) these calls are distinctly disyllabic, and the booming calls are lower in pitch, in correlation with the larger gular sacs.

In all other species of cranes, the unison calls are shorter, more penetrating, and lack booming, although the upper throat area may be expanded. Further, the sexes usually stand side by side while calling, and the wings are often raised or drooped. The sexes call in synchrony, but the calls as well as the postures assumed by the two sexes are different from one another.

In the genera *Bugeranus* and *Anthropoides* the calls are of a determinate length (up to 7 seconds). The two species of *Bugeranus* (wattled and Siberian cranes) have several features in common, including a relatively high-pitched call in both sexes and a rapid uncoiling of the neck of the male as he begins his display. However, unlike other cranes, in the Siberian crane the male begins the display, and unlike the situation in the wattled crane the display is of indeterminate length (Archibald, 1976). Males, and sometimes also females, lower the black primaries in the Siberian crane, but in the wattled crane the wings are held tightly against the body (fig. 10).

In the genus *Anthropoides*, the unison call is typically introduced by the guard call, and both calls are low, grating, and tend to lack harmonic development. The female typically begins the display, and one female call is normally uttered for each male call. In the demoiselle crane, the female begins by calling while extending her head back behind the vertical axis, while the male holds his head nearly vertically. In the blue crane the female holds her extended neck and head slightly behind the vertical throughout the display, while the male holds his head back even further and droops his primaries while raising his humeri, exposing the dark flight feathers (fig. 10).

In the genus *Grus*, the display is of indeterminate length, depending on intensity of stimulation, with the female usually beginning the call. In most species the female utters two or even three calls per male call. According to Archibald, three species groups in the genus *Grus* can be recognized on the basis of variations in the unison call.

The species group *canadensis* consists of the sandhill crane alone. In it, both sexes keep their wings folded throughout the display, and there is little wing-raising on the part of the male. With each call by the female, her bill is elevated about 45 degrees and is returned to the horizontal between calls. Males vary considerably in their head and wing movements.

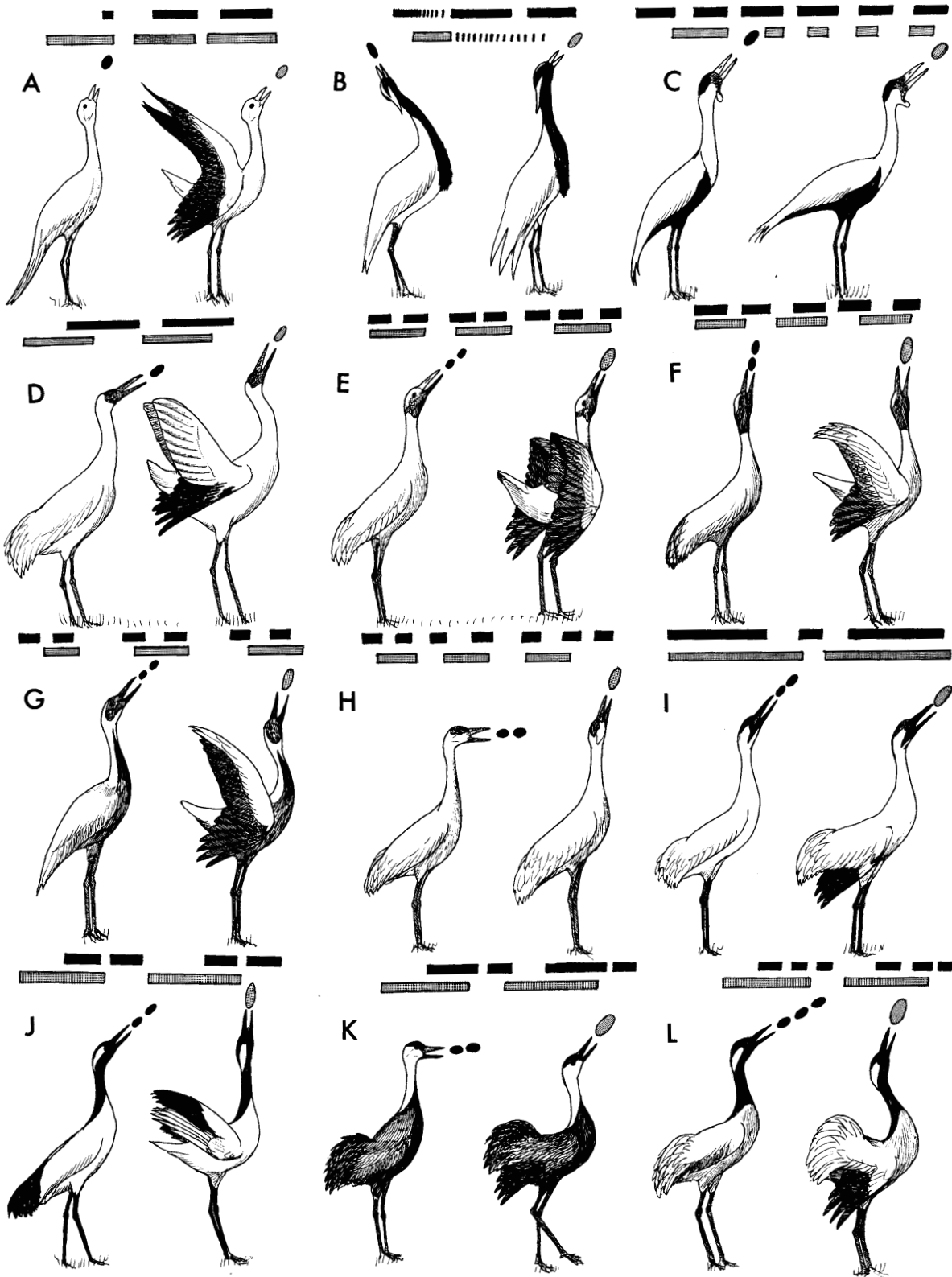
The species group *antigone* includes the sarus, Australian, and white-naped cranes. In these species the female begins the display, initially elevating her bill to or beyond the vertical but later returning the bill to a less extreme angle. The male extends his head and neck to an extreme posture beyond the vertical, and lowers the primaries while raising the humeri throughout the display. The pair typically stand side by side, sometimes even touching one another (fig. 10). In the Australian crane the large gular sac is inflated at the end of the display, and one or two long and very low-pitched calls are uttered, presumably homologous to the booming calls of *Balearica*.

The species group *americana* includes the hooded, Eurasian, whooping, and Japanese cranes. The display is usually initiated by the female, with a long scream-like call followed by a series of shorter calls that average two or three per male call. The female initially extends her head and neck beyond the vertical, but later moves it more forward, while the degree of the neck extension and angular position varies with species and situation. Likewise, the amount of wing elevation and feather erection in males varies with degree of stimulation and threat. Pair members often walk toward the threatened object during the display. According to Archibald, the unison call of the Japanese crane varies between populations, with the Japanese form typically producing a call in which the female utters two or three short calls for every male call, while the mainland population females utter a long call followed by a short call for every male call.

Crane Vocalizations and Tracheal Variations

It has long been known that there is a relationship between the structure of the trachea in cranes and their remarkably loud and penetrating calls. Topsell (1972) reported that the French naturalist Pierre Bollonius (1517-1564) determined by dissection that the "throat bole" of cranes differed from those of all other birds, in that it "is fastened to the fleshe, as deepe as the ribbes without dependance on the intralls," and that this is the "true cause why their voices be hearde, before their bodies be seene." By 1575 the tracheal configuration of the Eurasian crane had been illustrated by V. Coiter, and subsequently most of the cranes of the world were described as to their tracheal condition. The monographic review by Berndt (1938), which deals with tracheal coiling in cranes, swans, and the relatively few other groups of birds in which it occurs, is still the most complete coverage of this subject.

On the basis of the work of Berndt and others, it is clear that the cranes exhibit a series of interspecific variations that provide a probable evolutionary progression of tracheal modifications affecting both the total tracheal length and the relationships of the trachea to the keel of the sternum.



10. Unison-call posturing of blue (A), demoiselle (B), wattled (C), Siberian (D), Australian (E), sarus (F), white-naped (G), sandhill (H), whooping (I), Japanese (J), hooded (K), and Eurasian (L) cranes. Durations of male (shaded) and female (inked) vocalizations are indicated by bars above. "Balloons" indicate typical number of female calls per male call. After Archibald (1974).

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In the generalized or "primitive" condition of the trachea in the crowned crane, the trachea passes back into the thoracic cavity directly (fig. 3). This is presumably the ancestral crane condition, and it might be noted that the recently found *Balearica*-like crane fossils from the late Miocene of Nebraska are sufficiently well preserved that many of the tracheal semirings are still intact, and these indicate a similar direct tracheal route (Gregory Brown, pers. comm.).

In all other surviving species of cranes the trachea of both sexes in the adult crane is looped downward to come into contact with the anterior edge of the sternum. In the wattled crane the loop is a simple S-shape, with the leading edge of the sternum recessed but not excavated to receive the tracheal tube (fig. 11). Evidently a very similar condition exists in the Siberian crane (Archibald, 1976).

In the genus *Anthropoides*, the condition is more like that of *Bucgeranus* than of *Grus*. In the demoiselle crane a more extensive degree of tracheal invasion of the sternum may be seen (fig. 11), but the anterior edge of the trachea is still fully exposed to view. This is also the case with the blue crane (fig. 11).

Within the genus *Grus*, all species exhibit a relatively extensive excavation of the sternum by the trachea, which ranges from a relatively simple looping in the sandhill crane to a double looping that extends to the very posterior end of the keel in the whooping crane (fig. 11).

One of the obvious effects of such tracheal invasion of the sternum is a considerable increase in total tracheal length. This is well illustrated in table 5, in which the total average tracheal length may be seen to vary from about 50 centimeters in the crowned cranes and the demoiselle crane to more than 160 centimeters in the Japanese crane. The most obvious correlation of variations in tracheal lengths among crane species has to do with the vocalizations of adult cranes (table 5). It may be seen that, as the tracheal length is increased to increased tracheal invagination of the sternum, the adult vocalizations become progressively more penetrating and "whooping." On the other hand, there is no clear-cut direct relationship between tracheal length and the mean fundamental frequency of the unison call (table 6), or to the number of harmonics that are usually generated. What does seem to be true is that species with longer tracheae tend to show less fluctuation of frequencies when calling, and also tend to show better harmonic development than those species lacking tracheal elongation. Thus, harmonics are most poorly developed in the genus *Anthropoides*, which lacks both tracheal elongation and gular sacs, while as many as eight harmonics are developed in the crowned cranes (which have gular sacs) and from five to seven harmonics are typical of sarus, white-naped, hooded, Australian, Eurasian, and whooping cranes, all of which have greatly elongated tracheae. On the other hand, the

Japanese crane exhibits little harmonic development, according to Archibald, in spite of its extremely elongated trachea. In common with the whooping crane, however, it shows a high degree of constancy of frequency during the unison and guard calls, especially among males.

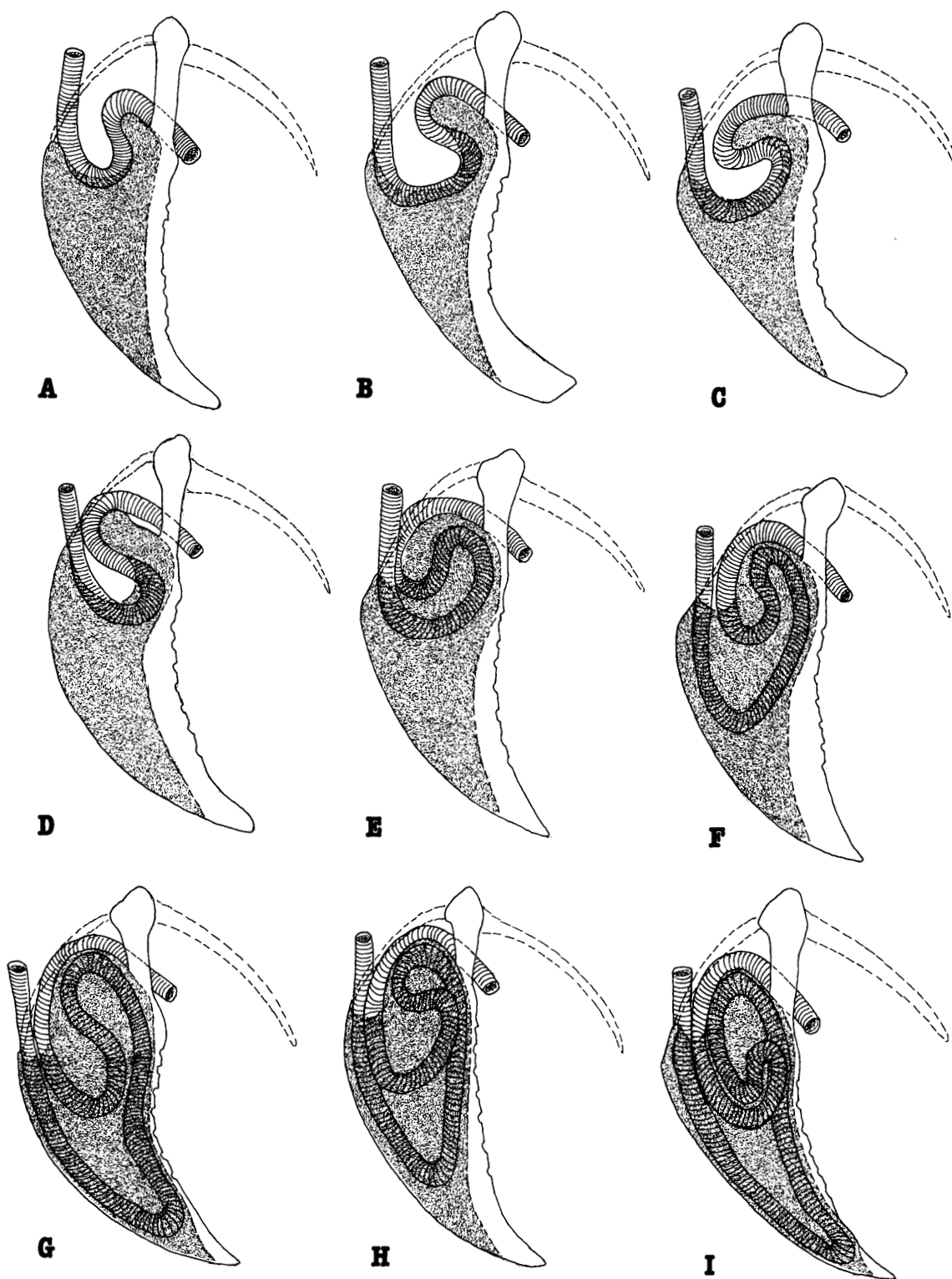
Niemeier (1979b) has investigated the possible resonating role of the trachea in the vocalizations of sandhill cranes during ontogeny. She determined that calls after the "voice break" exhibited their greatest amplitude development at frequencies coincidental with the harmonic frequencies that would be generated from an open tube equal in length to the tracheal length of a bird. Thus, as in the swans and other Anatidae (Johnsgard, 1971), the crane's trachea evidently operates like an open-tube acoustical system. However, Niemeier also found that at the upper end of the trachea's length (in birds approaching a year or older), the trachea may be as much as 2.26 times longer than would be necessary to produce the fundamental frequencies actually generated by the birds. Adult-type bugling and similar calls were observed only after the trachea had reached a length in excess of 55 centimeters, and a diameter in excess of 1 centimeter.

It would thus seem that the cranes have "accepted" the respiratory penalties associated with an unusually long trachea (and thus an increased volume of "dead" tracheal air to be exchanged with each breath) for certain acoustical benefits. These benefits are evidently not lowered vocal frequencies *per se*, but instead may be associated with increased acoustic potential for harmonic development (and thus increased overall carrying power). Or more highly specific and individualized "tuning" of the syrinx may be possible, associated with individual differences in tracheal lengths, and possibly unique vocal characteristics might facilitate individual recognition. Both would have considerable advantages to birds such as cranes, which clearly rely heavily on vocalizations for their social signals. Evidently tracheal elongation must have certain acoustic advantages over the gular sacs for vocal resonance: otherwise one would have predicted that the latter device would have been retained and used in *Grus*, while in fact only the Australian crane seems to have retained or developed a functional gular sac.

Tracheal and Syringeal Development*

Elongated tracheae, arranged *in situ* in loops or coils, are presently known to occur in some 57 species of birds representing six orders (Gruiformes, Galliformes, Anseriformes, Ciconiiformes, Charadriiformes, and Passeriformes). There are actually four different types of anatomical associations of the coiled or looped tracheal tube in the class Aves. Tracheal coiling may be (1)

*This section contributed by Dr. Myra Mergler Niemeier, Iowa State University



11. Adult tracheal and sternal anatomy of wattled (A), demoiselle (B and C), blue (D), sandhill (E), sarus (F), Eurasian (G), and whooping (H and I) cranes. In part after Berndt (1938).

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TABLE 5

Crane Vocalizations and Sternal Characteristics

<i>Species</i>	<i>Body Index*</i>	<i>Tracheal Invagination†</i>	<i>Vocal Characteristics‡</i>
East African and South African Crowned Cranes	827	6.03	Mellow, disyllabic; also lower-pitched booming with gular sac, male lower than female, with fewer harmonics
West African Crowned Crane	763	7.04	Mellow, goose-like honk; higher-pitched booming with gular sac, male lower than female, and fewer harmonics
Blue Crane	887	57.44	Low-pitched, broken calls, little harmonic development, male lower than female
Demoiselle Crane	705	39.52	Low-pitched broken calls, no harmonic development, male lower than female
Wattled Crane	1,131	46.83	High-pitched scream, harmonics to ca. 5 kH., male lower than female
Siberian Crane	1,050	45.63	Musical call, harmonics to ca. 5 kH., male lower than female
Australian Crane	996	122.17	Very penetrating whooping, male calls lower than female and modified by gular sac, harmonics to ca. 5 kH. in female
Sarus Crane	1,105	109.9	Very penetrating whooping, most harmonics under 4 kH. in female, male lower than female
White-naped Crane	961	168.5	Very penetrating whooping, most harmonics under 4 kH., male lower than female
Sandhill Crane	797	64.53	Loud but less penetrating and pulsed calls, harmonics to ca. 6 kH., male lower than female
Whooping Crane	1,039	179.0	Very penetrating whooping, most harmonics under 4 kH., male lower than female
Japanese Crane	1,074	198.75	Very penetrating whooping, most harmonics under 3 kH., male lower than female
Hooded Crane	805	139.0	Loud but less penetrating whooping, male relatively high-pitched but lower than female, harmonics to ca. 5 kH.
Black-necked Crane	983	??	Very penetrating whooping
Eurasian Crane	905	150.5	Very penetrating whooping, most harmonics under 4 kH., male lower than female

*Sum of exposed culmen, wing (chord), and tarsus in millimeters, from Wood (1976) except for black-necked crane.

†Based on measurements of Wood (1976); distance from anteriormost point of sternum to most posterior point of tracheal invagination, in millimeters.

‡Based on descriptions of Walkinshaw (1973) and Archibald (1975).

**Measurements not available, reported as "extensive" by Walkinshaw (1973).

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TABLE 6

Tracheal Lengths and Fundamental Frequencies of Unison Calls, Various Cranes

Species	<i>Average Tracheal Length (in centimeters)*</i>			<i>Fundamental Freq. (Hz)†</i>	<i>Tracheal References</i>
	<i>Intrasternal</i>	<i>Extrasternal</i>	<i>Total</i>		
West African Crowned Crane	0	51.0(3)	51.0(3)	♂ 440-860 ♀ 590-920	Berndt, 1938 Archibald, 1975
East African Crowned Crane	0	53.5(2)	53.5(2)	♂ 470-970 ♀ 540-970	Archibald, 1975
Blue Crane	9.6(2)	55.0(2)	64.6(2) 58.7(3)	♂ 860 ♀ 1,240	Berndt, 1938 Archibald, 1975
Demoiselle Crane	9.7(1)	44.8(1)	54.5(1)	♂ 840 ♀ 1,400	Berndt, 1938
Wattled Crane	0	86.6(1)	86.6(1)	♂ 1,400 ♀ 1,700	Archibald, 1975
Australian Crane	—	—	106.9(8)	♂ 570 ♀ 880	Archibald, 1975
Sarus Crane	28.9(5)	—	88.1(4) 107.7(2)	♂ 1,090 ♀ 1,270	Berndt, 1938 Archibald, 1975
White-naped Crane	—	—	121.8(3)	♂ 770 ♀ 1,270	Archibald, 1975
Lesser Sandhill Crane	13.0(2)	43.0(1)	56.0(1)	♂ 510 ♀ 900	this study
Greater & Florida Sandhill Cranes	—	—	59.1(11)	♂ 500-550 ♀ 890-900	Niemeier, 1979b
Whooping Crane	71.0(1)	76.0(1)	147.0(1) 151.7(2)	♂ 790 ♀ 690-890	Coues, 1874 Archibald, 1975
Japanese Crane	—	—	162.8(1)	♂ 1,030 ♀ 1,110-1,190	Archibald, 1975
Hooded Crane	—	—	118.2(2)	♂ 770 ♀ 1,150-1,200	Archibald, 1975
Eurasian Crane	47.6(3)	—	109.6(3) 118.2(6)	♂ 1,030 ♀ 1,100-1,190	Berndt, 1938 Archibald, 1975

*Sample size indicated in parentheses, mean indicated for samples of more than one.

†Mean "basal frequency" of main portion of unison call, according to Archibald (1975).

superficial, that is, beneath the skin on the surface of the pectoral muscle or abdomen, (2) in association with the clavicle, (3) coiled within the thoracic cavity, or (4) within the sternum. Occurrence of this intrasternal housing of the trachea is second to the most common condition of superficial tracheal coiling. Intrasternal tracheal coiling is found in the majority of swan and crane species and is not found in any other avian family.

The order Gruiformes has received considerable attention in reference to tracheal structure. The most extreme degree of intrasternal tracheal elongation and convolution in this order is seen in various adult members of the family Gruidae.

Berndt's (1938) extensive review of the literature prior

to the mid-1930s concerned tracheal and sternal anatomy in the cranes, excluding the white-naped crane, the hooded crane, the Japanese crane, and the black-necked crane. In 1973, Walkinshaw summarized the tracheal anatomy of all 15 species of cranes and presented subjective assessments of the tracheal length of one species relative to another (see table 5).

The relationship between the growth of the sternum and the trachea was documented by Schneider (1788-89, cited in Berndt, 1938), who showed that the sternum was not completely ossified in a pullet of the Eurasian crane, thus implying a developmental aspect to this sterno-tracheal relationship. In this example, only the "foremost and uppermost portions of the keel were

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ossified" (Schneider, 1788-89). Yarrell (1827) was apparently the first individual to note the developmental relationship between the sternum and the trachea in cranes with convoluted tracheae. In his examination of two specimens of the Eurasian crane he noted that one was "evidently a young bird by the state of the bones in which the insertion of the trachea is not carried so far as in the 'older bird'." Yarrell (1827) assumed that the greater "depth of insertion" (of the trachea) occurred only in male cranes. However, lack of sexual dimorphism relative to crane tracheal morphology is supported by Portmann (1959) and G. W. Archibald (pers. comm.).

W. K. Parker (1868) described and illustrated sternal and shoulder girdle structure in crowned cranes, in the Japanese crane, and in the sarus crane. Of particular interest is his description and illustration of the "shoulder bones and sternum of a recently hatched Manchourian [Japanese] Crane." Like Schneider (1788-89), Parker stated that the lateral parts of the sternum ossify first. Parker also described the association of the sternum and the trachea in developing Japanese and sarus cranes. The newly hatched Japanese crane showed only a shallow depression in the anterior surface of the sternum which accommodated a slight flexion of the trachea. This depression was described as being much more extensive in a "half-grown" sarus, where "the tracheal loop turns suddenly upwards, apparently causing non-development and absorption of the bone, nearly to the lower coracoid lip" (Parker, 1868). Thus, Parker was the first to propose a possible mechanism by which the trachea is able to invade the sternum.

Roberts (1880) investigated the ontogeny of the tracheosternal apparatus in the sandhill crane. He examined an embryonic crane collected in Minnesota (probably a greater sandhill crane) that was about to hatch. Roberts described the trachea as "simple" (not entering the sternum) and described the sternum as being "entirely cartilaginous." Roberts was the first to state that tracheosternal development is an age-dependent phenomenon. He also described the adult position of the trachea within the sternum in both the sandhill crane and the whooping crane. (Tracheal coils extend to the posteriormost perimeter of the sternum in the whooping crane, but are confined to the anterior portion in sandhills.) He described the rest of the keel as being "composed of two frail plates separated by a thin layer of bony meshwork" (Roberts, 1880).

Coues (1892) referred to the tracheal structure of two "species" of sandhill crane, *canadensis*, the "Northern" sandhill crane and *pratensis*, the "Southern" sandhill crane, noting that "the trachea is at first simple and straight . . . [in the adult] the anterior half of the keel . . . is excavated to receive the [tracheal] folds." Pycraft (1913) described the same developmental phenomenon and speculated on the reciprocal processes involved in sternal excavation and tracheal invasion.

Age-dependent development of the sternum and trachea apparently caused Forbes (1882) to incorrectly assume that the female wattled crane possesses a highly convoluted trachea and that the male's is straight (as in both sexes of the Siberian crane).

Portmann (1959) was the first to correctly summarize tracheosternal development in swans and cranes. He explained that tracheal elongation and convolution attains the adult form "after several months" in the cranes (no species specified), unlike the swans, which do not attain the adult tracheal morphology until they are over one year of age. Portmann described the changes that take place in the cranial portion of the gruoid sternum as a result of tracheal penetration, which was previously diagramed by Berndt (1938). G. W. Archibald (pers. comm.) also noted differences in tracheal structure in six newly hatched to newly fledged sandhill cranes.

Because the early, primarily anecdotal accounts of tracheal morphology in presumably immature cranes were chance findings for a variety of crane species of unknown age, no systematic study had been done to illustrate the process of tracheosternal development in known-age cranes with elongated tracheae. Niemeier (1979b) investigated this process in Florida cranes and greater sandhill cranes by x-raying captive-reared individuals with ages ranging from 3 days to 14 years.

Tracheal growth within the sandhill crane sternum was found to proceed as a gradual penetration of the initially cartilaginous tracheal loop into the cartilaginous sternum. The lateral portions of the sternum ossify first. The trachea reached its mature length (approximately 60 cm—see table 5) between 70 and 90 days of age, implying an average tracheal elongation rate of 0.6 cm per day.

The process of intrasternal tracheal elongation and coiling can be viewed as a dynamic interplay between the developing trachea and sternum. As the tracheal loop forces its way into the sternum, a concavity must be developed to allow for tracheal penetration. In early stages, this concavity is apparently the result of sternal growth. But, as the process of ossification begins, breaking down and rebuilding of sternal cartilage or bone is obviously necessary to accommodate the coiling of the tracheal loop.

Although tracheal development in these cranes is usually complete at two to three months of age, further coiling of the tracheal loop (found in 10, or 44 percent, of the 23 specimens examined) may be the result of a delay in sternal ossification or temporal extension of the building up and breaking down of intrasternal bone or cartilage. This may be especially true in the case of the greater sandhill crane, where intrasternal tracheal coiling is apparently more extensive but tracheal length is not significantly greater than it is in the Florida race. Tracheal elongation must be appreciably more rapid than sternal excavation for tracheal coiling to occur.

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That is, the process of sternal enlargement must be slower than the process of tracheal elongation to force the tracheal loop to coil within this space. In fact, the rate of tracheal elongation is about five times that of sternal growth.

A space forms between the trachea at the point of flexure and the concavity on the anterior surface of the sternum. This indicates that the sternal excavation necessary for early penetration of the tracheal loop into the sternum is facilitated by sternal growth.

At various points during its ontogenetic development, the sandhill crane reflects the adult tracheal condition found in other species of cranes. This varies from the slight penetration of the trachea into the sternum in the unhatched chick (reflecting the tracheal condition of the adult Siberian crane and the wattled crane) to the moderately coiled trachea characteristic of adults of several species of *Grus*. Lastly, the adult status of extensive tracheal coiling is similar to (or even exceeded by) the tracheal coiling found in the Japanese, whooping, Eurasian, and black-necked cranes (Walkinshaw, 1973).

The problems of possible respiratory inefficiency associated with an elongated trachea have apparently been avoided in cranes by several means. The constant positive relationship between tracheal diameter and tracheal length (to 50 cm) indicates that, to this point at least, the sandhill crane avoids increased tracheal resistance to the airstream by increasing tracheal diameter relative to length. This idea has been suggested by Hinds and Calder (1971) for avian species whose tracheal volumes far exceeded those predicted by their body mass as a result of tracheal convolution; the sandhill crane's tracheal volume exceeds these predictions by 3.2:1 in males, second only to the 3.8:1 ratio of the trumpeter swan (*Cygnus buccinator*).

Unlike the mammalian larynx, which is a pre-bronchial structure (that is, it is located anterior to the bronchi), the most common type of avian syrinx is associated with the bronchi and is designated as a tracheobronchial type. Nonpasserine birds such as cranes have the most simplistic type of syrinx, formed of membranes in the inner and outer walls of the trachea at the point where it branches into the two bronchi. Tension on these two sets of tympaniform membranes is apparently controlled, in part, by only two sets of muscles, which are external to the trachea itself. Contraction of the sternotracheal musculature allows the syringeal membranes to bow into the lumina of the bronchi, creating slits through which air passes, thus setting the membranes into vibration (Sutherland and McChesney, 1965).

Because of their increasing size but consistent thinness (approximately 0.01 mm) during development, the internal tympaniform membranes are thought to be the primary sound-producing structures in cranes. The external tympaniform membranes were found by Niemeier (1979b) to be much smaller and thicker, with a high degree of variability in thickness. Both the internal and the external tympaniform membranes have been implicated as the sources of sound production in other types of birds.

The fundamental, or pitch-determining, frequencies emitted by the vibrating syringeal membranes (the voice of a bird) have historically been thought to be determined by tracheal length. This relationship, however, is not at all clear-cut, and evidence has been accumulated both for and against this effect in birds. Sandhill cranes show an independence of emitted carrier or pitch-determining frequencies and tracheal length during development.

