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A sociogram for the cranes of the world

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Abstract

The behavioral repertoire for the world's 15 species of cranes includes over 100 behavioral acts with clear social significance. Each species performs at least 60 discrete social postures, vocalizations, displays, and activities. Because all but a handful of the stereotyped social displays are common to all species, the presence or absence of social displays was useful only to a limited degree in comparing the relatedness of established crane taxonomic groups. However, the breadth of the repertoire for each species and for the family Gruidae tentatively places cranes at the apex of social complexity (at least for stereotyped displays) in the animal world. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

This study is based on observations of captive cranes of all species (Table 1), with supplemental observations of all species in the wild. Previous studies of the social repertoire of cranes include: the classic ethogram of the red-crowned crane by Masatomi and Kitagawa (1975), and Masatomi's (1983a) work detailing copulatory sequences in *Grus* species of cranes. Archibald (1976a) used social displays, especially the Unison-call (a form of antiphonal duet) in an attempt to decipher crane phylogeny. Katz (1979) employed some aspects of crane social behavior to quantify seasonal changes in mated pairs of hooded cranes. Nesbitt and Archibald (1981) described some agonistic displays for sandhill cranes. Partial sociograms are available for the following species: whooping crane (Allen, 1952; Kepler, 1976), Siberian crane (Poulsen, 1975; Sauey, 1976), Eurasian crane (Poulsen, 1975), and sandhill crane (Voss, 1976a,b; Tacha, 1981).

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Table 1
Current nomenclature of the world's cranes

Common name	Abbreviation in Table 2	Scientific name	Species group
Black crowned crane	B Cr	*Balearica pavonina*	Crowned crane group
Gray crowned crane	G Cr	*Balearica regulorum*	Crowned crane group
Wattled crane	Watt	*Bugeranus carunculatus*	Long-train group
Blue crane	Blue	*Anthropoides paradisea*	Long-train group
Demoiselle crane	Dem	*Anthropoides virgo*	Long-train group
Siberian crane	Sibe	*Grus leucogeranus*	Siberian crane
Sandhill crane	Sand	*Grus canadensis*	Sandhill crane
White-naped crane	Wh-N	*Grus vipio*	Bare-faced group
Sarus crane	Sar	*Grus antigone*	Bare-faced group
Brolga	Brol	*Grus rubicunda*	Bare-faced group
Eurasian crane	Eura	*Grus grus*	Eugrus group
Hooded crane	Hood	*Grus monacha*	Eugrus group
Black-necked crane	B-Nk	*Grus nigricollis*	Eugrus group
Red-crowned crane	Red	*Grus japonensis*	Eugrus group
Whooping crane	Whoo	*Grus americana*	Eugrus group

A partial ethogram, including only the non-social behavior for the world's cranes, has been published (Ellis et al., 1991). This is the social ethogram: it consists of two parts. First is the sociogram (sensu Wilson, 1975), a description of all social displays, together with higher level behavior sequences, here termed activities (e.g. Dance or Attack). The second part is a tabulation (Table 2) of the presence and importance of each social ethon (a non-restrictive term for behavioral acts as simple as a reflex or as complex as an activity: sensu Ellis, 1979) for each species.

Social signals in many groups of animals are difficult to recognize and disentangle. Many are subtle, are graded in their effects and expressions, and have a variety of effects on the recipient (see Wilson, 1975:199). Also, different observers sometimes apply different criteria in naming and separating displays, thereby making comparisons between taxa very difficult (Nelson, 1978). The large number of displays we describe for cranes, in part, reflects the relative ease with which an experienced observer can distinguish their rather obvious social signals. Because our primary goal was to name and characterize homologous displays in all species, we were forced to generalize the description of some ethons to allow for variation between species. The result is that this paper and Ellis et al. (1991) together provide a nearly complete compendium for the behavioral repertoire of all species of cranes. However, our descriptions are, for many ethons, too general to represent an ethogram for any species. As such, this paper supplies the structure for future ethograms for all species.

While we present all ethons that have a social context, our primary focus is on social communication, which is defined as the transfer of information (Hailman, 1977) often resulting in the overt alteration of behavior of the recipient. We recognize that some crane displays (e.g. Pre-Attack) function interspecifically (Viess, 1981).

The reader should be aware that, while we have attempted to report likely sign vehicles, effective stimuli, or releasers (i.e. those aspects of each signal that influence the response of the communicant), it was beyond the scope of this paper to perform the necessary experiments to do so thoroughly. In many agonistic encounters, brightly-colored bare skin is prominently featured, but whether this is the actual sign vehicle that releases or retards aggression, or whether it acts in concert with body position and motion or other features of the display are unknown. The elucidation of such releasers in cranes must await additional research.

The family Gruidae (Table 1) is an ancient group whose earliest known fossils are from

Eocene deposits ca 50000000 years old (Olsen, 1985). Cranes have body parts conspicuously molded for use as visual and auditory signals over long distances, and since they move slowly, relative to many other animals, the forms of their displays can be readily perceived and analyzed. Even so, many subtle signals (such as iris dilation) have only recently come to light, and others may as yet remain undiscovered.

Archibald (1976a) had previously used only a single social display, the Unison-call, to distinguish species groups. The phylogeny resulting from this approach has been largely confirmed by recent molecular genetics studies (Dessauer et al., 1992; Krajewski and Fetzner, 1994). Our approach was to look less intently at any one display, but to evaluate the whole spectrum of social displays toward identifying species groups on the basis of presence or absence of displays. Our study benefitted from ample time (ca 30 years) and a pooling of observations from numerous students of crane behavior.

2. Methods

All 15 species of cranes have been held in captivity at one or both of our institutions (Patuxent Wildlife Research Center, two species (including four subspecies), 31 years; and International Crane Foundation, 15 species, 28 years). The use of captive animals has long been recognized as an essential component of behavioral research (Lorenz, 1935). Indeed, a continuum of research opportunities exists between the field and the lab (Lehner, 1979), and both are needed to allow researchers to observe the minute details (from captive animals) and proper context (from free ranging animals) of animal social behavior (Menzel, 1969). Most of our observations were made on captive birds held in relatively large outdoor enclosures (many netted; with the result that occupants of these were capable of flights up to 30 m) designed to allow a full expression of social displays. Because some individual animals develop abnormal behavior in captivity (Tinbergen, 1962), all of our descriptions are based on observations of more than one individual, and, whenever possible, have been augmented by work on wild cranes. Where certain behavioral anomalies (such as fence pacing or the development of homosexual pairs) have appeared, pen or other modifications were made to eliminate them (Kepler, 1976, 1978; Viess, 1981). We feel confident that the social displays described herein are typical of wild birds, although we recognize that their frequency of performance has been greatly altered by captivity.

We have greatly benefitted from the special opportunities derived from living in close proximity to breeding pairs of all species, and especially from working with hand-reared birds. Most hand-reared birds respond toward approaching humans as for intruding conspecifics or, in some instances, as for an approaching mate. This situation enabled us to vary the stimulus situation (i.e. our presence) to thereby determine the hierarchy of social displays. At the approach of a human, tame or imprinted birds first show alert behavior, then low-intensity threat displays, then, if the human continues to approach, they display more intently, and may finally attack by lunging, stabbing, etc. The result is that a decade of field observations, especially for the less social species, may not yield the number of observations of some of the more intense social displays that can come from a single stroll through our captive colonies. We also note that many of the subtle features of crane social behavior (e.g. Iris-expansion, Feather-tuft-erection) have gone undetected or unreported until this study because they are inconspicuous except when viewed from very near.

In the compendium that follows, we deal with the form and context of social (auditory and visual) displays in cranes. In describing each social ethon, we included orientation of body parts, sounds, movements, feather positions, and even subtle cues such as iris expansion or the degree of bare skin coloration and expansion. We also mention probable sign-vehicles (e.g. color or pattern) that characterize the displays (Hailman, 1977).

We recognize that, in describing the behavior of a species, it is often difficult to separate ethons at the appropriate level. More specifically, it is important to recognize that some behavioral acts are merely components of more complex displays. For example, we noted that two species of cranes

Table 2
Social behavior of the world's cranes[a]

Ethon	B Cr	G Cr	Watt	Blue	Dem	Sibe	Sand	Wh-N	Sar	Brol	Eura	Hood	B-Nk	Red	Whoo
I. Vocalizations															
A. Peep	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Food-begging	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C. Nesting-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D. Contact-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E. Pre-flight-call	P	P	+	+	+	+	+	+	+	+	+	+	+	+	+
F. Flight-call	P	P	P	P	+	+	+	+	+	+	+	+	+	+	+
G. Alarm-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
H. Guard-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
I. Unison-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
J. Location-call	P	P	P	+	+	+	+	++	+	+	++	++	++	++	++
K. Stress-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
L. Distress-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
M. Moan	P	P	?	?	?	+	+	+	+	+	+	+	+	+	+
N. Hiss	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
O. Pre-copulatory-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
P. Copulatory-call	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+
Q. Thoracic-click	−	−	+	−	−	−	P	−	−	−	−	−	−	−	−
II. Agonistic displays															
A. Alert	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Iris-expansion	−	−	++	−	−	++	−	−	−	−	−	−	−	−	−
C. Bare-skin-expansion	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+
D. Bare-skin-present	+	+	+	−	−	+	++	+	+	+	++	++	++	++	++
E. Feather-tuft-erection	++	++	++	+	+	+	++	−	sl	++	++	+	+	+	++
F. Gular-expansion	+	+	−	−	−	−	−	sl	+	+	−	−	−	−	−
G. Tertial-elevation	−	−	−	−	−	+	+	+	++	+	+++	+	+	++	+
H. Head-rub	+	+	?	?	?	+	++	++	++	+	sl	sl	sl	+	sl
I. Pre-strut	+	+	+	+	+	+	+	+	+	+	++	++	++	++	++
J. Strut[b]	+ v	+ v	+ v	+ v	+ v	+ vH	++ vH	+ Vh	+ v	+ v	++ VH	++ VH	++ H	++ Vh	++ Vh
K. Head-flick	+	+	++	++	+	sl	−	+	−	−	−	−	−	−	−
L. Dorsal-preen[c]	+	+	+	+	+	+++D	+slD	+slD	+slD	+slD	++D	++D	++D	++D	+DR
M. Ventral-preen	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+
N. Wing-flick-flight	P	P	P	+	P	+	+	+	+	+	+	+	+	+	P
O. Bill-down-hold	+	+	P	P	+	+++	+	+	P	+	+	++	++	+	++
P. Bill-down-growl	−	−	P	P	P	++	+	+	P	+	+	+	P	+	+
Q. Bill-down-sweep	+	+	−	−	P	++	−	−	+	?	+	?	?	−	−
R. Blow-bubbles	−	−	−	+	+	++	+	?	+	?	?	?	?	+	?
S. Stab-nibble-tug	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
T. Head-lower-ruffle	+	+	++	++	+	−	−	−	−	−	−	−	−	−	−
U. Ruffle-bow	−	−	−	−	−	++	++	+++	++	++	+	+	+	+	+
V. Wing-spread-hold	+	+	+	sl	?	−	−	−	−	−	−	−	−	−	−
W. Wing-spread-flap	+	+	++	++	+	+	−	+	+	+	+	+	−	+	−
X. Tail-wag	+	+	++	++	+	−	−	−	−	−	−	−	−	−	−
Y. Stomp	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Z. Leg-quiver	P	P	+	+	P	P	+	P	+	+	P	+	+	+	+

Table 2 *(Continued)*

Ethon	*B Cr*	*G Cr*	*Watt*	*Blue*	*Dem*	*Sibe*	*Sand*	*Wh-N*	*Sar*	*Brol*	*Eura*	*Hood*	*B-Nk*	*Red*	*Whoo*
AA. Catapult	−	−	−	−	−	−	−	++	*sl*	+	−	−	−	−	−
BB. Butterfly	−	−	−	−	−	−	−	−	−	−	+	++	++	−	++
CC. Arch	−	−	−	−	−	−	−	−	−	−	−	−	−	+++	−
DD. Hoover or Neck-crane	+	+	−	−	−	++	+	+	+	+	+	+	+	+	+
EE. Crouch	+	+	+	+	+	+++	++	+	+	+	++	++	+	+++	++
FF. Pre-attack	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
III. Attack and mob															
A. Run-flap	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Hiss	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C. Gape	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D. Bill-stab	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E. Jump-rake	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F. Wing-thrash	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
IV. Defensive and submissive displays and activities															
A. Wing-flare-cower	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Cower	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C. Cower-crouch	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D. Distraction-display	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E. Bunching	*P*	*P*	*?*	*P*	+	*?*	+	*?*	*?*	*P*	+	*?*	*?*	*?*	*?*
F. Flee	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G. Pre-copulation	*P*	+	+	+	+	+	+	+	+	+	+	+	+	+	+
V. Concordant behavior															
A. Contact-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Pre-flight	+	+	+		+	+	+	+	+	+	+	+	+	+	+
C. Pre-flight-call	*P*	*P*	+	+	+	+	+	+	+	+	+	+	+	+	+
D. Flight-call	*P*	*P*	*P*	*P*	+	+	+	+	+	+	+	+	+	+	+
E. Flight	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F. Allopreen	+	+	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*
VI. Pair related behavior															
A. Unison-walking	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Unison-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C. Dance	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1. Spread-hold	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2. Gape	+	+	+	+	+	+	+	+	+	+	*P*	*P*	*P*	*P*	*P*
3. Gape-sweep	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
4. Tuck-bob	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
5. Leap	*P*	*P*	+	+	+	+	+	+	+	+	+	+	+	+	+
6. Object-toss	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7. Run-flap-glide	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+
8. Hoover or Neck-crane	+	+	−	−	*?*	+	+	+	+	+	+	+	+	+	+
9. Bill-stab	−	−	+	*sl*	*sl*	++	+	+	++	+	+	+	+	+	+
D. Pre-copulation	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E. Copulation-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F. Copulation	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
VII. Nest preparation and maintenance behavior															
A. Sideways-toss	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Sweep-drop	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Table 2 *(Continued)*

Ethon	*B Cr*	*G Cr*	*Watt*	*Blue*	*Dem*	*Sibe*	*Sand*	*Wh-N*	*Sar*	*Brol*	*Eura*	*Hood*	*B-Nk*	*Red*	*Whoo*
C. Nest-probe	*P*	*P*	*P*	*P*	*P*	+	?	*P*	+	+	*P*	*P*	*P*	+	+
D. Tread	+	+	*P*	*P*	*P*	*P*	++	+	+	*P*	*P*	*P*	*P*	+	*P*
VIII. Parental behavior															
A. Oviposition	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. High-step	+	+	+	+	+	+	++	+	+	+	+	+	+	+	+
C. Waddle	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D. Shuffle	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E. Settle	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F. Bill-tuck	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G. Incubation	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
H. Brooding	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
I. Shading	+	+	+	+	+	+	+	+	++	++	+	+	+	+	+
J. Tread	*P*	+	*P*	*P*	*P*	*P*	+	+	+	*P*	*P*	*P*	*P*	+	*P*
K. Nesting-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
L. Present-morsel	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
M. Distraction-display	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
IX. Filial behavior															
A. Peep	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. Contact-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C. Food-begging	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D. Wing-quiver	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E. Accept-morsel	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F. Stress-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G. Distress-call	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

[a]Key to cell codes: ?, It is unknown if this species performs this ethon and knowledge insufficient to conjecture; +, this species performs this ethon; −, this species does not perform this ethon; ++, this species performs this ethon to a great degree; +++, this species performs this ethon to a greater degree than other species; P, this species probably performs this ethon; sl, slightly, species performs an ethon that suggests this ethon.

[b]Strut variations: V = vertical Strut is normal form (v = occasional form), performed with body axis raised >20° above horizon. H = horizontal Strut is normal form (h = occasional form), performed with body axis horizontal or <20° above horizon.

[c]D = Drop (wing lowered during performance); R = rarely seen (e.g. DR = wing drop rare for this species).

conspicuously flare the feathers of the thigh when Strutting. Because Thigh-feather-flare was never noted outside the context of some more complex display, we do not include it here as a separate display. More difficult to decide if appropriate to separate were Iris-expansion and Feather-tuft-erection. Although both appear as separate displays, we are nonetheless somewhat uneasy in presenting them separately because each is also a component of more complex displays. When seen alone, they may merely be the precursors of, or evidence of, an inclination to perform a more complex display.

We have somewhat arbitrarily divided the social repertoire into nine general categories (Section 3.1–Section 3.9). The first to be presented is the vocal (or auditory) repertoire (Section 3.1), which is also presented again by weaving the calls into the functional classes of the visual displays (Section 3.2–Section 3.9). Unfortunately, there is overlap between categories even for visual displays because some ethons appear in several contexts. For example, elements of Attack (Section 3.3) appear also in the Dance (Section 3.6C) and are discussed in both contexts. Similarly, the Growl that is part of the Bill-down-growl threat display seems identical to the Nesting-call of a parent crane calling to its hatching chick, so it is treated in both places.

While our emphasis in this paper is on ethon titles and general descriptions, we provide some information on behavioral sequences (e.g. the order of appearance of ethons within a typical Dance bout). Our nomenclature generally employs the use of dashes to link descriptive words (e.g. Jump-rake). Because a one word title is sometimes sufficient (e.g. Alert), we capitalize the first letter in each ethon title to alert the reader that we are writing restrictively about, for example, the Alert social display. When speaking non-restrictively about, for example, an attack by a predator, the word 'attack' is not capitalized whereas when a crane employs elements of Attack, the word is capitalized. When referring to non-social ethons described by Ellis et al. (1991), we also capitalize the first word in each ethon title.

Although we attempted to apply descriptive titles to all visual displays, most vocalizations are not easily described (an exception is the Thoracic-click), so each is titled by context (e.g. Pre-flight-call). To save space, we used acronyms in the paragraph where a particular ethon is described, but for clarity, only there. For example, in its descriptive paragraph, Gular-expansion is referred to as G-e, but elsewhere, all references to Gular-expansion are spelled out.

The primary method of accumulating data for this report was to make careful observations and still photographs while rearing and caring for captive cranes. Immediately after observing rarely performed ethons, we also took detailed notes of the form and context. Super-8 movie films were exposed and notes were taken on behavioral sequences. The films were viewed and tracings were made of selected frames. These tracings and still photographs were then abstracted into the illustrations that accompany the text. After years of familiarizing ourselves with crane social behavior, in 1988 we joined forces to identify and name each ethon and to prepare behavior categories. We subsequently observed even more carefully in an attempt to identify new ethons and new performance contexts. During the subsequent ten years, we also attempted to verify each cell in the species-ethon contingency table (Table 2). For example, Iris-expansion, a very subtle feature first noted in the Siberian crane, was found in other species only after careful scrutiny of many captive pairs.

3. The sociogram

Social ethons are presented below in text outline form that matches the compressed outline in Table 2. The table also provides data on which species perform each ethon and to what degree. For some cells within the table, further study will confirm or dispute our assessment of the importance of that ethon for a particular species. The order of presentation is roughly by age (young to old), by volume (quiet to loud), and by order of appearance in behavioral sequences (early to late).

3.1. Vocalizations

In ethology, titles for ethons are typically 'descriptive', but for vocalizations, 'functional' titles (providing primary context) are often more useful (Grier, 1984). Much intergradation exists between calls with the result that the range of vocalizations appears as a continuum with identifiable peaks, each of which is given a title. Because various species perform the calls very differently, some calls classed together here (by context of performance) may not be true homologs (similar in origin).

Below, we arbitrarily present vocalizations separate from the other social ethon classes. However, we recognize that calls are most often given as components of complex social displays. Where a call is the major or only component of a social display, the call is presented a second time in the appropriate place in the outline in Table 2. The scope of this work precludes presenting sonograms for each call for each species. Nevertheless, we recognize that in ethograms for each species sonographic analysis will be required.

A. *Peep* (Voss, 1977; pip call). A quiet, brief whistle grading into an even briefer chirp or extended into a purr. Beginning 2-3 days before hatching and grading into the Contact-call which continues throughout life.

B. *Food-begging* (Archibald, 1976a; Food-begging-call). A rapid series of brief chirps in the chick grading into a single, hoarse, prolonged chirp in fledglings. At least for tiny chicks, this call intergrades with the Peep and Contact-call.

C. *Nesting-call* (Archibald, 1976a; N-c). A quiet purr or growl given at a rate of about one to two calls/s) is normally given in long series. Quieter and less rigidly cadent than the Copulatory-call. This call is given by adults while nest building, while inspecting nest contents (eggs, chicks, or even an empty nest), and while Brooding or Feeding chicks. During a complete performance, the bill is pointed downward and the bill tip is held very near the chick or substrate. In the whooping crane, an identical call is performed during the Bill-down-growl social display. For the Siberian crane, the Nesting-call sounds closer to the Stress-call. For some species (i.e. red-crowned, hooded, Eurasian, and sandhill), the female is much more prone to give this call than the male.

D. *Contact-call* (Masatomi and Kitagawa, 1975; Alert-call; Archibald, 1976a; C-c). Cranes quietly communicate while foraging and during other maintenance activities using this call, which may actually be two or more similar calls that intergrade with the quieter Peep and louder Pre-flight-call. In adults, this call is a quiet, brief, hoarse gargle usually given at intervals of several seconds. The exception is the adult Siberian crane, in which the C-c is one continuous horn-like note also given at intervals of several seconds.

E. *Pre-flight-call* (Archibald, 1976a; Flight-intention-call). A brief hoarse gargle observed in *all species* but the crowned cranes. Like the Contact-call, but louder, honk-like, and usually given in long series with about one call per second. Very often seen in birds preparing to fly.

A second call, performed by red-crowned and hooded cranes, is given in the same context as the P-f-c, but only during the mating season and almost always by a female. It is also given at intervals like the P-f-c and sounds like a nasal or hoarse version of the P-f-c, but is believed to be distinct.

F. *Flight-call* (Nesbitt and Bradley, 1988 unpubl., F-c). A loud call given at short intervals by cranes aloft. For some or most species (but not the Eurasian crane), the F-c is like a truncated Guard-c.

G. *Alarm-call* (Archibald, 1976a; A-c). This call is evident in all species of cranes. It is a brief, loud, low-frequency blast (higher pitched in the Siberian crane) given alone or in bouts with individual calls separated by intervals of several seconds. Each call is composed of a series of hoarse subnotes that are given so rapidly that they are nearly inseparable to the human ear. In the sandhill crane and perhaps all other species, the A-c sounds identical to the first call of a Guard-call series. The common context for all species is the detection of a distant predator or another threat.

H. *Guard-call* (Archibald, 1976a; G-c). In the sandhill crane and all other species, pairs and flock mates respond to the approach of intruding conspecifics and some other disturbances by performing loud, guttural squawks (often in series).

In a flock, many birds may be calling at once, but in pairs, the male and female alternate calls in true antiphonal fashion. It is typically performed in series and somewhat like the Unison-call except in the G-c the male and female calls are temporally much alike although the female is higher pitched.

G-cs are often given in series with an interval of one to several seconds between calls. The sandhill crane G-c largely replaces (i.e. may be equivalent to) the whooping crane Alarm-call. Crowned cranes give rather loud, honk-like G-cs. For the black crowned crane, G-c is a simple 'boom' while in the gray crowned crane, it is a disyllabic 'ka-wonk'. For the Siberian crane, it is a single, unbroken, high-pitched, short call.

I and J. *Unison-call* (Walkinshaw, 1949; U-c; Armstrong, 1963 (in Masatomi and Kitagawa, 1975), antiphonal song). All cranes perform antiphonal duets (Archibald, 1976a) which are sexually dimorphic in all species except the crowned cranes. U-cs have been effectively used to determine sex in paired birds (Kepler, 1978) and have been employed to determine phylogeny (Archibald, 1976b). Although much variation exists between species, in general, both birds call standing side by side with necks upright and, when highly aggressive, standing on tip toes to increase height. For *Anthropoides* and *Bugeranus*, each duet lasts 5–7 s, with one male call emitted for each female call. Demoiselle cranes keep their wings folded throughout the duet, but the female elevates her bill to almost or beyond the vertical, while the male calls with bill slightly above the horizontal. Blue and wattled males elevate their humeri briefly at the end of the duet. Siberian cranes also emit one male call per one female call, but the duet can continue for several minutes. Mates call alternately, the male lower pitched than the female, resulting in a duet resembling a European police siren. All other *Grus* species also have duets of indeterminate length; however, for each male call the female usually emits 2–3 shorter and higher calls. For some species and sexes (i.e. sandhill (both sexes), sarus, brolga and white-naped (only females)), the wings are closed throughout the duet. The female always begins the duet in sarus, brolga and white-naped cranes, and the male always elevates his wings and drops the primaries (Fig. 1) in turkey-strut (*Meleagris gallopavo*) fashion. The Siberian, whooping, red-crowned, black-necked, Eurasian, and hooded cranes sometimes walk slowly while duetting and the wings of both sexes may be elevated with primaries lowered. During low intensity displays, birds duet without elevating their wings.

Crowned cranes perform a long series of synchronized Guards-calls and a gular *Boom* (gray crowned cranes) or *Honk* (black crowned cranes) in place of the U-c. The head is held down with the bill drawn against the neck. As a Boom (or Honk) is given, the bill is swept quickly to the side. Members of a pair give alternate Booms or Honks in series that sometimes last several minutes. Remarkably, the Boom serves a Guard-call function in the black crowned crane and as a U-c in the gray crowned crane.

J. *Location-call* (Archibald, 1976a; L-c). A very loud trumpet-like blast. If performed in a bout, at least several seconds of silence follow each call. When widely separated across a marsh, pair mem-

Fig. 1. Unison-call, white-naped crane (male is at left).

bers L-c in an apparent effort to determine mate location. To the human ear, the L-c is very like, although more drawn out than, the first note of a Unison-call.

K. *Stress-call* (Archibald, 1976a; S-c). The plaintive prolonged nasal chirp of a chick that grades into a loud wailing in the adult. Seen in context of prolonged hunger, thermal stress, or threat of capture.

L. *Distress-call*. Probably the full expression of the Stress-call, but in the adult whooping crane (and all but the crowned cranes), D-c is a long, multi-note, grating scream given in series during capture and handling. Crowned cranes in distress emit a prolonged honk given in extended series.

M. *Moan*. An energetic moan is emitted by some cranes during the most intense portion of the Ruffle-bow social display (e.g. sandhill, Siberian, sarus, brolga, and white-naped cranes). In the Red-crowned, it is given in transition from Crouch to Ruffle-bow. The sound is either a nasal buzzing or, more likely, a syringeal vocalization. It is performed with the bill closed. The Moan is so inconspicuous as to escape detection in the wild. Even in captivity, it can only be heard from, at most, a few meters.

N. *Hiss*. A loud hissing, emitted with bill closed or agape, is evident during the Pre-attack display and during an actual Attack. Probably performed by all species.

O and P. *Precopulatory-call* and *Copulatory-call* (Archibald, 1976a; P-c). Much like the Nesting-call, the P-c begins as a Contact-call, then becomes regular and louder growl. For five species, (i.e. Eurasian, hooded, whooping, black-necked, and red-crowned cranes), the P-c grades into a loud scream, the C-c. For all other species, the P-c is also the call given during actual copulation.

The P-c is performed in long series in which one to two calls are given per second. Sometimes a series will continue for 10 min without interruption until Copulation is complete. While giving the P-c, the bill is directed skyward and the bird advances in a slow rhythmic gait (very often with its mate in tow) as described for the Precopulatory-display (Section 3.6, D and E). The P-c is a soft purr in the crowned crane.

Q. *Thoracic-click*. This noise, evident only in wattled (and perhaps sandhill) cranes, is given for a short period following capture. It appears as a quiet, but conspicuous thump or throb. On first hearing, it sounds like a loud heart beat, but it is given at about one second intervals (i.e. cadence too slow for heart beat). From careful inspection, we believe its origin is thoracic rather than buccal, nasal, or syringeal, with the result that it is most likely merely a pneumatic sound rather than a vocalization with social significance.

3.2. Agonistic displays

Cranes use at least 32 agonistic displays not including vocalizations.

A. *Alert* (Masatomi and Kitagawa, 1975; A). When a crane becomes aware of a distant intruding conspecific, a predator, or some other alarming stimulus, it adopts a characteristic posture with its head extended maximally up and somewhat forward while watching the stimulus. Typically the bird remains still, briefly. All species exhibit the A posture, but mated males typically elevate the head higher while females extend the neck more forward. The dominant bird (also normally a male) in a group will normally stand taller (i.e. show more A behavior) and have a more expanded red cap, face or wattles than subordinate birds. Adult males assume a greater role in watching for threats to the pair or family than do the females (e.g. Tacha, 1988:16). While A certainly carries a behavioral message to other cranes, it may also merely be the most efficient means of surveying the environs.

B. *Iris-expansion*. Captive male Siberian and wattled cranes clearly exhibit this behavior. It is also somewhat evident in whooping cranes. Typical context is a defensive male approaching a territorial violator. In such encounters, the female typically remains in the background and shows I-e to a lesser degree if at all.

C. *Bare-skin-expansion* and *Bare-skin-contraction*. Except for the two species that lack bare patches or wattles, cranes during display expand their unfeathered areas to show dominance or aggressiveness and contract them when ill or subordinate.

In the whooping crane, both the red papillose crown and the red-black mustache strip are extended (Fig. 2). Although these areas are concealed by feathers in juvenile birds, they are nonetheless expanded during display.

D. *Bare-skin-present*. When an intruder is far off, a dominant or territorial bird may Bare-skin-expand or stand Alert, but do nothing else to threaten. As the intruder approaches, for the species with red caps, the displaying bird will turn its bill away from the intruder and thereby maximize the red surface area presented, all the while using its peripheral vision to maintain visual contact with the intruder. Periodically, the displayer interrupts its performance of B-s-p to look directly at the intruder for a second or two, then resumes its rather odd stance of looking down and away from the object of its display. Only those species (13) which have bare skin areas present them.

E. *Feather-tuft-erection*, *Head-fluff*, and *Head-sleek*. The two species that lack specialized bare skin areas compensate by displaying special feathered areas on the head or neck. The demoiselle crane erects its white, post orbital plume. The blue crane flares (H-f) its cobra-like nuchal hood. Context of performance is as for Bare-skin-expansion and Bare-skin-present. The converse of H-f (and F-t-e) is H-s.

Most of the cranes that expand bare skin areas also erect small feather tufts. For some species, the movement of these tufts is inconspicuous even in captivity. For the black-necked crane, the flaring of feathers of the auricular area is more conspicuous than for any other species. The phylogenetically aberrant crowned cranes conspicuously flare their crowns in threat contexts, but also perform a normal variation of the F-t-e.

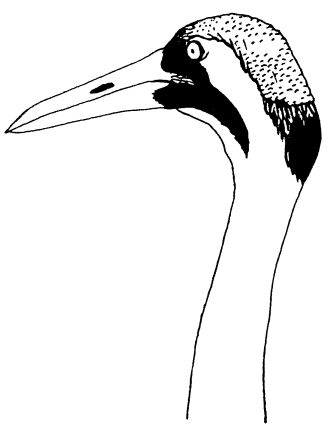

Fig. 2. Bare-skin-expansion, whooping crane.

Fig. 3. Tertial-elevation and Strut, Eurasian crane.

F. *Gular-expansion*. Three of the five species that inconspicuously or never exhibit Feather-tuft-erection do perform G-e in contexts like that for Feather-tuft-erection and Bare-skin-expansion. Most apparent in the closely related sarus and brolga cranes, this display consists merely of expanding the pharynx while facing an intruder.

G. *Tertial-elevation* (Masatomi and Kitagawa, 1975; Adornment). Not performed by the crowned cranes or the three long-train species, T-e is evident in all other species (Table 2) and most pronounced in the Eurasian crane (Fig. 3) for which the tertiaries are raised past perpendicular with the plane of the back. T-e appears as a separate display and as a component of more elaborate displays, especially Strut and Unison-call. When so displaying, the crane most often turns so its lateral aspect is visible to the intruder.

H. *Head-rub*. The crown and side of the head are rapidly rubbed on the back or wing. Most often performed in company with ritualized preening, this display appears as a displacement activity in moderately intense agonistic encounters. Commonly seen in three species (Table 2), H-r is also occasionally performed by at least nine other species including both crowned cranes. H-r is performed more often by females. By context, H-r seems to indicate some ambivalence between approaching and avoiding an intruder.

I. *Pre-strut* (Masatomi and Kitagawa, 1975; adornment). This static display is seen in all fifteen species. It is a modification of Alert posture with the added components of Bare-skin-expansion, tertiary-elevation, and elevation of thigh feathers (some species only). It sometimes includes a lifting component wherein the bird stands on its toes with the foot pad off of the substrate. As for Alert, this display is primarily performed by territorial males. P-s is at approximately the same level of intensity as, and is often followed by, Guard-calling or Unison-calling.

J. *Strut* (Masatomi and Kitagawa, 1975; adornment-walk). Performed by all species, this display (Fig. 3) is a specialized walk wherein the crane turns sideways to present its lateral aspect to the recipient and walks in slow, measured steps. Between steps, each foot is lifted high and toe extension is exaggerated. Bare-skin-present is conspicuous in the sandhill crane, and tertiary elevation is especially evident in the Eurasian crane. Two general forms are evident: either the axis of the body is nearly horizontal or much more vertical (Fig. 3). Table 2 indicates which form is most often seen in each species. Other components evident in extreme performances include a lateral flaring of the thigh and tibio-tarsi feathers (especially in whooping and black-necked cranes) and occasionally dropping of the primaries (whooping crane).

K. *Head-flick* (Masatomi and Kitagawa, 1975; irrelevant-head-shake). Five or six species (Table 2) show a quick, but conspicuous, sideward tossing of the bill in display context. In the blue crane, a bill-clacking or bill-rattle component is also present. In the related wattled crane, a rattling sound is also made, but by the wattles slapping against the head rather than by a clicking of the bill. In these two species, it is frequently performed as part of Head-lower-ruffle, discussed later.

Fig. 4. Dorsal-preen, whooping crane.

L. *Dorsal-preen* (Masatomi and Kitagawa, 1975; Irrelevant-back-preen; Voss, 1977; Preen Display). Ritualized preening is probably the most frequently performed non-static, social display. The back, tertiaries, or scapulars are the primary sites of bill contact (Fig. 4). Several components of the display suggest that other than normal preening is involved: first, the D-p is consistently performed at the same, rather small location; second, the preening components are abbreviated and interrupted (sometimes resulting in the bird merely contacting the spot with its bill for several seconds without nibbling the feathers); third, after a few seconds with the bill on back, the bird very often lifts its head to observe the recipient, then returns to preen or point at the same spot; fourth, a consistent wing-drop component (Fig. 4) often accompanies D-p especially in the Siberian crane, but also in nine other species; and finally, D-p is also very often part of a display sequence beginning with Alert, then Pre-strut. An interesting D-p component especially evident in the Siberian crane is Iris-expansion maximizing display of the yellow iris.

M. *Ventral-preen* (Masatomi and Kitagawa, 1975; Irrelevant-leg-preen). As for Dorsal-preen, all species but the crowned cranes perform this. Normally in V-p, the crane preens and/or contacts a small area at the junction of the belly, thigh, and proximal tibio-tarsus. A peculiar neck extension component identifies this as a display. V-p is very often the final component of the Hoover and Ruffle-bow displays discussed later.

N. *Wing-flick-flight*. This display grades smoothly into normal flapping flight and can be differentiated only when extreme. When displaying, the wing stroke is shallower, the glide between strokes longer, and the upward flick for the next stroke is more rapid. Although it has been observed in ten species, all species of cranes probably use this display. Cranes W-f-f when patrolling territorial boundaries, when pursuing intruders, and during courtship.

O, P and Q. *Bill-down-hold*, *Bill-down-growl* and *Bill-down-sweep* (Voss, 1977; Foraging Display). At least two of these displays have not previously been described. However, Poulsen (1975) may have entitled one of them Bill-to-ground. Some form of these displays (Fig. 5) is surely performed by 13 species and probably performed by the remaining two species (Table 2). Performance of B-d-h consists of lowering the head until the bill touches or nearly touches the ground and holding this posture. For the crowned cranes, B-d-h is the complete display. All other species probably (five species) or surely (eight species) add a growl component that sounds like the Nesting-call. Sometimes a Siberian crane will B-d-g while turning slowly, occasionally making a complete circle. Usually one mate performs these displays at the approach of an intruder. These displays are especially pronounced in the Siberian crane, a species which also adds a component (B-d-s) in which the neck sways side-to-side causing the bill to sweep left and right in an arc ca 50 cm in length.

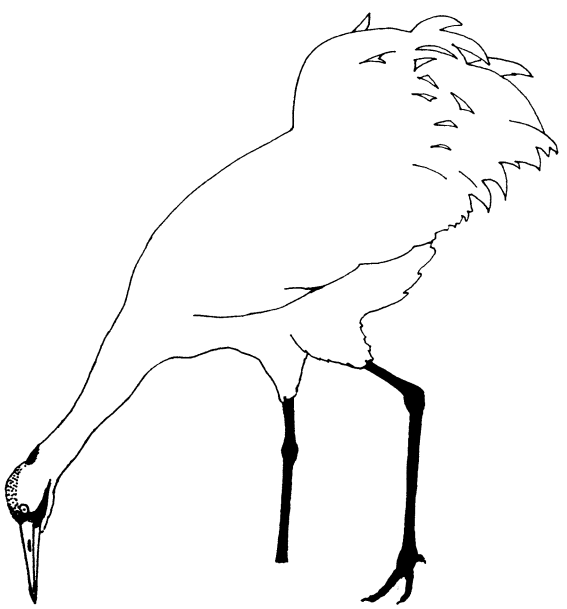

Fig. 5. Bill-down-growl, whooping crane.

We propose three possible origins of these displays. First, the Bill-down component, from a distance, looks like a standing adult attending a chick. Next, the growl is similar to or equivalent to the Nesting-call, and in some performances, the adult nibbles at twigs in a manner suggesting nest building especially when coupled with the sweep component of the Siberian crane. These displays appear then to be ritualized chick care and/or ritualized nest building. Either could convey to the recipient that the displaying crane has a deep commitment to the site and probably could be expelled only with difficulty. Alternately, this behavior may be ritualized foraging as suggested by Voss (1977).

R. *Blow-bubbles*. In the Siberian crane and a few other species (Table 2), a threatened crane may perform what appears to be Bill-down-growl while standing in water. For Siberian cranes, the bill is flicked side-to-side, as if stirring the water, with the result that the display appears to be ritualized feeding. Alternately, B-b is merely an aquatic performance of Bill-down-growl or Bill-down-sweep.

S. *Stab-nibble-tug* (Masatomi and Kitagawa, 1975; irrelevant-ground-stick; Voss, 1977; Foraging Display). This display, common to all species, is often closely linked with Bill-down-hold, Bill-down-growl, Bill-down-sweep and Crouch (Section 3.2, EE). During most performances, a crane, while being approached by an intruder, nervously Stabs at the ground and/or Nibbles and/or Tugs

at vegetation (at least three separate foraging action patterns (Ellis et al., 1991) are involved). Some performances suggest ritualized nest building, but most performances appear as true displacement activities that have not been ritualized. Although this is an aggressive display, the context shows a strong fear component as well.

T. *Head-lower-ruffle*. This display is found only in two crane groups, the crowned cranes plus the Long-train Group (the three species in Table 1 that have long trailing tertials). It is a homolog of the Ruffle-bow discussed next. In a typical performance, the head is dipped forward and *rapidly shaken*. Most often performed while walking.

U. *Ruffle-bow* (Masatomi and Kitagawa, 1975; wing-shake-bow; Voss, 1977; Body-wing-shake Display). As stated above, R-b replaces the Head-lower-ruffle of five species. R-b (Figs. 6 and 7) is performed by the bird presenting one side toward the intruder/recipient, then commencing what appears to be a maintenance Ruffle-shake (Ellis et al., 1991). First, the feathers are elevated, then the body begins gyrating side-to-side as the wings lift slightly then slap closed, in left and right cycles of increasing crescendo and vigor until the body of the bird whirs back and forth in a flurry of shaking. Two versions of Ruffle-bow are known.

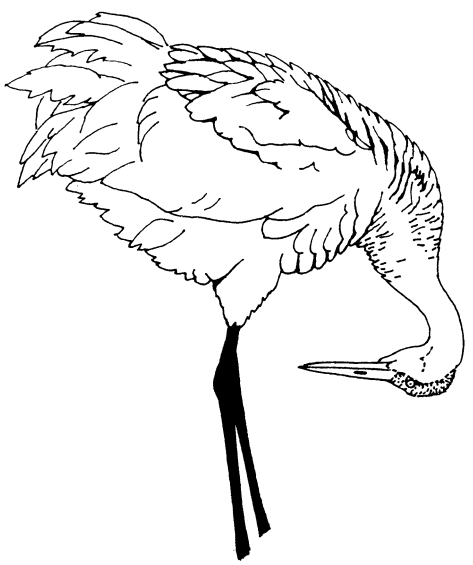

Fig. 6. Ruffle-down-down, sandhill crane.

Fig. 7. Ruffle-bow-up, whooping crane.

For the species that show R-b-down (Fig. 6, e.g. sandhill crane and four other species), when the gyrations reach a peak, the head is thrown forward and down with the bill pointed rearward, the bird rises onto its toes and a quiet Moan, ca 2 s in duration, is emitted. Gyration then ceases and most often (for the sandhill crane), the bill contacts the feathers of the leg and the crane Ventral-preens. For R-b-up (Fig. 7), the head is extended up and forward and the bill is tucked neck-ward and held for a second or two as shaking frequency reaches a zenith.

The Moan component, known for ten species, is nasal in quality and emitted with the bill closed.

V. *Wing-spread-hold*. The wings are lifted high and wide and held spread for $\approx 1-5$ s. Only the two crowned and the wattled cranes perform this display. It appears as a homology to the display described next. Evidence for the homology is a slight lowering of the head hinting at the sweep component of the next display.

W. *Wing-spread-flap*. Most of the world's cranes perform some form of this homolog of the crowned crane's Wing-spread-hold (Table 2). The wings are spread wide and high, then are rapidly

swept in a wide arc forward and down, producing an audible whoosh. This is a common display of the white-naped and Siberian cranes. For six species, as the wings flap, the head and neck sweep through a wide arc forward so that they lie under the forward extending wings. In the blue crane, the head and neck feathers flare (Head-fluff) as the head sweeps forward.

X. *Tail-wag*. T-w is the quick side to side tail movements performed in brief bouts of five to ten cycles each. This inconspicuous display is found only in the three species with the longest trailing tertiaries (wattled, blue and demoiselle) and the crowned cranes. A performance is seen in a display sequence with the ritualized preening that follows Wing-spread-flap or Stomp (below). T-w is seen as a movement of the tertiaries trailing above the tail, or the tail may be seen below the tertiaries, elevated for some other display.

Y. *Stomp* (Masatomi and Kitagawa, 1975; stamp). All species Stomp their feet in an audible left-right sequence that lasts $\approx 1-2$ seconds and increases in crescendo until it becomes a blur of foot movement. The legs are held nearly straight throughout so the foot movement is slight. S is always seen as part of a display sequence. It is typically followed by Leg-quiver discussed next.

Z. *Leg-quiver*. This element of some agonistic displays is subtle, but readily visible from close range. We hypothesize its presence in all species, but the movement is slight enough that it must be sought to be noticed. The displaying bird stands Alert with its straightened legs moving in a high frequency, low amplitude shiver. As for the preceding, L-q is an element in a series. A typical sequence for the whooping crane is Ruffle-bow, Stomp, L-q, Hoover.

AA. *Catapult*. All elements of this display are performed only by the white-naped crane, but incomplete performances are also seen in the sarus and brolga cranes. The C is perhaps merely an elaboration on the Wing-spread-flap display (Section 3.2, W). In both, the wings are spread, held high, then flapped deeply as the head and neck are thrust forward and down. The C employs the added element that the neck is then catapulted rapidly upward and arched far over the back, held ca 1 s, then typically lowered forward as the bird commences Ventral-preen.

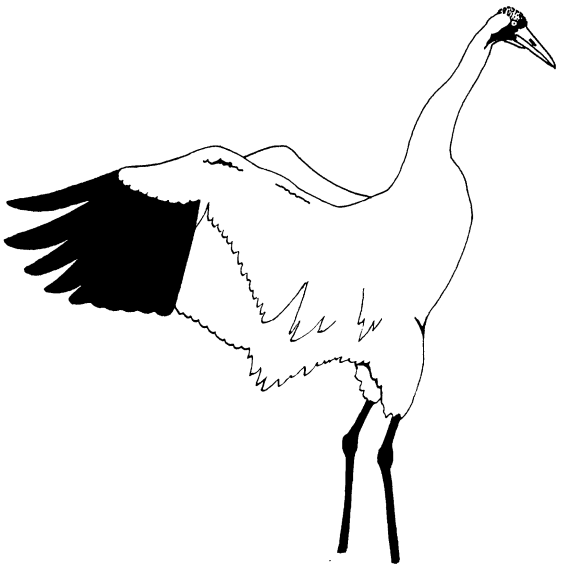

Fig. 8. Butterfly, whooping crane.

BB. *Butterfly*. The whooping crane's equivalent to the Arch, the B (Fig. 8) includes lifting of the three-quarters open wing high and back and then straining or 'holding the pose'. Unlike the Arch (next), the bill is pointed forward and down. Both Arch and B have elements of and appear as precursors to the Hoover (Section 3.2, DD).

CC. *Arch* (Masatomi and Kitagawa, 1975; Arch). A (Fig. 9) is probably the red-crowned crane's homolog to the Catapult (White-naped Group, Table 2) and the Butterfly (whooping crane). The high-intensity A usually follows several other, less intense, displays (e.g. Dorsal-preen) and signals near extreme agonistic tendency. Performed by arching the neck over the back with the bill pointed $\approx 80°$ above horizontal. Simultaneously, the wings are lifted (while remaining partially folded) maximally above the back. The bird holds the pose one or more seconds, then lowers wings and returns bill to horizontal.

DD. *Hoover* or *Neck-crane* (Masatomi and Kitagawa, 1975; Low-bow and High-bow; Poulsen, 1975; bill to ground (but see also Section 3.2, P)). H (Fig. 10) involves two general forms of neck posturing, both are reminiscent of the stem (neck) and handle (head) of a vacuum cleaner, hence the

Fig. 9. Arch, red-crowned crane.

title Hoover. The two versions are Hoover-up (extend neck maximally upward and slightly forward, tuck bill down, and strain) and Hoover-down (extend neck maximally down and slightly forward, point bill down, and strain). In both versions, the body axis is high anteriorly. Curiously, the sandhill crane and Siberian crane do Hoover-down while all of the last five species in Table 2 do Hoover-up except the hooded crane which does both. H very often follows alighting and very often involves or follows a wing-spread-up component.

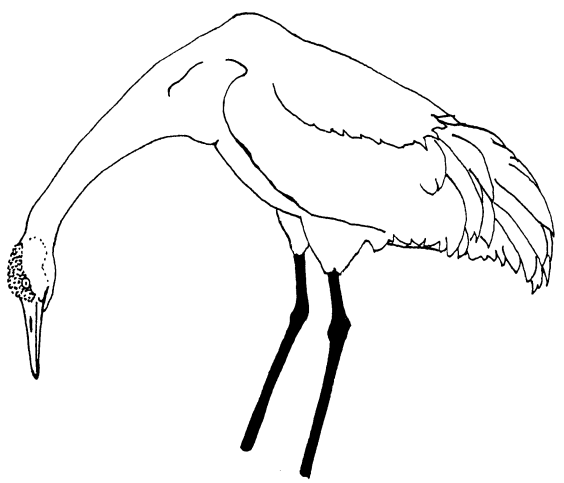

Fig. 10. Hoover, sandhill crane.

H is closely related to the Butterfly and Arch. In the sarus, brolga, and white-naped cranes, it only appears following alighting or some other display and is never performed alone. For the red-crowned crane, H performance, at least sometimes, is accompanied by rising onto the toes and by a quiet Moan or Growl. In the red-crowned crane, the near wing is occasionally lowered and the far wing spread and lifted during performance of Hoover. Sometimes both wings are held high when red-crowned cranes perform Hoover. Female hooded cranes have an interesting variant in which the far wing is lifted during H-down, then the bird exhibits a two-wing up-spread while still in H-down.

EE. *Crouch* (Masatomi and Kitagawa, 1975; irrelevant-crouch; Voss, 1977; Crouch Display). This, and the next ethon, are the most intense agonistic displays. They immediately precede outright Attack if the intruder approaches further. Two versions of C are seen. In both forms, the bird lowers to Lie posture as if Incubating and compresses the neck feathers. In the Siberian and crowned crane version, the wings are normally left completely closed, but in all other species, some degree of spreading is occasionally exhibited. High intensity displays involve more spreading. Having the wings spread also enables a more rapid Attack should the intruder continue to approach. In most species, most of the time, C is accompanied by much bill contact with nearby vegetation (Ellis et al. (1991) terms are Stab, Pecking, Nibble, Tug, and Thrash). C in the Siberian crane is unique in that the bird, when once crouched, always holds its bill motionless. Crouch appears to be a form of ritualized Incubation and probably signals to an intruder that the performer has a great investment in the territory (i.e. is nesting).

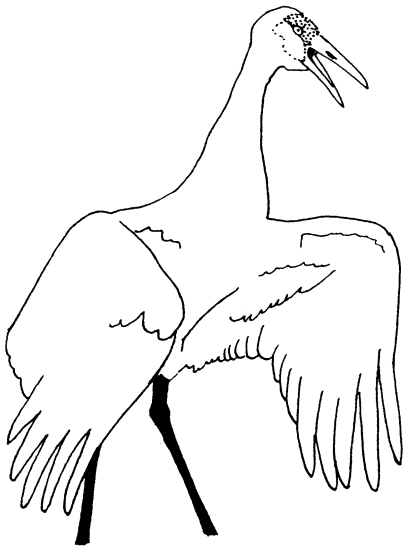

Fig. 11. Pre-attack, sandhill crane.

FF. *Pre-attack* (Voss, 1977; Spread-wing Display). As the crane approaches (or backs away from) an intruder in preparation for Attack, it will typically spread and droop its wings so primary and secondary tips droop or touch the vegetation (Fig. 11). The neck is extended upward and slightly forward with the head facing the intruder. Alarm-call, Guard-call, and Hiss often accompany a display. Young colts are particularly prone to display P-a just prior to Attacking another chick.

3.3. Attack and mob

A and M are 'activities' involving many action patterns. An A normally is preceded by, and often is interspersed with and followed by, several social displays, but is in itself not a display but rather an attempt to dispel or kill an intruder. All species show all of the following A action patterns. In addition, pre-fledged chicks of some, and perhaps all, species use some and probably all of the food dismemberment ethons (described in Ellis et al., 1991) when attacking siblings.

Mobbing, a group rush at a predator or another common enemy, has been known for the Eurasian crane since at least the 13th century (Wood and Fyfe, 1969). M may be present in most or all species, at least in the context of adults defending mates or young.

A. *Run-flap*. If the intruder is at a distance, the crane may Run while Flapping to enter combat or may R-f to flee. R-f may be followed by agonistic display rather than combat.

B and C. *Hiss* and *Gape*. In an Attack, the bird may loudly Hiss and Gape widely at the target.

D. *Bill-stab* (Masatomi and Kitagawa, 1975; upright-peck; Nesbitt and Archibald, 1981; Bill Sparring). A rapid thrust of the bill (closed or slightly open) is used to injure the target. Predators (e.g. dog (*Canis familiaris*) and human) have been killed by a stab of a crane's bill (Bent, 1926:227).

E. *Jump-rake* (Masatomi and Kitagawa, 1975; Kick). The crane leaps into the air (Fig. 12) and slashes at its opponent with its talons. The strongly curved inside talon is believed to inflict most of the damage.

F. *Wing-thrash*. Some damage can also be inflicted by slapping the wings against the opponent/intruder, but rapid and repeated W-t probably serve more to confuse and distract than to injure.

3.4. Defensive and submissive displays and activities

All cranes are believed to have all of the following displays. These are most often performed by ill birds, chicks, and subordinate adults. They are normally accompanied by Bare-skin-contraction

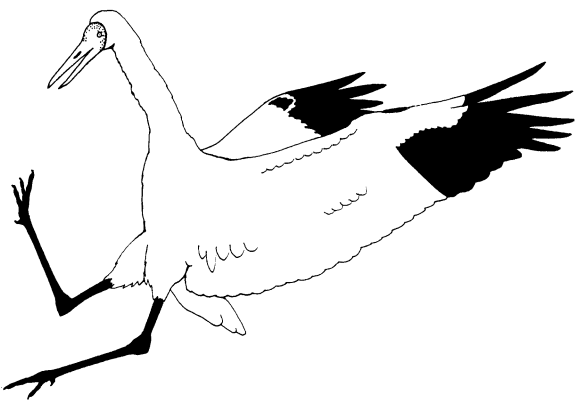

Fig. 12. Jump-rake, Siberian crane.

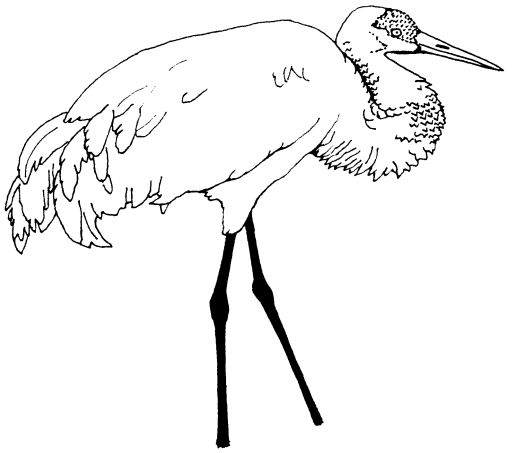

Fig. 13. Cower, sandhill crane.

and/or Head-sleek and Feather-tuft-compression, the converse of dominant displays (Section 3.2, C–F). Bunching and fleeing, while fitting under this heading, are activities rather than displays. Some pair-related ethons (most notably the Pre-copulatory display (Section 3.6, D)) also appear in appeasement contexts.

A. *Wing-flare-cower*. Like Pre-attack, the wings are spread and drooped. Differs in that the head is held low with the neck fluffed and curved down and forward (as in Cower, discussed next). May grade into Pre-attack when intruder presses.

B. *Cower* (Masatomi and Kitagawa, 1975; Neck-retracted-submission). In C (Fig. 13), the body axis is nearly horizontal, the neck is curved down with the head held low and retracted, and the feathers of the head and neck are elevated (Fluffed). Very submissive young and ill cranes commonly show this display. In chicks, this display is normally accompanied by the following related and intergrading calls: Peep, Contact-call and Food-begging-call. Masatomi and Kitagawa (1975) identified a Head-down-submission involving the head lowered near the ground rather than neck coiled. We consider these as two forms of C. A third form, wherein the bill is drawn near the Fluffed, but not retracted, neck, has been seen in juvenile birds observing their parents engaged in a territorial fray (M.A. Bishop, Personal communication).

C. *Cower-crouch* and *Lie-crouch*. C-c can be separated into two versions because of great contextual and slight physical differences. C-c is the extreme performance of Cower: it differs only in that the subordinate or depressed bird (most often a chick) lowers to Sit or Lie posture while performing. When performed by an adult on the nest, it becomes Lie-crouch and lacks the neck Fluff component. When approached by a predator, an Incubating adult will L-c with the neck forward outstretched or wrapped around the body to one side. By performing L-c, the adult is probably not signaling subordinance as in Cower, but rather is probably trying to avoid detection. Once the intruder is very close or shows that it has located the adult, the performer will often rise and defend its nest, flee, or try to lure the intruder away.

D. *Distraction-display* (Masatomi and Kitagawa, 1975; Diversionary display). An adult attending eggs or young may, if approached by a fearsome predator, move diagonally away from the nest and thus lure the intruder past the offspring. Often this behavior (i.e. luring away) is accompanied by a special display. The D-d involves drooping and dragging one or both wings over the vegetation while walking away from the intruder. The head is also held low and the bird may vocalize Distress-call. This display is probably homologous to the 'broken wing display of shorebirds'.

E. *Bunching*. Some cranes flee at the approach of an avian predator while others (including greater sandhill cranes, *G. c. tabida*; Rod Drewien, Personal communication) rush into a compact group and point bills skyward in an obvious attempt to deter the predator from attacking.

F. *Flee*. Another option for a crane is to Walk, Run or Run-flap while Fleeing from an intruder.

G. *Pre-copulation* (Masatomi and Kitagawa, 1975; Irrelevant-wing-open). Described in Section 3.6, G, the female form of P-c (Fig. 14) occasionally appears in appeasement context when a subordinate crane of either sex performs this display at the approach of a more aggressive bird. P-c is not infrequent in pre-fledged chicks 6 weeks of age and older.

3.5. Concordant behavior

All cranes are to some degree gregarious. Several displays, vocalizations, and activities promote coordinated movement, and obviate actual Attacks within a social unit. Pair related ethons, while of the same genre as those discussed below, are presented separately in Section 3.6.

A. *Contact-call* (Section 3.1, D). This quiet growl is given at several second intervals as cranes quietly forage together. It grades in a continuum from the whistle-like Peep of the chick to the louder Pre-flight call and Flight-call of fledged chicks and adults.

B and C. *Pre-flight* and *Pre-flight-call* (Masatomi and Kitagawa, 1975; Intentional posture; Section 3.1, E). In a group situation, when a crane adopts the unique neck-stretched-forward-and-up P-f posture (Fig. 15), it faces into the wind and gives P-f-c, a louder version of the Contact-call. If other cranes decide to also depart, they align themselves with the first, pose in P-f, and also call. Soon others and perhaps all in the group join in. Then one and perhaps all Run-flap and lift into Flight. A Neck-fluff version (suggesting fear) is occasionally seen in the whooping crane, sandhill crane, and perhaps others.

D and E. *Flight-call* and *Fly*. Crane's normal method of Flight (an activity comprised of several action patterns: Soar, Glide, Flap, etc.; Ellis et al., 1991) is by constant flapping (i.e. powered flight). However, on migration they often use thermals as supplementary sources of power (Pennycuik et al., 1979). Cranes also save energy in level, powered flight by Flying in 'V' or 'chevron' formation (Walkinshaw, 1973; Pennycuik et al., 1979). Flying in formation is aerodynamically more efficient, allowing trailing birds to make use of an 'upwash' of air that spreads laterally behind and beyond each bird's wing tips (Burton, 1990). Unlike most birds that F in formation, cranes at least sometimes F slightly higher than the bird immediately in front of them. Aerodynamic efficiency may be thereby compromised to a degree. Even so, they gain some lift from the preceding bird and also benefit by improved visibility (Burton, 1990). Wing-flick-flight was discussed earlier (Section 3.2, N). Some additional Flight displays are probably present as suggested by Bent (1926:227), but not yet known well enough to delineate here.

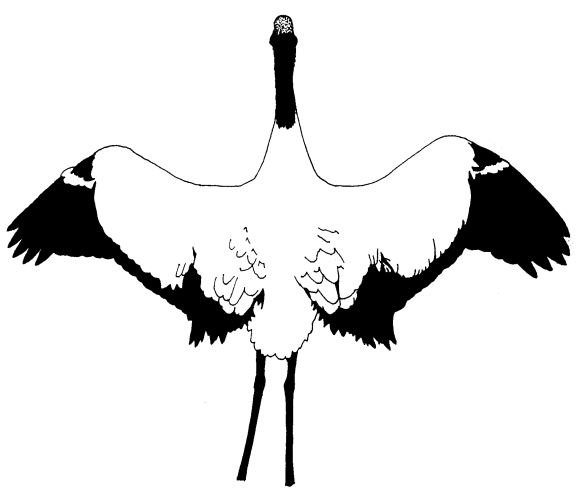

Fig. 14. Pre-copulation, black-necked crane (female).

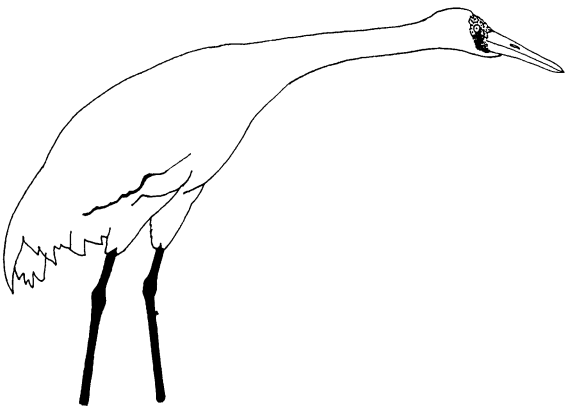

Fig. 15. Pre-flight, Siberian crane.

F-c is probably identical to the Pre-flight-call, separate only by context. Given while birds are aloft, it is believed to be given even by a bird Flying alone. In this context, F-c may serve to locate other birds.

F. *Allopreen*. Both species of crowned cranes Preen the back and neck regions of family members and mates. A often appears in conflict situations and, as such, it may serve as a displacement activity or otherwise limit aggression.

3.6. Pair related behavior

Pair formation and maintenance in cranes, just as for other bird groups, involves the full range of agonistic displays, elements of Attack, and several displays unique to pairing. Further, many non-social ethons are performed in synchrony as mates travel together, forage a short distance apart, Alarm-call, and perform a host of social and maintenance activities simultaneously and in close proximity. The ethons below are in order, from least to most complex, and from first performed (in new pairs or at the onset of a new breeding season) to those that culminate. Not discussed below is Feather-painting (Ellis et al., 1991), an activity that may have social significance.

A. *Unison-walking*. Paired cranes very often Walk side-by-side or, more often, the male leads with the female a few paces behind. This behavior is especially evident when an intruder is present. As the intruder approaches, the male may Strut with the female in tow performing U-w.

B. *Unison-call*. Described earlier (Fig. 1; Section 3.1, I), duetting is important in pair formation and maintenance for all species.

C. *Dance*. D is an activity sometimes involving most agonistic displays (Section 3.2), all elements of Attack (Section 3.3), and some unique action patterns. Elements of D appear in play contexts both for adults and young. D differs from agonistic displays by its much more active and flowing nature. Birds in D very often avoid looking directly at the recipient, especially when it is very near. In D, it is common to observe incipient performances and grades of intensity in performing. Variation in 'behavioral quality' is thereby more evident than in most or all other activities. At least in captivity, D is much less developed in crowned cranes than in other species.

1. *Spread-hold* (Masatomi and Kitagawa, 1975; Pre-leap). One bird widely fans and lifts its wings while at intervals peering at its dance mate. S-h is sometimes performed while Walking or Running.

2 and 3. *Gape* and *Gape-sweep*. In G, the bill is held open, often for several seconds. In G-s, the open bill is rotated laterally (ca 20–50°) away from the recipient, then returned toward. Mates often G, G-s, and perform the previous display in tandem, and all three displays often lead into a Dancing bout.

4 and 5. *Tuck-bob* and *Leap* (Masatomi and Kitagawa, 1975; Stoop). These very active displays are most often seen when a pair dances, but bouts of T-b sometimes erupt in a closely crowded flock. As nearby birds become excited, they begin Gaping and Leaping and rushing about. To perform these displays, a crane rapidly elevates its head, sometimes Leaping from the ground, then just as swiftly crouches low (Fig. 16) with the body axis depressed forward, and the neck tightly coiled. Sometimes a crane holds this coiled pose for a second or two, but more often it shoots up and down in several rapid cycles of tucking, then bobbing up high. The wings are partly spread in many, but not all, performances. L may lift a crane a meter or more, and is always accompanied by some degree of wing spreading and Flapping.

6. *Object-toss* (Masatomi and Kitagawa, 1975; Throw). Sometimes a crane will Dance alone for several seconds before its mate enters the fray. Even when Dancing solo, dancers very often O-t. To perform O-t, a bird Bill-stabs and then grasps a feather (most often), a grass stem, or some other light object and tosses it skyward with a quick upward flip of the bill. The object is thereafter Gaped at or Bill-stabbed or Jump-raked (Fig. 12) as it floats down. Running, Flapping and Leaping are components of all well developed Object-toss bouts.

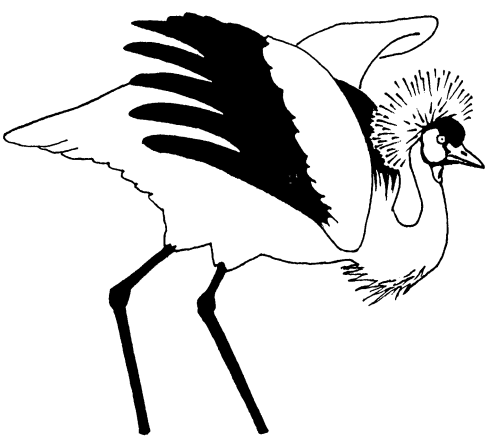

Fig. 16. Tuck-bob, gray crowned crane.

7. *Run-flap-glide*. In the course of a Dance, one crane (typically the female) becomes intimidated by the wild gyrations of its mate and retreats in R-f-g (actually three separate action patterns), then comes rushing back Running and Flapping and sometimes Gliding along, barely touching the ground. Both birds then whirl and rush about in skipping steps, half aloft, half Running.

8. *Hoover* or *Neck-crane* (Masatomi and Kitagawa, 1975; Low-bow and High-bow; Section 3.2, DD). In the midst of a Dance, but especially at the onset when only one crane is excited, the non-performing crane will often H (Fig. 10) or perform some other moderate-intensity agonistic display, as if to ward off advances by the dancer.

9. *Bill-stab* (Section 3.3, D). During a Dance bout, one or both cranes will often B-s at its partner. Almost always these Bill-stabs are given from too far away to be genuine attempts to injure.

D and E. *Pre-copulation* and *Copulation-call* (Masatomi and Kitagawa, 1975; Irrelevant-wing-open, Wing-spread, and Bill-raise; Voss, 1976a; P-c). All cranes have a conspicuous P-c display. Details of typical sequences of behavior before and after Copulation are supplied by Masatomi (1983a) for six species. A typical performance for a whooping crane male or female is for one adult to walk slowly in short measured steps with bill pointed skyward (Fig. 17; neck fully extended up and slightly forward). The bird emits a quiet growl (C-c) in short (ca 0.5 s), rapid bursts separated by very brief (ca 0.2 s) quiet intervals. In a typical copulation bout, both birds stroll along, one behind the other, bill-up calling. Eventually (and sometimes very shortly), the female (Fig. 14) spreads her wings very wide laterally, with secondaries drooped, and allows the male to approach from behind. The full performance of P-c for her then includes this wing-spread-droop component which the male 'normally' lacks. The female's P-c display is sometimes given by a subordinate bird (even a male and sometimes even large colts (Voss, 1976a)) in response to the approach of a dominant bird.

F. *Copulation* (Copulation-call). Like Attack and Dance, C really is an activity involving several component action patterns. Like Attack, it also is not a social display. Rather it is the culmination of many social displays. In the C sequence, the pair approach in Pre-copulatory display, but then the male (or sometimes the female; Masatomi and Kitagawa, 1975:835) Walks and Flaps onto the back of his mate. The mounting bird lowers to Sit (i.e. rests tarsi on back of his partner) while still Flapping to balance, then presses his tail left or right around the tail of his mate and cloacal contact is completed. We estimate that cloacal contact lasts for 3 to 10 s in successful bouts. Some tail-wagging and minor pelvic thrusting may also be present but is inconspicuous. Most often the male dismounts by sliding forward off the front of the female, but may step backward (Voss, 1976a). Typical bouts of C are followed by some agonistic display (Masatomi, 1983a,b) including Unison-calling for many species.

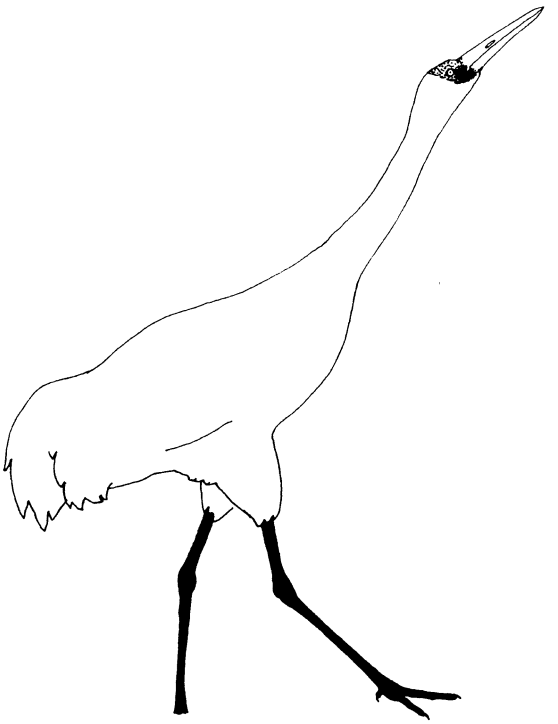

Fig. 17. Pre-copulation, Siberian crane (male).

For the Eugrus Group (five species), a somewhat distinct C-c exists. For these species, the call given in Pre-copulation increases in crescendo until it becomes a wailing scream, the C-c.

3.7. Nest preparation and maintenance behavior

All species are believed to have all of the following action patterns in their repertoire. However, demoiselle cranes and blue cranes often build insignificant nests or no nests at all. As such, many individual birds likely never perform some or all of the action patterns listed below.

None of the action patterns discussed below, and in the next section (Section 3.8), are of necessity performed in social settings. However, we include them here (and excluded them from the ethogram of non-social behavior (Ellis et al., 1991) based on the logic that all reproductive efforts of all species are social in nature.

A. *Sideways-toss*. Stems/twigs are moved toward the nest site and onto the nest platform using S-t. An individual stem may be sequentially moved closer and closer in stages until it is finally deposited on the mound. Typically, an adult will Stand facing away from the nest and S-t many twigs toward the nest, then move to a new site and repeat. It may take days before a particular stem actually arrives at the mound by this means. We believe that S-t is the more important ethon for male nest building, while Sweep-drop (below) is primarily used by the female.

B. *Sweep-drop*. Similar to Sideways-toss but lacking the fling component and including a distinct drop component, this action pattern is used more for actual placement of twigs on the mound and rearranging stems on the nest while Incubating.

C. *Nest-probe*. The bill is inserted by sequentially being thrust deeper and deeper into the nest. The primary function of this action pattern is probably to test for water encroachment on the nest. In warm climates, it may function to measure heat of decay as for the Megapodes. It is performed primarily while Incubating.

D. *Tread*. Probably all species of cranes trample the nest surface to compact vegetation prior to Incubation, and T is probably present in the repertoire even of species that normally nest without a nest but observations are not available. See also Section 3.8, J.

3.8. Parental behavior

Most of the ethons listed below have a direct functional nature and are not primarily displays, if at all. Only the last three (i.e. Section 3.8, K, L and M) have a conspicuous display role.

A. *Oviposition*. Egg laying is of necessity stereotyped by physical limitations in long-legged cranes. The female typically Sits (i.e. breast up, heels down) in something of a Cower posture (Fig. 18; head down, neck retracted) and quivers slightly (strains as egg moves into and out of her cloaca) at intervals, then expels the egg with a brief dip of the lower abdomen. Sometimes an egg actually drops a few cm before contacting the nest.

B and C. *High-step* and *Waddle*. H-s involves exaggerated foot lifting movements (i.e. the foot is lifted higher and held up longer than in normal Walking) and is exhibited when approaching and leaving the eggs, as when commencing or finishing an Incubation bout. When near the eggs, a crane lowers to Sit, Incubate posture, and uses the side-to-side movements of W to move forward over the eggs. In W the heels rest on the substrate and the feet either lie limply on or dangle above the nest.

D and E. *Shuffle* and *Settle*. As the adult lowers into Lie Incubation posture, it first Shuffles its legs closer and closer to the eggs, then in a separate action pattern, it Settles over the eggs and beds the eggs in its feathers by rocking side-to-side. In some performances, the wings are also

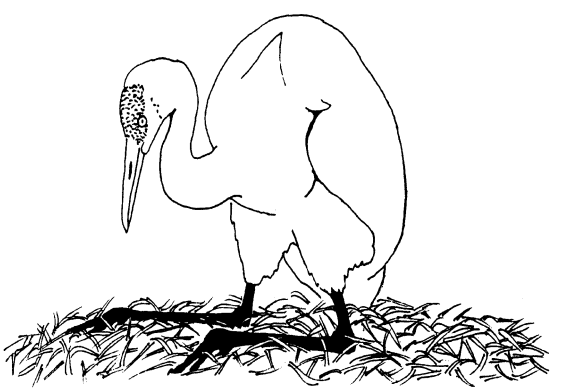

Fig. 18. Oviposition, sandhill crane.

involved, supporting the weight of the bird as it Shuffles and Settles.

F. *Bill-tuck*. At intervals through each incubation day, the ventral side of the bill is pulled across the eggs and rotates them. In cranes, B-t most often results in the small end of the egg being lifted over the large rather than the egg rolling about its long axis.

G and H. *Incubation* and *Brooding*. Although incubation (Lying over eggs) and Brooding (Lying, Sitting, or even Standing over chicks) are physically and functionally alike, we include both terms because they are so widely accepted. When Brooding in Lie posture, the breast contacts the substrate (eggs and/or nest), whereas for Sit the breast is not supporting, and the weight is borne by the heels, tarsi, and sometimes the drooped wings. Chicks, when being Brooded, move about beneath the breast and wing and sometimes protrude from the feathers of the back.

I. *Shading*. Cranes Shade eggs and/or young in Stand, Sit, and Lie postures. The wings may be tightly closed or spread to a greater or lesser degree. When Shading, an adult may turn its back to the sun, but for some S bouts, the sun is not behind the crane. Cranes are not known to slightly lift or slightly extend their wings at intervals while S as seen in some other birds (Ellis, 1979), nor are there unique positions that distinguish it from Incubation/Brooding.

J. *Tread*. Several species of cranes (Table 2) are known to T on vegetation to open a brood yard or a foraging area (up to 3 m in diameter) for a chick (Pomeroy, 1980). Probably all species perform this activity sometimes. Walking is the primary component, but the step used is somewhat different. In normal Walking or Running, the foot closes so the toes lie parallel as the foot lifts, passing through the vegetation. When Treading, however, the toes are left spread for use in flattening the vegetation.

K. *Nesting-call*. Described earlier (Section 3.1, C), this quiet, brief growl of the adult is repeated in rapid series and is most often heard during Incubation and while the chicks are small. It sounds similar to the growl given during Bill-down-growl. Adults use this call when responding to the chick's Peeps before hatching and in all other contexts when an adult attends a chick (even fledged young).

L. *Present-morsel* (Masatomi and Kitagawa, 1975; Feed). Parent cranes hold food items near or at the tip of the bill while presenting them to a chick. The adult lowers its head, extends the bill laterally toward the chick, and growls (Nesting-call). Sometimes adults present a morsel, drop it, then pick it up and present and drop it many times in succession.

M. *Distraction-display* (Masatomi and Kitagawa, 1975; Diversionary display). D-d was discussed earlier (Section 3.4, D).

3.9. Filial behavior

Chicks are strongly interactive with their parents, calling, approaching, following, and Pecking the adult's bill. Distinct ethons are described below.

A and B. *Peep* and *Contact-call*. Described earlier (Section 3.1, A), P is first heard as soon as the chick breaks into the air cell (2–3 days prior to hatching), and continues with modifications until the chick is independent. P grades into the C-c of chicks and adults, but P-like calls are emitted by ill or subordinate birds even as adults.

C and D. *Food-begging* and *Wing-quiver*. To F-b, a chick orients toward an adult, holds its neck retracted (as in Cower) but with the bill pointed up, Peeps, and Pecks lightly at the adult's bill. A W-q component is often present in F-b context and perhaps when soliciting Brooding.

W-q is performed by lifting the wings slightly away from the body and simultaneously fluttering them, shiver-like, at low amplitude and at high frequency (about two to five strokes/s). In tiny chicks, W-q is normally accompanied by vigorous Peeping, less so in older chicks. W-q is rare or absent in colts older than one month.

E. *Accept-morsel*. Chicks Peep and Peck at the adult's bill to remove food items. Young and older birds use the same Peck to steal food from another crane, but normally would not Peep while doing so.

F and G. *Stress-call* and *Distress-call*. The Peep of a neonate is very like the S-c and D-c. For large colts and adults, these three calls and the

Contact-call intergrade, but they are distinct enough at the extremes, and differ in context enough, to convey different messages to other cranes and merit separate titles here.

4. Discussion and conclusions

Cranes have a tremendously complex repertoire of stereotyped social behavior. Although comparisons of the number of displays between taxa is difficult (Nelson, 1978) because one author may divide a complex display into several components while another author treats each display as a single unit, comparisons between taxa are possible. Descriptive ethology is founded on the premise that discrete behavioral acts can be identified. Even more obvious, the ability of animals to interact socially implies that discrete social signals exist and are decipherable by conspecifics. If they are decipherable by conspecifics, then, with careful study, the ethologist can also tease apart the social alphabet of a species.

Moynihan (1970) provided a rough yardstick of the complexity of the social repertoire of 27 species of vertebrates. He reported that the number of social displays per species within each vertebrate class varied from 10 to 26 for fish, 15 to 28 for birds, and 16 to 37 for mammals. The apex was 37 for rhesus macaques (*Macaca mulatta*), a well-studied primate. When we revisited the subject in the light of subsequent work with birds, we found general agreement with Moynihan's (1970) tally. For example, about 25 displays are described for the black-necked grebe (*Podiceps nigricollis*; Prinzinger, 1974), 20–30 are known for each species of Sulidae (Nelson, 1978), 27 for the green heron (*Butorides virescens*; Meyerriecks, 1960), 22 for the golden eagle (*Aquila chrysaetos*; Ellis, 1979), and about 20 displays for the mourning dove (*Zenaida macroura*; Sayre et al., 1993). Hailman (1977) estimated that 50 displays might be an upper limit in non-human animals.

The crane social repertoire (Table 2: 60-plus stereotyped social ethons per species (even when nest-related ethons and complex activities are not included)), as described herein, would tentatively place cranes at the apex of behavioral complexity, at least for stereotyped social behavior. However, this does not mean that cranes are more complex socially than any other animal group. Mammals, most notably primates, have a much wider range of social expression because they present signals over a broader spectrum of display intensity. They also use more subtle calls and more variety in facial expressions than we have found in cranes. Wilson (1975:185) referred to graded signals or signal enrichment to express these concepts. Further, the nearly infinite number of social expressions possible through the use of language places man apart from all other vertebrates. However, when considering only the number of stereotyped social displays, cranes surface as presenting the most complex repertoire known. We are aware that our level of detail in teasing apart separate ethons is greater than that employed in some studies (e.g. Sayre et al., 1993). However, we have resisted the temptation when 'dissecting' displays to count components as separate displays.

Fortunately for our efforts to identify discrete behavioral units, most crane displays are both consistent and conspicuous. This stereotypy and the extraordinary complexity of their social repertoire stems, we believe, from three factors: first, cranes are solitary on the breeding grounds, second, most are gregarious when not breeding, and third, all have lethal bills. These traits result in first, a need to advertise their breeding territory over long distances (where only conspicuous and stereotyped displays will serve), second, a need to interact socially over short distances when in a flock, and third, a need to avoid combat least severe injury or death result. Nelson (1978), in speculating about the complexity of sulid social repertoire, added two more possible factors, namely large body size and great longevity. It will be most interesting to see if future studies can identify unrelated vertebrate taxa that exhibit similar traits (i.e. species that show seasonal territoriality, lethal capabilities, etc.) and determine if these taxa have developed social signals of comparable complexity. However, we expect that in the final analysis cranes will retain what now appears to be their position as premier among birds and perhaps among all other animals in the number of salient social displays.

Recently, molecular studies have been used to clarify phylogenies (Ingold et al., 1989; Krajewski, 1989, 1990; Dessauer et al., 1992; Krajewski and Fetzner, 1994). All of these clearly separate crowned cranes into a separate subfamily. The Eugrus Group also seems discrete from the remaining species (Love, 1990; Dessauer et al., 1992; Love and Deininger, 1991). One remaining point of controversy is in the placement of the wattled crane (Krajewski, 1989; Krajewski and Fetzner, 1994). The molecular genetics studies agree that the blue crane is probably the wattled crane's nearest relative. Our behavioral treatment agrees that the wattled crane is closely related to the blue and demoiselle cranes. The frequency, and especially the precise motions, of four wattled crane displays (i.e. the Head-lower-ruffle, Wing-spread-flap, Tail-wag, and Head-flick) are strikingly like those of the blue crane. A wattled-blue link is also supported by external plumage similarities, biogeography, and the propensity of the two species to hybridize in the wild (Johnson, 1985).

For the Siberian crane, the molecular genetics studies (Krajewski, 1989; Krajewski and Fetzner, 1994) indicate, as does much of the divergent agonistic repertoire, that the latter species is not closely related to any other species. Wood's studies of morphology, however, are largely consistent with Archibald's conclusion that the wattled crane is allied with the Siberian crane (Archibald, 1976a,b; Wood, 1979). However, one analysis clustered the blue and wattled cranes together.

From our attempt to use behavior to separate species and to identify species groups, several generalizations arise. First, most non-social ethons are common to all species (Ellis et al., 1991). In addition, ethons related to rearing young, to defending, and to attacking are conservative and therefore shared by all species. As expected, we found that agonistic displays are less conservative (i.e. more divergent) and are therefore more useful in defining taxonomic groups. However even here, comparisons (Table 2) revealed very few displays that could, on the basis of presence or absence alone, be used to define taxonomic groups. Interpretation of results in Table 2 is further confused by the fact that some displays are closely related to (or arbitrarily separated from) others with the result that the absence of one display in one species means very little if a second species exhibits a display that is obviously a homologous variant. An example of this are the Bill-down displays (Table 2; II, O-R). It is probably of little significance that the crowned cranes do not have a growl (II, P) component for their similar displays, Bill-down-hold and Bill-down-sweep (II, O and Q), that are almost certainly homologs of Bill-down-growl performed by all other species.

The most conspicuous generalizations from Table 2 are as follows: Copulatory-call (I, P) separates the Eugrus Group from all other cranes. Ventral-preen (II, M) separates the two crowned cranes from all other species. Three displays, Head-lower-ruffle (II, T), Ruffle-bow (II, U), and Wing-spread-hold (II, V), together suggest that crowned cranes and the Long-train Group are related, but separate, from all other cranes. Realize, however, that once again II, T and II, U are related (i.e. probably homologous) displays. Some differences fit no consistent pattern. For example, if the crowned cranes are related to the Long-train Group as suggested by II, M, II, T, and II, V, why do all species except the Long-train Group exhibit Neck-crane (II, DD)? Some other separations are suggested by the table, but do not merit mention without further study.

Because almost all displays (Table 2) proved to be common to all species, the differences between species lie primarily in the expression of display components not in the presence or absence of the displays. These observations, together with Archibald's success in generating a robust phylogeny (Archibald, 1976a,b) (later supported by the molecular studies) using divergent components of a single social display (the Unison-call), lead us to speculate that detailed comparisons of the fine components of at least some of the social displays will in the future prove more useful in defining evolutionary relationships than was possible from our gross treatment of the presence/absence of the displays themselves.

From all molecular and behavioral comparisons, including this study, it is clear that all but the African crowned cranes are phylogenetically

very close. Once the African crowned cranes are separated, the second most distinct group includes the five species in the Eugrus (Archibald's 1976a *americana*) Group. Strongly suggested is the grouping of three species in the long-train (Archibald's 1976a *Anthropoides*) group. Other relationships are still unclear. An important question involves identifying affinities of the Siberian crane, and clarifying the relationships between the brolga and white-naped cranes (C. Krajewski, Personal communication).

Perhaps the most remarkable aspect of the presence-absence data, as presented in Table 2, is that so many displays are present in all species. While we are fully aware of the potential that interspecific similarities may be due to convergence rather than descent from a common parent, we assert that these similarities are so extensive (see discussion of criteria for determining homology in Tembrock, 1963) not only in the form of each display, but also in the context of performance and, just as important, in the responses commonly elicited by each, that our observations support the concept that the displays, as described and grouped herein, are true homologs (versus analogs) and support the theory that all cranes are closely related. Decades ago, morphological studies of external appearance, osteology, and intrasternal tracheal coiling generated a phylogeny (Peters, 1934; Archibald, 1976b; Johnsgard, 1983) that has been little changed by molecular genetics studies during the past 10 years (Krajewski, 1989) and little altered by our, apparently less powerful, presence/absence data for social displays.

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