

Signal Behavior in Cranes (the Siberian Crane *Sarcogeranus leucogeranus*, the White-naped Crane *Grus vipio*, and the Red-crowned Crane *Grus japonensis*) in the Context of the Ritualization Hypothesis

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Abstract—Signal behavior of three crane species was chosen to test the logic of the ritualization hypothesis. Its claims to explain the origin and functioning of the “highly ritualized” communication signals in birds are discussed. It is shown that such signals are observed in a wide range of situations, including those in the absence of a social partner for communication (perceiver). In its presence a signal may be performed in a way that it cannot be perceived by the partner. The same actions (“ritualized preening”) vary in length and intensity, and such variability is present in nearly all situations. In each situation, it is difficult to discriminate between the ritualized preening and actual comfort behavior. It may take place even when a social partner is present. Short preening that may be readily considered as ritualized signals are more common in the all situations, including those with an absent partner. The endogenous cyclicality in unison calling by mates indicates that communication cannot be regarded as a simple exchange of signals in accordance to the ‘stimulus-reaction’ principle. Similar actions by the more ancestral Siberian crane may appear to be more ritualized than in the evolutionary advanced Red-crowned crane. All these findings contradict the concept of emancipation and ritualization of behavioral actions during evolution and selection for increasing communication efficiency. According to that hypothesis, during this process such actions, due to selection for more efficient communication, evolve into discrete meaningful communication signals (displays). They stand out against the background of the monotonous, unexpressive (non-signal) everyday behavior and thus appear as the main carriers of information serving principal communication functions. A more realistic approach seems to be the understanding of communication as a process of a continuous mutual fine-tuning of the social partners’ behavioral attitudes towards each other. In either participant, its behavior is an integral structure, inseparable into categories of more or less important signals (flow of behavior). Even minor changes in performance by one individual reflect alteration in its motivational state which, in its turn, changes that of the other participant and the subsequent lines of its behavior.

Keywords: animal communication, methodology of description; divergency of behavior; comparative ethology; ritualization hypothesis, cranes.

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In the recent decades, cranes have received increased attention from ornithologists. This interest is mainly due to the high vulnerability of these birds to progressing changes in environmental conditions in many of their habitats, which necessitates their special protection and, if required, restoration of populations of endangered species. This situation prompted the development of rearing methods for captive cranes for later release of such pairs into the wild. It opened up new opportunities for studying a number of crane behavioral patterns that are difficult or impossible to observe in the wild in detail.

Owing to such circumstances, ornithologists were successful in conducting studies aimed at the analysis of signal behavior in cranes. The primary area of research was comparative ethological analysis aimed at understanding the taxonomic structure of cranes with a view to understanding their phylogeny and evolution. However, it is important to note that many of these studies focused mainly on the behavioral actions that are most conspicuous for the observer (in particular, typical unison calling by members of mated pairs; see Archibald, 1975). Authors that attempted to detail the sequence of signal behavior of a species describe it as a set of stereotyped postures (displays) rather than as

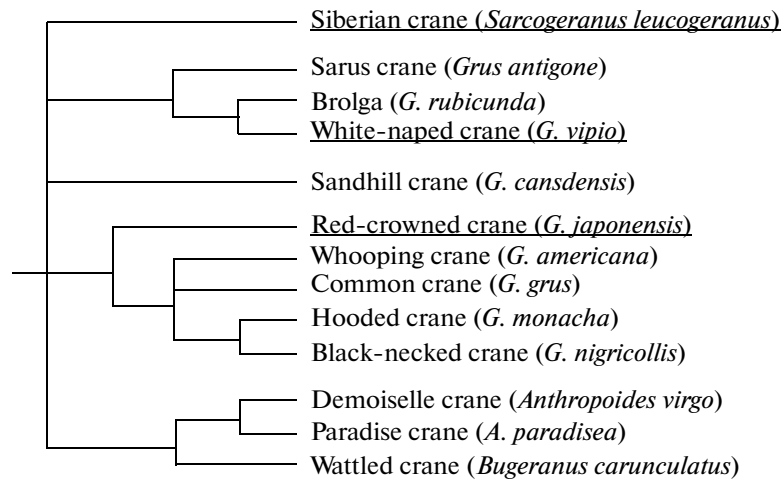


Fig. 1. The phylogeny of *Grus* cranes according to comparative molecular studies (from Meine, Archibald, 1996).

an integrated structure with its own inherent logic (Masatomi, Kitagawa, 1975). Due to this, many interpretations of the outlined approach look superficial, not to say naive, to a professional ethologist (see e.g. Ellis et al., 1998 as an example).

The material for this paper was collected and analyzed following a dramatically different approach. In contrast to the aforementioned elementaristic methodology, we attempted to examine species-specific signaling as an orderly system with its inner regularities. Following this we will present the fullest possible pattern of signal behavior of the Siberian crane which has been at best incompletely described in earlier publications (see Kurochkin 1987: 323–325).

All papers devoted to signal behaviors of cranes emphasize that many of their movements and postures may be considered ritualized actions. The researchers are based on the apparent similarities between these signals and the elements of everyday behaviors, in particular the comfort behavior. On the basis of the established viewpoints resulting from the so-called ritualization hypothesis (Tinbergen, 1952), it is concluded that these actions secondarily acquired the signal function in the evolution through transformation of the initial components of everyday behaviors under natural selection.

However, there is a controversy with regard to the applicability of these viewpoints to studying signal behavior in cranes and the hypothesis's consistency with the current level of biological knowledge. Since the similarities between a large number of signal actions and elements of comfort behavior in cranes are not inconspicuous, these birds prove to be a perfect subject for discussing the issues raised on the basis of experimental data. This is the topic that dominates the discussion of our empirical results.

SUBJECT OF RESEARCH, MATERIALS AND METHODS

Subfamily Gruinae includes 13 extant species in addition to 7 extinct species (Fig. 1). According to the paleontological data, the age of this group is estimated at 5 to 24 million years (Brodkorb, 1967).

The results of molecular studies suggested a division of the extant *Grus* species into four clusters (Krajewski, 1988; Krajewski, Fetzner, 1994). Two clusters are monotypic; however, the Siberian crane is so dramatically distinct from other *Grus* species that some authors assign it to a separate genus *Sarcogeranus* (Meine, Archibald, 1996). Here we will discuss the behavior of the Siberian Crane alongside that of two other *Grus* species from different clusters. The three species of interest are underlined in Fig. 1. Their position in the dendrogram clearly shows a significant level of divergence. From this standpoint it will be interesting to determine the level of variation in motor patterns associated with the signal behavior which were inherited from a common ancestor that lived several million years ago.

The data were collected during several years. Preliminary results for the three species were obtained from 2002 to 2004 and 2006 in the Moscow zoo nursery near the settlement of Sychevo (Moscow Province, Volokolamsk District). Systematic observations on the Red-crowned Crane (one pair in an outdoor aviary) were performed for seven days during the pre-nesting period in 2006 in Oka State Nature Reserve. Aggressive behavior of semi-wild red-crowned and white-naped cranes was observed from April 17 to May 3, 2007 in Khingansky State Nature Reserve. Signal behavior of the Siberian Crane in the pre-breeding period is described on the basis of seven-day systematic observations of two pairs in aviaries between 12 and 22 April, 2009 (two days missed due to a cold

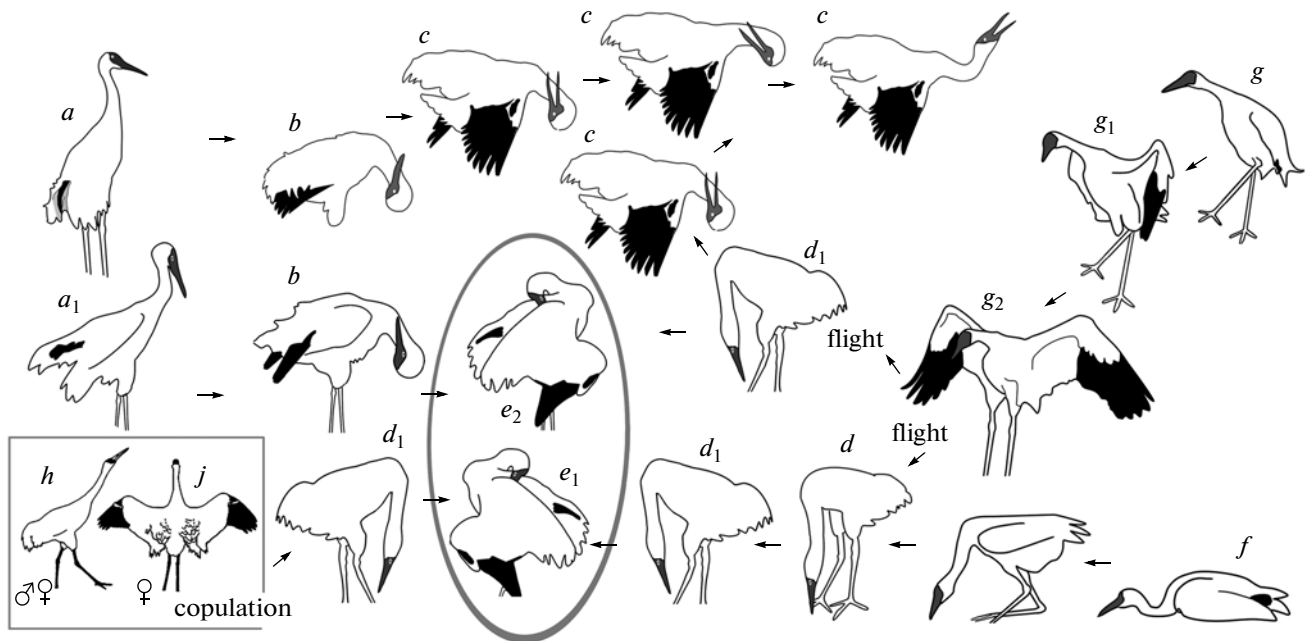


Fig. 2. The motor patterns of the Siberian Crane signal behavior. See text for references.

spell). In this case the overall observation time was 36 hours.

During the initial period of nonsystematic observations, all forms of signal behavior were recorded by video tape for further classification. At this stage, we stimulated the signal activities in the cranes by approaching them (up to the aviaries). Their responses towards approaching humans were considered a manifestation of threat. In this regard unison duets that are frequently performed by cranes in response to such an external stimulus were an exception.

In the subsequent period of observations this factor was eliminated whenever possible. In Khingansky Nature Reserve its influence was nil because all interactions were video-taped from a great distance. In the Oka Nature Reserve where it was not possible to record at a distance greater than four to five meters from the aviary netting, recordings were started 30 minutes after the observer's arrival so that the birds could get accustomed to his presence and did not respond to it. The pairs were board-fenced to prevent from visual contacts between them and could only hear their conspecifics. During the entire observation period, the observer remained nearly motionless, sitting in one place. In 2009 when observing the Siberian cranes, we recorded by video tape and took notes on behavioral sequences (interactions including unison calls and postures) through recording by audio tape.

All motion activities were recorded using Sony CCD-TR570E and CCD-TR3400E video cameras. The results of analyzing the acoustic behavior were reported elsewhere (Opaev et al., 2008). The chronometric behavior analysis was done on digitalized video

recordings by the time section method (resolution 0.04 s) by Pinnacle Studio™ and Adobe Photoshop™ software. Tracings of frames were abstracted into illustrations using Corel Draw™ software.

Frequency distribution of behavioral act durations was tested for normality by Shapiro-Wilks W-test recommended for small sample sizes (Shapiro et al., 1968). Since most distributions were significantly non-normal, the non-parametric Mann-Whitney test was used for pairwise comparisons.

To evaluate the deviation of duet sequences from random behavior over time, the number of duets was counted per successive 10-minute intervals.

To test the occurrence of unison calling for randomness, the number of such calls per 10 minutes was compared to the binomial distribution which should be expected when an event is relatively frequent but random (Davis, 1990). For comparison, the Kolmogorov-Smirnov test was used.

RESULTS

Signal behavior of the Siberian Crane. The complete repertoire of actions that may be considered communication signals is given in Fig. 2. Nearly all actions were sequential without interruption, so that in some cases it is difficult to say whether it is a single signal or whether this communicative effect results from the recipient's response to a sequence of two, three, or more actions artificially singled out by the observer as independent signals. However, only for the sake of convenience, the behavior repertoire is divided into

nine behavioral actions (postures and motor patterns) with the following brief descriptions:

a–*a*₁ in Fig. 2. Intense feather shaking which more or less regularly precedes actions *b*–*c* and *b*–*f*.

b. Initial element identical for two different actions, i.e. for bouts in a unison duet and for dorsal preening (see below, *e*).

c. A bout of an individual in a unison duet. Only the onset of the action, never detailed before, is shown.

d. A posture with the neck strained and lowered, and the bill pointed downward and touching the ground (hoover or neck-crane). In a strained social context this posture may be held for long periods accompanied by very typical slow steps, stabbing the ground, nibbling and tugging at vegetation (stab-nibble tug, Fig. 2).

e. Irrelevant dorsal preening which is the final element in the *a*–*b*–*e* and *a*–*d*–*f* sequences. It is nearly invariably accompanied by a typical dull booming (Opaev et al., 2009).

f. Recumbent posture. In a strained social context this posture may follow *d* and frequently precedes the sequence *f*–*d*–*g* (as shown in Fig. 2).

g. Peculiar (signal) flight preceded by the *g*₁ and *g*₂ postures. Following alighting, the *d*–*f* sequence, or less frequently, the *d*–*c* sequence occurs. In the *g*₁ posture, a male can strut, which is also used in the *h* posture. Several wide steps may be made during alighting.

A rarely occurring action with two to four wingbeats followed by the *d* posture or the *d*–*e* sequence is likely a reduced version of these sequences.

h posture. Posturing in the arousal of sexual motivation. In precopulation this posture is simultaneously adopted by both partners. An individual not ready for copulation rapidly ceases this performance.

j. Precopulatory posturing of a female in the *g*–*h* sequence. This is the only action with unequivocally communication function. However, in certain cases this performance can grade into the *g* preflight posture which is either followed by signal flight or eventually reduced to a daily posture.

For completeness' sake the dance should be mentioned that these cranes perform very rarely and that is expressed as alternation of brief bows, runs with wingbeats, and sometimes jumps up. As in other crane species, an element of dancing could be grabbing small objects from the ground and throwing them into the air.

Signals usually considered as threat signals As stated earlier in the Methods section, most actions observed at the first stage of observations were regarded as threats towards the observer. At this stage the material was collected without any association of recorded actions with a particular individual and the stage of its annual cycle. Therefore, the data on two pairs and one non-sexed individual is presented as a pooled sample. The list of behavioral patterns observed at this stage includes almost all postures and actions shown in Fig. 2

with the exception of the *h* and *j* postures. This fits the current point of view that actions *a*–*g*, excluding the unison duet *c*, refer to aggressive behavior (e.g. see Kurochkin, 1987). However, Sauey (1985), treats the latter actions as territorial aggression, too.

When the observer approaches the aviary very closely, the Siberian crane comes closer to the net and walks along in slow steps with the bill pointed downwards and stabbing the ground, which is accompanied by movements that resemble nest-building behavior (uprooting grass and throwing it sideward from its feet). At each step the bird extremely slowly lifts its forward foot higher than the level of its head (Figs. 3*a*–3*c*). Subsequently the Siberian crane adopts the *d*₁ posture that within less than a second is followed either by the *e* posture (Figs. 3*h*–3*j*) or a fall on the belly (the *f* posture). In either case, walking in slow steps usually resumes. It should be noted that feet lifting is also typical of birds near their nest under construction. This means that it is a typical element of the nest-building behavior.

In the context of this paper, of great interest is the *e* posture that is apparently associated with comfort behavior. There is a good reason why it was termed irrelevant dorsal preening. In our sample consisting of 50 video records with the *e* posture observed, the association of this action with the comfort behavior was only documented in eight cases (16%). Analysis of video records showed that bill was held between the back and tertials for 1.0. to 17.6 s (*n* = 27, mean 8.28 s, median 7.65 s). During this period, in two cases weak head movements were observed (intention movements); in four cases one-time bill contacts with the back feathers; and only in two cases did brief actual dorsal preening occur shorter than 20 s. Frequency distribution analysis by three nonparametric tests showed that it was bimodal with short and long preenings, and a small number of acts lasted for the time around the mean or median (Fig. 4).

Even though this is not statistically supported, one can assume that the distribution contained both so-called “ritualized” patterns and initial elements of displacement preening. As shown later, it proved true when the observations were systematic at the second stage.

Of the 50 *e* postures recorded by video tape, 20 (40%) were insertions in the slow walk sequence (see Fig. 3); five (10%) occurred after the recumbent posture (Fig. 5 bottom), and three (6%) were the final element of the peculiar flight *g* (Fig. 5 top) that in this particular case was an overt attack at the observer. All these 28 actions were performed at the very aviary netting or close to it and can be undoubtedly regarded as a response to the observer, presumably a threat.

However, it can hardly be said of the 22 bouts when the crane adopted the *e* posture in the center of the aviary. Such situations took place after the bird was accustomed to the observer; therefore, its behavior was not apparently human-related. The *e* posture seemed

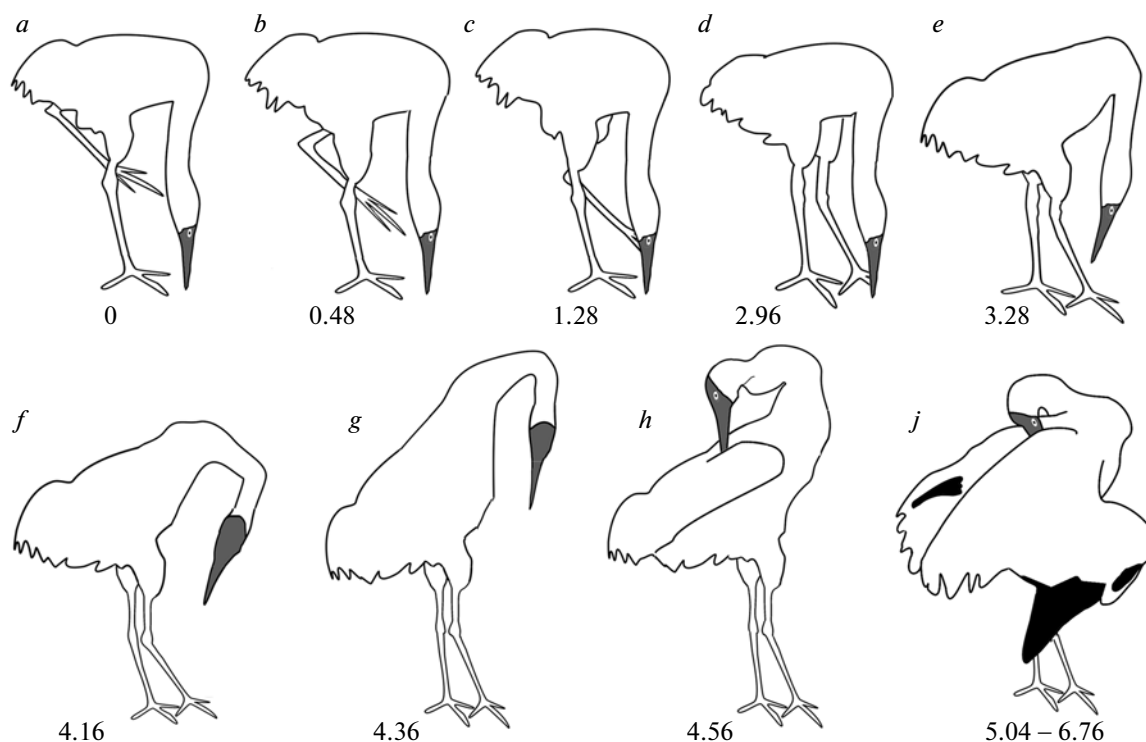


Fig. 3. Version 1 of the *e* posture performed by the Siberian Crane. The figures show cumulative durations, s.

spontaneous in 18 (36% of the total sample and 81.8% of the sample under consideration herein) out of 22 bouts and not included into any sequence of motor patterns. A typical example is the sequence “rest state—the *e* posture—rest state.” At least in one case the *e* posture was almost simultaneously adopted by both partners.

The remaining four bouts that demonstrated association between the motivation for the *e* posture and behavioral patterns usually treated as sexual (to be more specific, mating) behavior, merit special mention. The unison duet calling is meant. For example, a male held the *e* posture when approached by a female. She immediately began her part of the unison call, and the male responded with his part of the unison call while his bill was between the back and tertials. This resulted in a typical long unison call. This means that the *e* posture here preceded the characteristic duetting behavior without delay.

In another bout the female held the *e* posture at the top of a hillock in the middle of the territory where the pair most often gave unison calls. When the male approached her, she resumed the *e* posture (12 s after the previous one). The female remained in this posture when the male came closer and performed intense feather shaking (Fig. 2a1). Before the male completed his posturing, the female began her unison call joined in by the male afterwards.

Yet another bout is worthy of note suggested a link between motivations for the *e* posture and the behavior known as unison calling. In this case a Siberian crane kept alone performed both actions not far from the aviary netting (i.e. as a response to the observer). After completion of the unison duetting, the bird walked slowly (*d*) and adopted the *e* posture 16 s later.

In connection with the above, it is worthwhile focusing on the details of motor patterns during the *e* posture. Two types of movements may be clearly distinguished. One (e_1 in Fig. 2) is given in Fig. 3 in details. It is a transition between the *d* posture and the *e* posture. Since in similar situations the former is the final element of slow walking with the head pointed downward, when the bird stabs the ground and tugs at vegetation, at the moment when the bird adopts the *e* posture, the bill, still holding vegetation, occasionally tosses it into the air (two cases on video records). In the other case (e_2 in Figs. 2 and 6), the motor pattern associated with transition from the everyday behavior into the *e* posture is identical to that of the beginning of unison duetting (Fig. 7). This is evident from the bill orientation: the bill tip moves up and backward so that it crosses the bird's neck for an instant. Our sample contains 15 cases of this movement in which the complete *e* posture sequence was recorded. As seen in Fig. 8, frequency distribution of durations of bill contact with plumage in these two movement types are similar in the sense that they are biased towards shorter contacts,

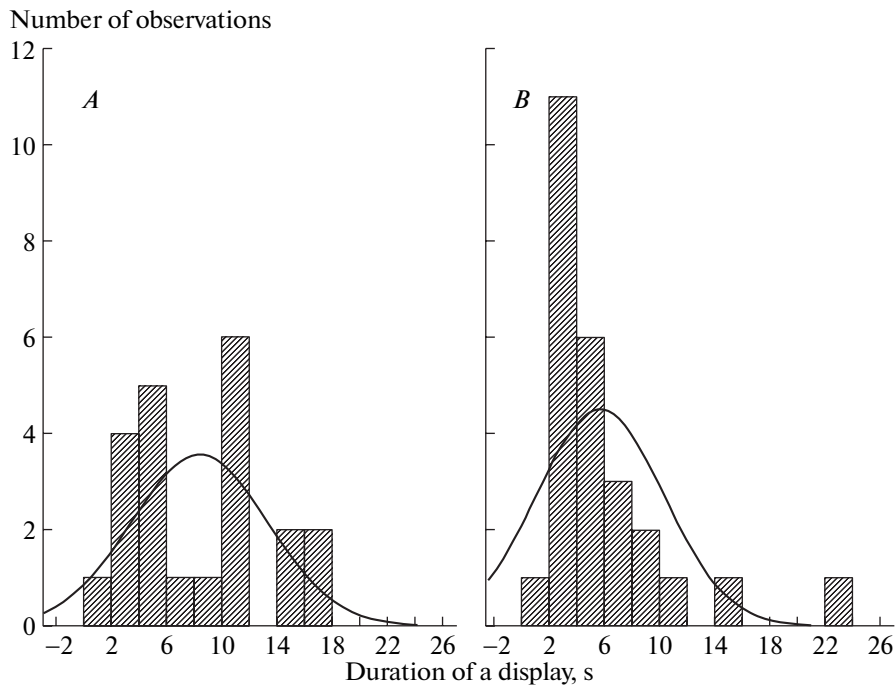


Fig. 4. Frequency distribution durations of the final component of the *e* posture in the Siberian Crane. *A* is in the presence of the observer; *B* in the prenesting period.

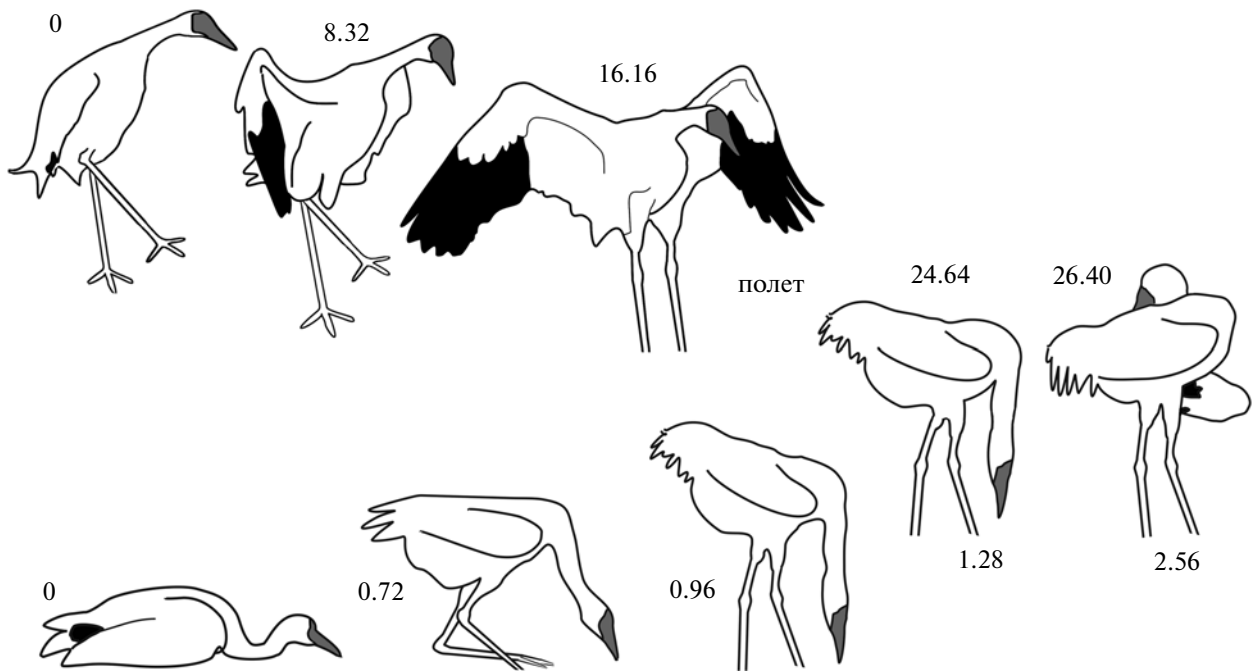


Fig. 5. The *e* posture after flight in the Siberian Crane (top) and after the recumbent posture (bottom). The notation is as in Fig. 3.

making the distribution significantly non-Gaussian. At the same time, no significant difference was shown between them.

In addition to the bill movements, the common element preceding the *e* posture and the beginning of

unison duetting is intense feather shaking. It was present in all cases of adapting version 2 of the *e* posture. This component is not fixed in the unison calling behavior. Of 14 duets video taped completely, only four included feather shaking.

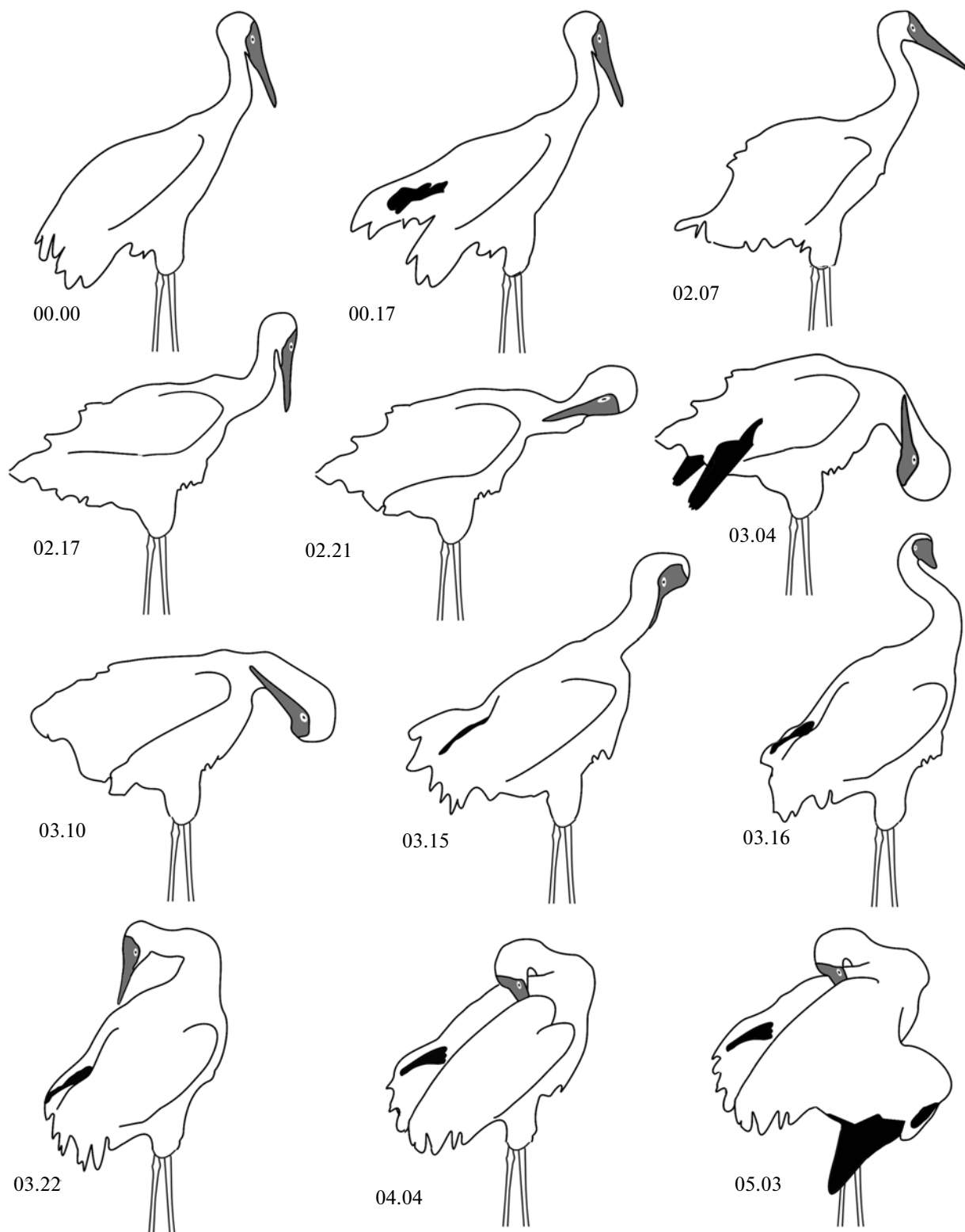


Fig. 6. Version 2 of the *e* posture of the Siberian Crane. The notation is as in Fig. 3.

Completing the description of the results obtained at the preliminary stage of observing species-specific visual signals in the Siberian crane, asymmetry in wing

movements in the *e* posture should be mentioned. It may be of interest whether the dropped wing is directed towards the recipient (in our case to the

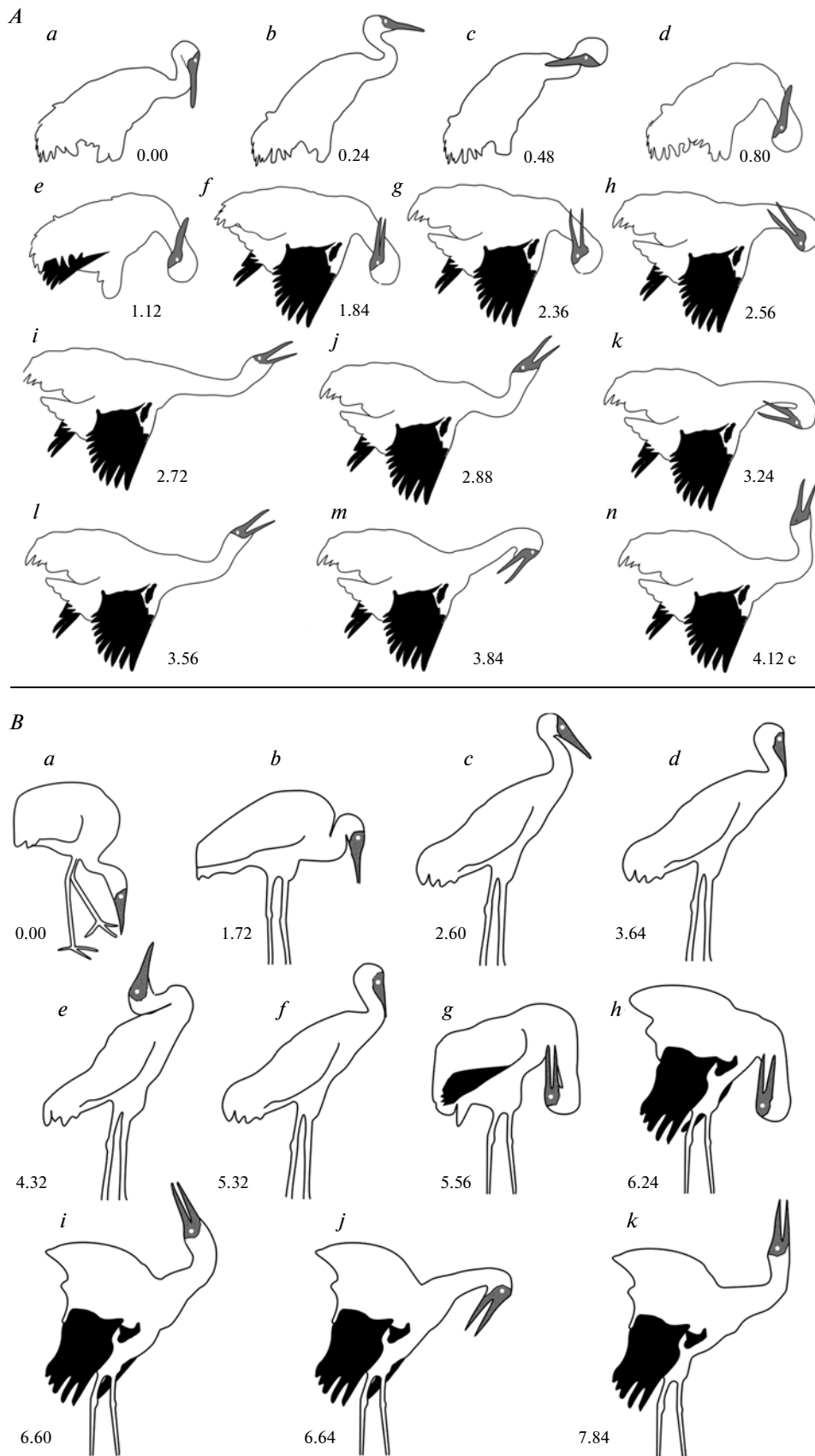


Fig. 7. Versions of the unison duetting in the Siberian Crane males. See text for references. The notation as in Fig. 3.

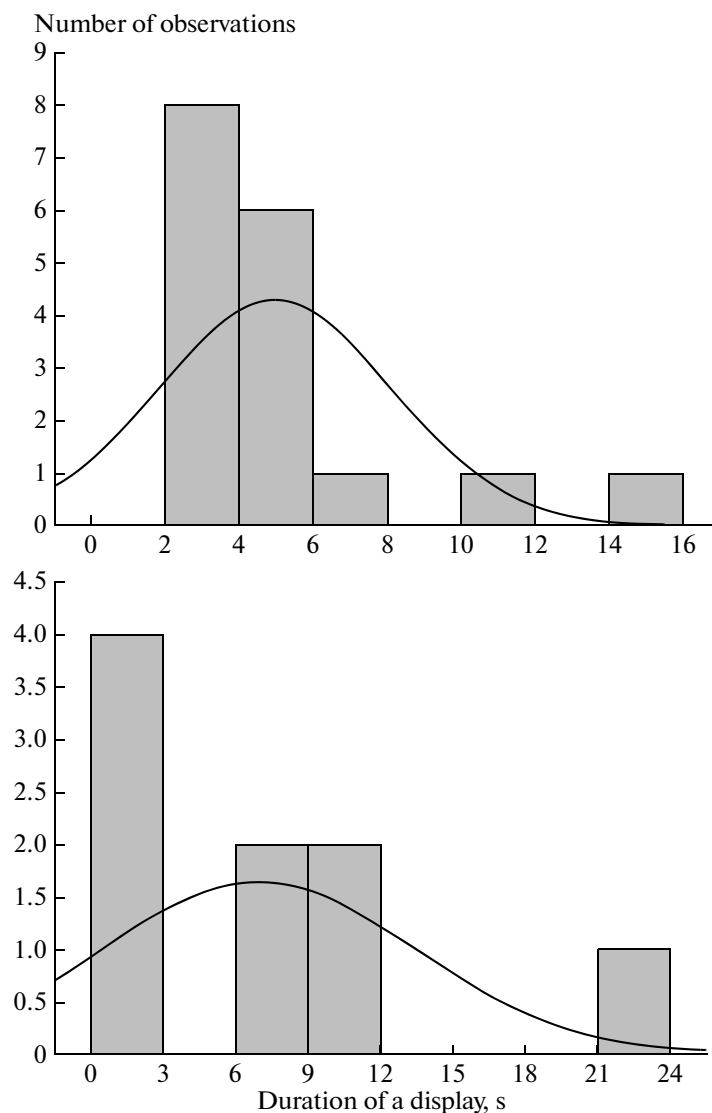


Fig. 8. Duration distributions of the final element of the *e* posture of the Siberian Crane. At the top, version 1 of the *e* posture; at the bottom, version 2 of same posture.

observer); i.e. whether the black-and-white wing pattern may be considered a releaser? Since the sample collected at this stage is generally anonymous, our video records do not allow us to clarify whether the particular individual only drops a certain wing in such situations, or it drops any wing depending on the side where the recipient is located.

In 29 cases cranes dropped the left wing; in 12 cases, the right wing. As a matter of fact, one bird that spontaneously adopted the *e* posture, it dropped the right wing three times (i.e. it performed a rare wing movement). Another interesting record demonstrates that one female five times adopted the *e* posture in response to a human standing in the immediate proximity to the aviary netting. Alternation of wing drops was random (left-right-left-right-left). Moreover, the left wing was presented dropped to the human

twice and to the opposite side once. The dropped right wing was once presented to both directions. This event seems to challenge the role of the wing pattern *per se* for a signal function.

Interaction signaling between Siberian cranes in the nesting period. This section is based on observations of two mated pairs seven – ten days prior to laying. The pair A laid the first egg the next day (April 23); the pair B, on day 3 (April 25) after the completion of observations.

The first stage we found was the lack of difference in their repertoire of threat acts from the one described earlier. When describing the crane behavior in the prenesting phase of the reproductive cycle, we paid attention to the pattern of use of the *e* posture that is treated as a component of threat behavior of the species.

Table 1. The total number of the *e* posture during observations

Pair	Date	Observation time in the morning	Sex of individuals			Observation time in the evening	Sex of individuals		
			female	male	sex?		female	male	sex?
A (<i>n</i> = 64)	13.04	2 h 40 min	1	2	7	2 h 35 min	1	2	
	14.04	3 h 40 min	8	9	—	2 h 15 min	—	2	—
	15.04	3 h 10 min	7	9	1	1 h 30 min	1	4	—
	16.04*	3 h 00 min	2	4	—	—	—	—	—
	22.04	1 h 40 min	2	2	—	—	—	—	—
	Total	14 h 10 min	20	26	8	6 h 20 min	2	8	—
B (<i>n</i> = 66)	13.04	—	—	—	—	2 h 35 min	8	4	1
	14.04	3 h 40 min	11	3	—	—	—	—	—
	15.04	3 h 10 min	15	6		1 h 30 min	1	—	—
	16.04*	3 h 00 min	6	3	1	—	—	—	—
	17.04	2 h 45 min	not determined	not determined	not determined	—	—	—	—
	18.04	0 h 50 min	2	3		—	—	—	—
	21.04	1 h 00 min	not determined	not determined	not determined	—	—	—	—
	22.04	1 h 40 min	1	1	—	—	—	—	—
Total	16 h 05 min	35	16	1	4 h 05 min	9	4	1	

Note: A dash indicates the absence of observations in the given time. — Indicates that the sex of mates was not determined at day 1.

*notes a decline in social activity before a fall in temperature.

As shown in Table 1, the frequency of this posture in this seasonal phase is quite high. Some pairs demonstrate a mean frequency of 2.23 and 2.06 and in the overall mean is 2.15 per individual per hour.

Our attempts to identify a specific context of the *e* posture were not successful (Table 2). Above all, this posture is apparently linked to both social and comfort behavior. This action was included in actual preening in 27 (20.8%) out of 130 recorded bouts. Frequency distribution of durations of that part of posturing when the bill remains in contact with the back plumage suggests the lack of a well-defined borderline between irrelevant (“ritualized”) and true (functional) preening (Fig. 4B). According to the video tapes, there is a tendency towards increased comfort movements of the bill (from 0 to 43) with increasing duration of the *e* posture.

Comparison of Figs. 4A and 4B shows that frequency distribution of durations in the context of agonistic and mating behaviors differ by the ratio of brief bill touches of the back and longer touches. The proportion of the former ones is significantly higher in the sample collected in the prebreeding period (between means $p = 0.06$, t-test, between medians $p = 0.03$, Mann-Whitney test).

As for the participation of the *e* posture in other activities apart from comfort behavior, it seems inherently fixed. This action is present in both individual interactions *per se* and in nest-building behavior components. However, most often (55 bouts, 42.3%) it is not possible to establish a clear link between the *e* posture and the preceding and following ones. Such performances were considered spontaneous. They are equally characteristic of periods of comfort, foraging, and social activities and, furthermore, are the final components of copulation (two cases are available).

Our observations are too complicated to be tabulated in detail. Any bout containing the *e* posture proves to be unique in one form or another. Therefore, Table 2 outlines a rough summary of the data. To show the behavioral sequence during communication in the strict sense, where the *e* posture could theoretically be treated as a signal action, we analyzed the patterns of mating behaviors in a 10 min bout video taped in real time (Fig. 9). It should be mentioned that this bout is not exceptional but is a typical example of coordinated behavior of both partners in the prenesting period. The number of such interactions is given in Table 2 under the column “previous action, *g*” where the letter designates a flight to the mate or synchronous flight of a mated pair (nine flights on the whole based on the total

Table 2. The characteristics of the @e@ posture in different situations. The number of recorded actions and their percentage in the total number of actions for the given pair, %

pair A (n = 64)	In response to the mate's action	<i>c</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	Dancing
		—	3 (4.7)	—	5 (7.8)	3 (4.7)	1 (1.6)
	The previous action by the sex partner	<i>c</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	Dancing
		1 (1.6)	—	4 (6.2)	6 (9.4)	1 (1.6)	1 (1.6)
	While a distance between the mates is shortening	4 (6.2)					
	During preening	8 (12.4)					
Spontaneously	27 (42.2)						
pair B (n = 66)	In response to the mate's action	<i>c</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	Copulation
		—	1 (1.5)	—	—	2 (3.0)	—
	The previous action by the sex partner	<i>c</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	Copulation
		7 (10.6)	—	1 (1.5)	3 (4.5)	2 (3.0)	2 (3.0)
	While a distance between the mates is shortening	1 (1.5)					
	During preening	19 (28.9)					
Spontaneously	28 (42.5)						

sample size, 6.9% cases of the *e* posture occurrence). It should be reminded that this flight was mentioned above to consistently precede the attack by the crane at the observer.

The analysis of the mutual orientation of the partners when one of them or both adopt the *e* posture does not support the contention that its components (e.g. a dropped wing) have any certain signal function (for details see Discussion).

As evidenced by Fig. 9, both versions of the *e* posture is not only a typical element of the sequences

including unison duets, but can barely be separated from unison duets in terms of any hypothetical motivations. We see that time intervals between these two actions may be extremely short (in this case, 2.5, 16, and 24 s). It clearly suggests that the *e* posture and unison duetting in similar contexts may be considered as parts of the single uninterrupted sequence of actions performed in the presence of the mate.

It is therefore useful to focus our attention on unison duets in the context of the mating behavior. Sauey (1985) concluded on the basis of the data on territorial

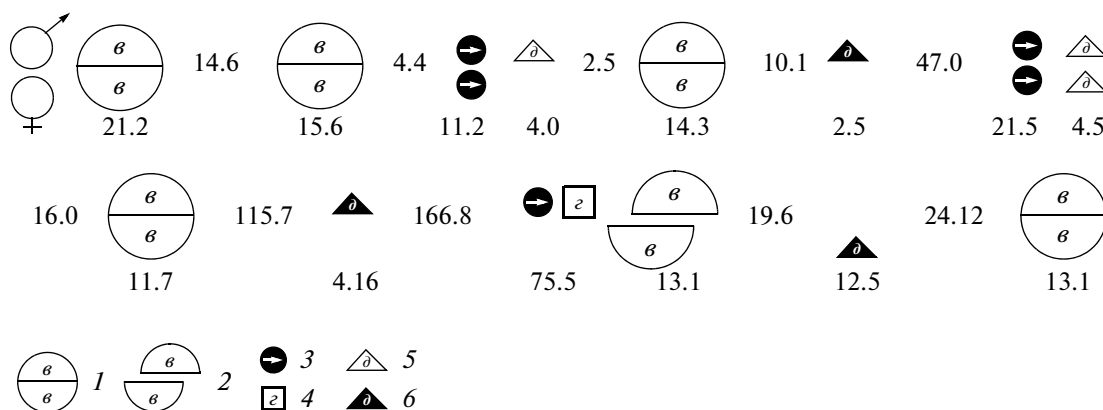


Fig. 9. Scheme of courtship play in pair of the Siberian Crane.

(1) Duet, mates start actions synchronously; (2) duet, mates start actions asynchronously; (3) flight; (4) *d* posture; (5) *e* posture, version 1; (6) *e* posture, version 2 (see Fig. 2). The figures designate the duration of the corresponding interactions.

Table 3. Frequency of unison duets in two pairs of the Siberian Crane

Pair	Date	Observation time in the morning	Spontaneous actions	@x _{cp}	External stimulation	@x _{cp}	Date	observation time in the evening	Spontaneous actions	@x _{cp}	External stimulation	@x _{cp}
A	13.04	2 h 40 min	24	9.0	17	6.4	13.04	2 h 35 min	13	5.0	1	5.0
	14.04	3 h 40 min	20	5.5	6	1.6	14.04	2 h 15 min	3	1.4	2	0.1
	15.04	3 h 10 min	13	4.1	9	2.8	15.04	1 h 30 min	3	2.0	3	2.0
	16.04	3 h 00 min	10	3.3	3	3.3	—	—	—	—	—	—
	Total	14 h 10 min	67	4.7	35	2.8	Total	6 h 20 min	19	3.0	6	0.9
B	13.04	—	—	—	—	—	13.04	2 h 35 min	8	3.1	1	0.4
	14.04	3 h 40 min	—	0.0	7	1.9	—	—	—	—	—	—
	15.04	3 h 10 min	3	0.9	1	0.3	15.04	1 h 30 min	2	1.3	1	0.7
	16.04	3 h 00 min	2	0.7	2	0.7	—	—	—	—	—	—
	Total	9 h 50 min	5	0.5	10	1.0	Total	4 h 05 min	10	2.4	2	0.5

behaviors of Siberian cranes in wintering grounds that “...unison duets are rather a threat than a mating display”. Our findings do not support that. When Siberian cranes were ready to copulate (the *h* posture in the male and female accompanied by relevant vocalization), they could start performing unison duets with nearly no delay. In three video taped cases time intervals between the precopulatory behavior and subsequent duetting were 12.4, 13.5, and 13.8 s. It is difficult to imagine that sexual motivation could be replaced by aggression within such a short period. Additionally, duets are common components in long interactions that are difficult to describe other than mating games (Fig. 9). It is worth mentioning that the mean duration of duet calling in our sample (13.04 s, $n = 31$) is considerably longer than that reported by Sauey (1985) who studied territorial behavior of Siberian cranes in wintering grounds (9.0 s, $n = 584$). It may suggest higher levels of motivation in mating duets than in activities considered as a part of territorial behavior.

The unison duet is a common component of the behavior of mate partners ready for egg laying. As Table 3 shows, the frequency of these actions in periods of high social activity occasionally reaches 12.2 per hour (pair A in the morning April 13). However, as evidenced by Table 3, different pairs may significantly differ by these parameters. A portion of the observed duets was thought to be stimulated by calls of neighbors including Siberian cranes, white-naped cranes, and common cranes in adjacent aviaries. However, in nearly all recording sessions in the pairs under study spontaneous unison duets were most common (Table 3).

A stimulated duet is performed without delay following an external acoustic stimulus with the mated partners sometimes located in different parts of the aviary. Similar interactions performed spontaneously are frequently, but not necessarily, preceded by typical motor patterns. The birds approach each other and

move in parallel several meters apart or follow each other. Immediately prior to duetting the male (less frequently both partners) lowers his head nearly touching the ground by his bill and shifts from foot to foot, slowly half-turning near the female. This locomotion is very similar to slow walking (see the description of pattern 4, *d*) used in other contexts as a threat. In this case each step is less evident in the sense that feet are lifted less high. This behavior was video taped in 10 out of 23 bouts that were not preceded by the *g* flight and taped in full, this initial interaction phase included.

In four cases the unison duet is performed when alighting after the *g* flight (in two cases a female alighting in the immediately proximity of the male). Three more cases contained the *e* posture between the *e* flight and unison duetting (Fig. 9).

When speaking of the motor patterns of duetting, it is important to note that it differs slightly, at least in males, from what was observed as response to an approaching human. In the breeding season the movements are performed with much greater amplitude (compare 7 *a* and 7 *b*). In terms of motor patterns they completely fit unison duetting in males in the most strained territorial conflicts during wintering (Sauey, 1985).

The analysis of the temporal distribution of duets suggests that their occurrence is governed by spontaneous (endogenous) cyclic changes in the motivation condition (e.g. see Panov et al., 2004). Frequency distribution of duet occurrence per 10-min interval is significantly different from the binomial distribution that should be expected if the duets were random. Intervals with a small (zero or two duets) and maximum number of duets (six) were observed more frequently, and intervals with an intermediate number of duets (three) were less common than expected (Table 4, Kolmogorov-Smirnov test, $D = 0.34$, $p < 0.01$). Duets that coincided in time with squawks by cranes from adjacent aviaries were not considered because they could

Table 4. Comparison of experimentally observed and estimated frequency distributions of duets at 10-min intervals

Показатель@	Number of duets at 10-min intervals						
	0	1	2	3	4	5	6
Total number of observations	10	11	10	0	1	0	1
Percentage of the total number of observations, %	30.3	33.3	30.3	0.0	3.0	0.0	3.3
Expected percentage, %	27.6	36.8	23.2	9.2	2.6	0.5	0.1

have been caused by these vocalizations. The result obtained may suggest that duets are performed in series, with brief pauses within series and with long pauses between them.

In other words, this case could be an example of the hydraulic model by K. Lorenz. This is also corroborated by other facts. For example, the pair B that performs duetting substantially more rarely than the pair A, had statistically longer duets (between means $p = 0.03$, t-test, between medians $p = 0.01$, Mann-Whitney test). Unison calling is longer in the pair B when the level of social motivations rises, i.e. during mating games of the pair A (Fig. 10). To put it differently, it suggests that the character of the actions under investigation and similar ones is determined to a greater extent by endogenous factors than by the context.

Based on the data presented, we have to conclude that among all studied behavioral actions ("signals") only nibbling on vegetation proves to be situation-spe-

cific. These actions were regularly recorded in the context of territorial behavior both in our preliminary observations and in free-ranging Siberian cranes in winter (Sauey, 1985).

Signal behavior in the White-naped Crane. A simplified scheme of the repertoire of actions that can be viewed, in accordance with existing tradition, as communication signals is given in Fig. 11. Like in the Siberian Crane, most signals of the White-naped Crane are interwoven into uninterrupted sequences; therefore, "extraction" of any discrete behavioral units from the flow of the behavior serving communication functions is hardly possible and can only be an artificial procedure.

As in the previous section, for the sake of convenience we single out seven motor patterns in the repertoire.

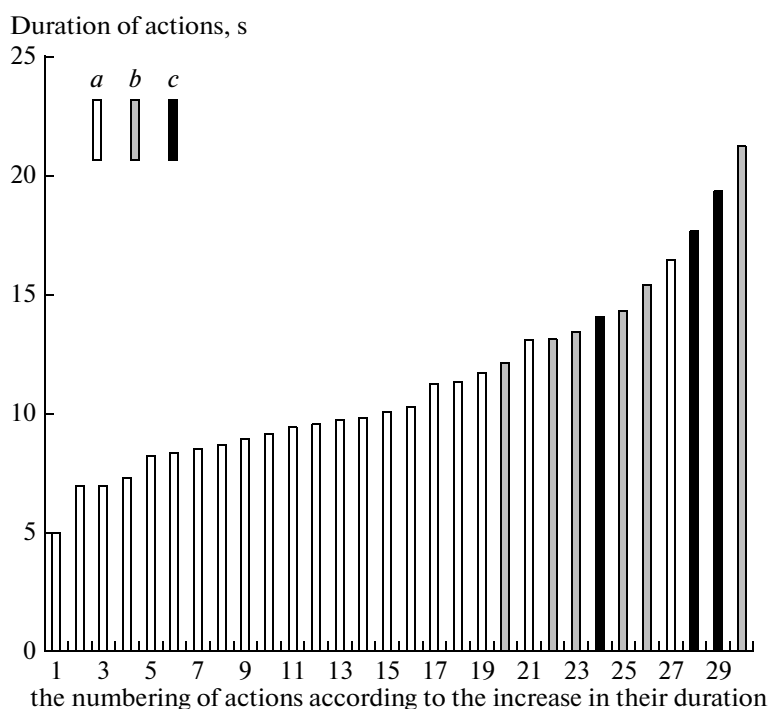


Fig. 10. Variation in the duration of duets. (a) A duet of the pair A in daily situations, (b) mating play of the pair A, (c) a duet of the pair B in daily situations.

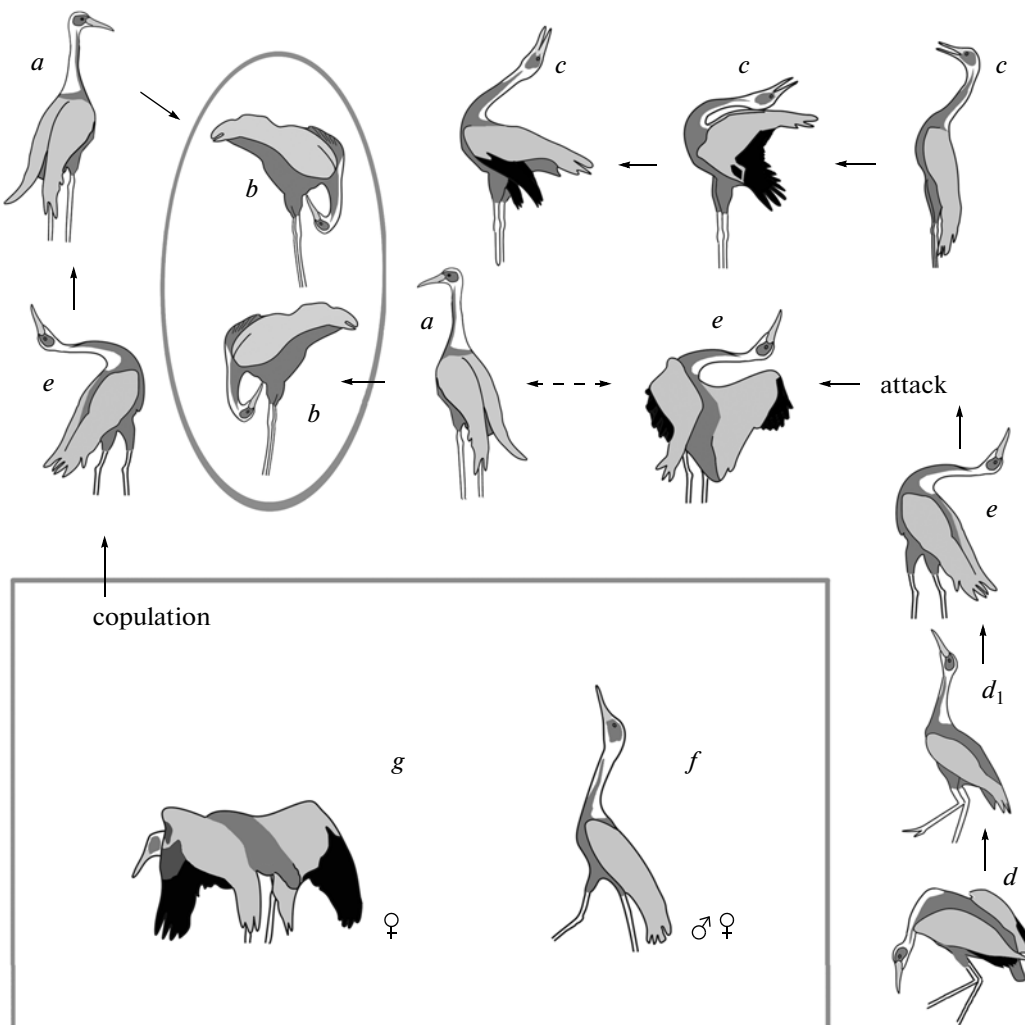


Fig. 11. The structure of signal behaviors of the Red-crowned Crane. See text for references.

(1) *a* intense feather shaking that follows alternate wagging of the left and right wings and almost always precedes the *b* posture.

(2) *b* a bow with subsequent bill contact with the breast (the *a* and *b* postures together constitutes what is called ruffle-down; see References).

(3) *c* action of the male in a unison duet (female behavior is significantly differs). Two initial transformations from an extended series of stereotyped movements are shown. Upon completion of duetting, the male preens his back for a second. This action as well as the head thrown backward in the beginning of duetting (Fig. 11*c*) points to the similarity between this posture and the *e* posture (see below).

(4) *d* a sequence of activities prior to attacking the intruder in a territorial conflict. Immediately prior to attacking, they adopt a posture quite similar but not identical to the *e* posture.

(5) *e* a sequence of activities partly fitting the description of a “catapult” in other crane species (in

particular in the Siberian Cranes). The difference is that after two or three vigorous wingbeats, the head is pointed backward (rather than forward and down) and grades into brief displacement dorsal preening (“warping” as termed by Masatomi, 1983).

(6) *f* the male posture prior to copulation. It is frequently held in a strut.

(7) *g* precopulatory female posture. This is the only performance with an unambiguous communication function. The copulation is followed by the *e* posture and then by the sequence *a–b* (Masatomi, 1983).

In a strained social context, the bird can temporarily adopt a recumbent posture that may be considered here as an element of agonistic behavior. Dancing occurs slightly more frequently than in the Siberian Crane (see photos under the heading “Birds: signal behavior” at www.panov-ethology.ru) Even if they differ in these two species, the difference is not significant whatsoever.

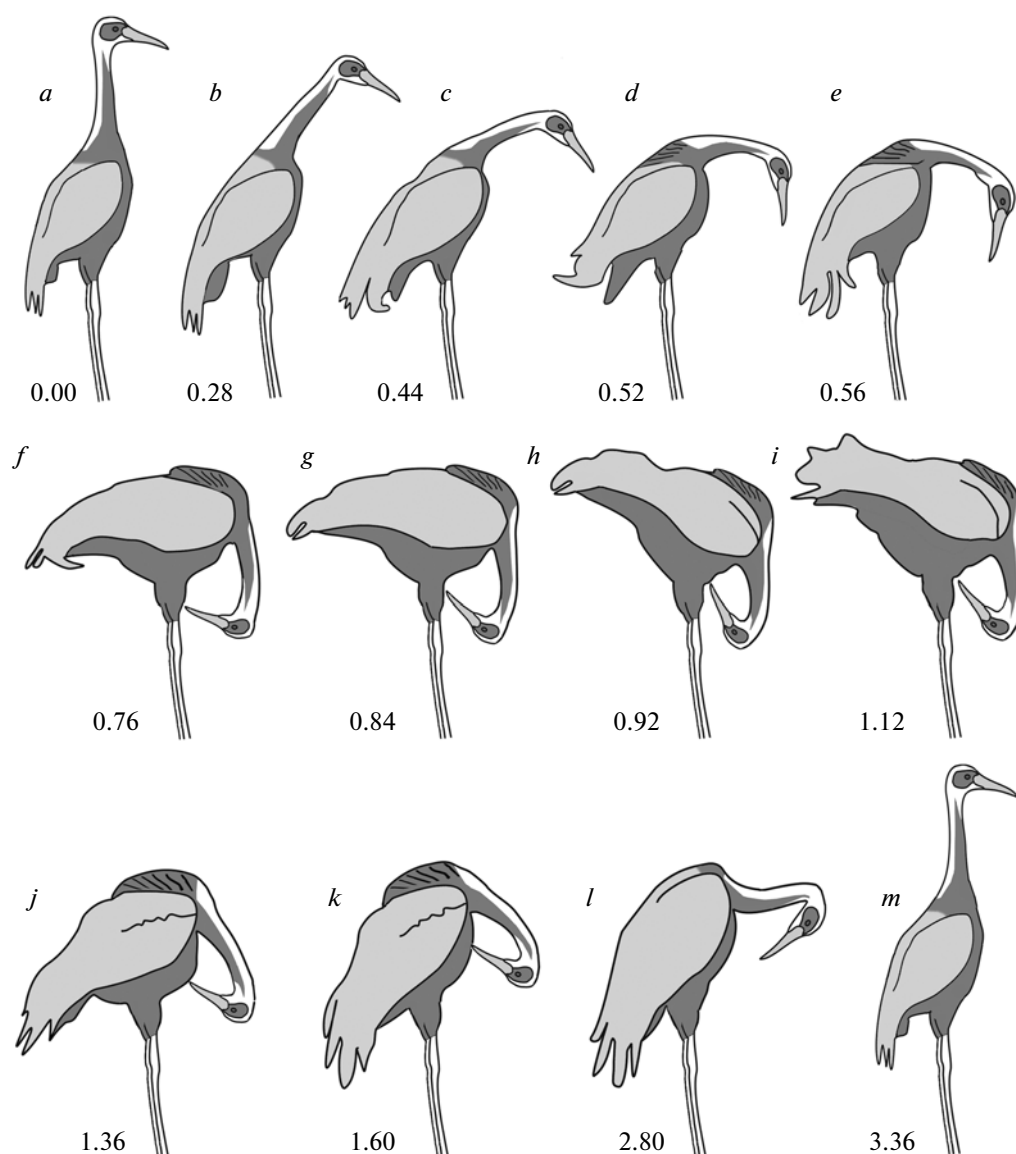


Fig. 12. The *b* posture of the White-naped Crane. The notation is as in Fig. 3.

It is easy to see that the discussed behavior of the White-naped Crane seems to be less elaborate compared to the Siberian Crane. An important difference is the “chains” of actions in their stereotype sequences are obviously shorter here. Meantime, the general mode of signals use in communication of white-naped cranes is not basically different from that of what we saw in the Siberian Crane. We mean the absence of situation-specificity in those behavioral actions that using conventional terminology can be called nothing other than “highly ritualized displays”. Two such motor patterns that will now be in the focus of our attention.

The *b* posture (Fig. 12) seems to be a frequently adopted by white-naped cranes. We cannot provide the mean frequencies for this posture over long periods

because we were not able to document sufficiently long continuous observations. For this reason our description is confined to several examples. In a video record of 11.5 min wherein a free ranging mated pair attempts to evict an intruding red-crowned crane, the female adopted this posture 7 times (plus two feather shakings with interrupted bows); the male, 3 times. In a 4 min video record wherein upon the intrusion of two conspecifics into the same mated pair’s territory four birds exhibited the *b* posture 9 times. These figures may be underestimates since we failed to get all individuals on camera. In a third routine situation, the performance sequence shown by a resident pair was as follows: the *b* posture of the male at 11:28, duetting at 11:30, the same posture of the female at 11:34, of the male at 11:35, of the female again at 11:36.

The contexts of the performance were different in these three cases. In the first case the pair demonstrate overt aggression towards the intruder (the female attacked the intruding red-crowned crane 4 times; the male, once). In the second case no aggression between the resident pair and intruders was observed. In the third case no intruders were visible whatsoever.

It should be emphasized that all described cases included elements previously listed as components of signal behavior, apart from the *b* posture. To be more exact, these were the duets (2 duets in the first case and one in both other cases) and also the *e* posture that followed every attack of the red-crowned crane by the white-naped crane and once was spontaneously adopted by the female far from the intruder.

We have information on the duration of bill contact with the breast in 59 *b* postures. The distributions obtained clearly show a link between this posture and preening. This is suggested by the presence of both nibbling the breast feathers (when the bill opens and closes only very slightly) and extended series in which preening actions were apparent. The latter are most common in the *b* posture in the context of agonistic behavior (Fig. 13). However, this distribution is not significantly different from other distributions, and they do not vary significantly, either (Table 5).

Other variations are given below. A bow after shaking may be incomplete so that the bill does not contact the breast. Two *b* postures occasionally follow one another with a short delay. In rare cases (in 5 out of 43 observations) the “bill at breast” posture is followed by brief back preening.

This final element is common to the *b* posture and the other motor pattern designated *e* (Fig. 14). After adopting this posturing the bill contact with the back feathers was video recorded in 13 cases (in 10 cases after duetting). Frequency distribution of preening durations is similar to that in the case of bill contact with breast (Fig. 15). Differences between the pooled sample on bill contact with the breast (Khingansky

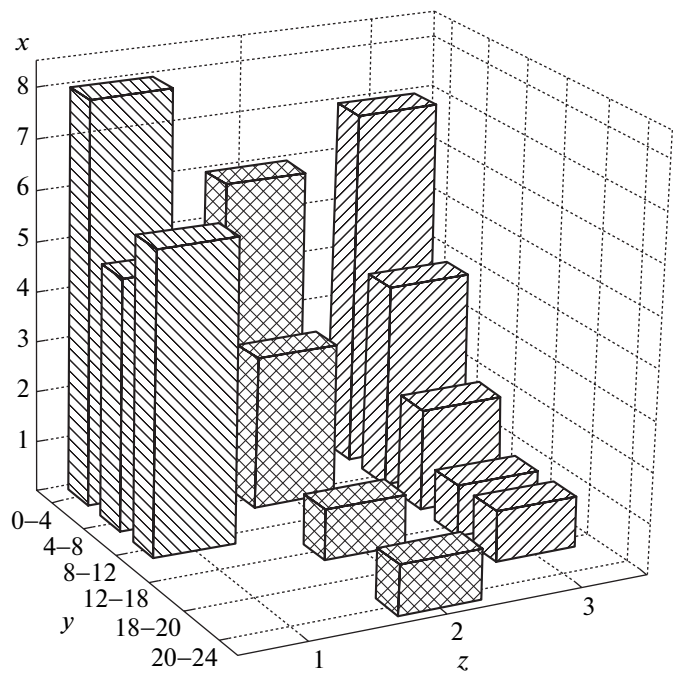


Fig. 13. Distribution of durations of the final component of the *b* posture (breast preening) for the White-naped Crane.

Nature Reserve and Sychevo breeding nursery, median 4.04 s) and the combined sample on dorsal preening are not significant (median 5.30, $p = 0.34$, the Mann-Whitney test).

Interestingly, the entire sequence of actions shown in Fig. 14 is only observed in the case of spontaneous performance of the posture (in particular as comfort behavior). In agonistic contexts the elements *b–d* are absent. Before attacking the intruder, the *e–j* sequence is only observed instantly, and immediately following the attack the *j–o* sequence is observed. Curiously, the crane frequently trips upon completing this motor pat-

Table 5. Comparison of different sample sizes in terms of the duration of the *b* posture in the White-naped Crane

Object of observations	Samples representing behavioral patterns and sex of individuals that adopted the posture	<i>n</i>	1	2	3	4	5	6	7
Free-ranging pair (Khingansky Nature Reserve)	1. Agonistic behavior	19	–	0.71	X	X	0.49	0.25	0.30
	2. Spontaneously a nonpaired individual	11	–	–	X	0.65	0.50	0.19	0.29
	3. Pooled sample	38			–	X	0.42	0.17	0.20
	4. Pooled sample size (without spontaneous displays of nonpaired individuals)	27				–	0.48	0.22	0.26
Aviary pair (Sychevo breeding nursery)	5. Male	15					–	0.84	X
	6. Female	6						–	X
	7. Pooled sample	21							–

Note: The Mann-Whitney test is used. The letter X designates that the comparison of the entire sample cannot be performed with its part. For example, agonistic behavior is a part of the sample “3 Pooled sample” and sample “4 Pooled sample size” (without spontaneous displays of non-paired individuals).

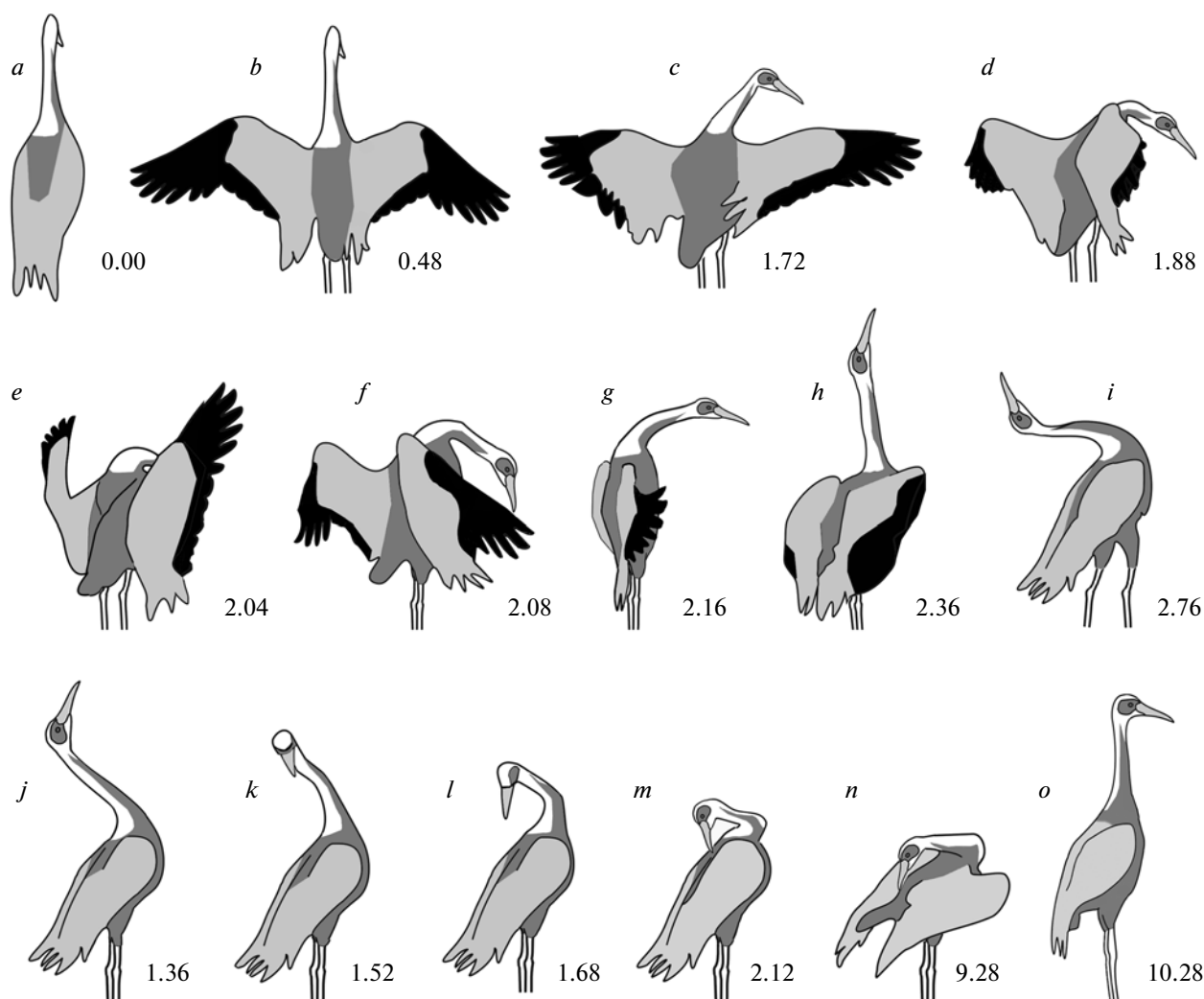


Fig. 14. Action *e* of the white-naped crane. The notation is as in Fig. 3.

tern. This is probably due to the loss of balance when the bird rapidly throws its head backward (0.4 s).

Here we established a link between the *e* posture and both comfort and aggressive behavior. However, in the terminology of classical ethology, this is a ritualized action that on a regular basis occurs as a vacuum activity, i.e. spontaneously.

Summarizing this section, it should be emphasized that all the components of the signal repertoire considered herein could follow one after another in various combinations, frequently with pauses of one minute or shorter. These sequences regularly include *b* and *e* postures. A few examples: *b* posture—duetting (and vice versa), *e* posture—duetting, *e* posture—dancing, etc. The absence of any situation specificity in the *b* posture and interactions in unison duetting are immediately apparent. Unfortunately, space limitations prevent a detailed discussion of evidence supporting this conclusion. Other components of the signal behavior of the White-naped Crane (e.g. interac-

tions during copulation) are beyond the scope of this article.

The signal behavior of the Red-crowned Crane has been described earlier in much more detail than those of the Siberian and White-naped Cranes. Unfortunately, most components were listed as static postures (Masatomi, Kitagawa, 1975), which, in our opinion, does not present an appropriate characterization of the species-specific signal system as an integral systemic entity.

Without repeating the facts mentioned by the Japanese colleagues, we will focus our attention on behaviors that can be similar to those described above for the two other species. We mean displacement preening and motor patterns taking place simultaneously. This preening generally directed at the same body parts as in the Siberian Crane (back) and white-naped crane (back and the ventral side). In the latter case, red-crowned cranes preen mainly sides of belly rather than breast, as white-naped cranes do.

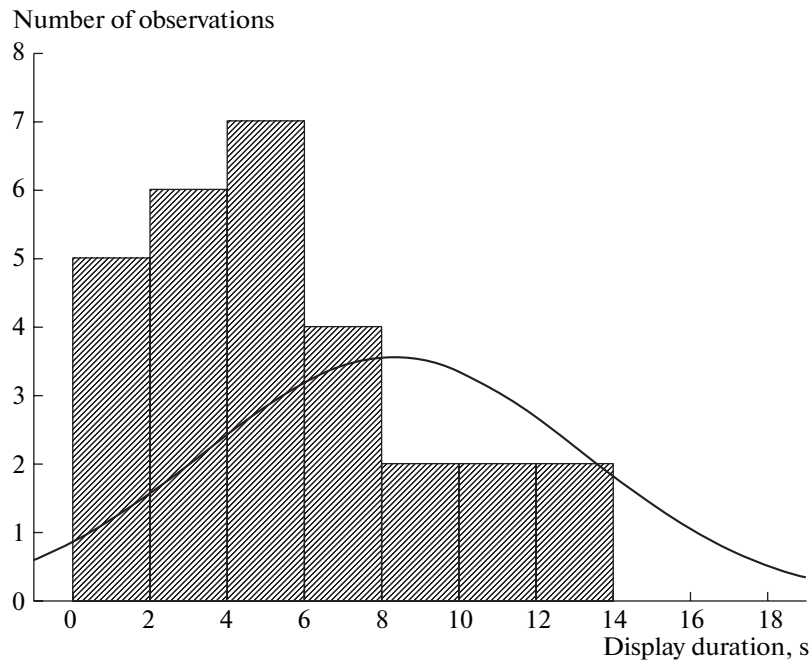


Fig. 15. Duration distribution of the final component of the e posture (dorsal preening) of the White-naped Crane.

A more significant difference of these performances in the Red-crowned Crane from those of the other two species is as follows. The site of displacement preening of the Siberian crane is only the back. The white-naped crane tends to preen the back and breast using different motor patterns. As for the Red-crowned Crane, both dorsal and breast preening components are included in sequences described and are sometimes performed for a rather long period. In agonistic social contexts, these sequences also include a special motor pattern, the arch posture (Fig. 16 f-h), or culminate in it. This posturing is accompanied by a brief dull growl.

This is very important for comparison of the three species because it demonstrates that Red-crowned Crane behavior is dramatically different from those in of the other two species. Whereas the behaviors of the Siberian and White-naped Cranes are apparently rigid and machine-like ones, the behavior of the red-crowned crane shows much more degrees of freedom.

As an example, six action sequences are presented (of 36 sequences appropriate for analysis). They appeared in the order indicated below one after another when a male red-crowned crane intruded a territory patrolled by a pair of white-naped cranes. All three birds were nervous, which resulted in attacks upon the intruder by the resident pair (or, less frequently, vice versa). The letters in the sequences are as in Fig. 16. The letter "l" stands for a left wing drop, and "r" for a right wing drop.

h(l)-a-a-a-h(r)-h(r)-a-a-h(l)-a-a-a-
h(l)-a-walk
h(l)-a-a-h(r)

a-h(r)-a-h(r)-a-h(l)-a-c-g-h(r)-h(l)-h(r)
h(r)-h(l)-a-h(l)-a-a-h(r)-a-a-c-g-h(r)-
h(l)-a
c-g-h(r)
 lie down-g-a(r)-a-walk

Bold letters denote the most consistent pattern: ruffle-bow-up-arch posture-wing drop followed by displacement dorsal preening. The same sequence without shaking is shown in the last sequence wherein the *g-h* combination (underlined) occurred when the bird was standing up from the recumbent posture. It simply had no time for shaking. The same situation (absence of introductory shaking) is observed in response to the attack by a white-naped crane. In one case the red-crowned crane adopted the arch posture; in another case the arch posture was followed by a wing drop and displacement dorsal preening. The arch posture was adopted by the red-crowned crane when it returned attack of the resident male.

The arch posture appears to be equally non-situation-specific as the e posture of the Siberian Crane (its similarity to the sequence *g-h* is beyond doubt) and as the b posture of the White-naped Crane. It turns out to be a highly characteristic dancing element in this species and is observed after copulation (Masatomi, 1983). According to our results, in the latter case this posture is accompanied by a wing drop and displacement dorsal preening, which is identical to behaviors in agonistic contexts. Finally, it can be performed quite spontaneously, i.e. as vacuum activity.

A rapid change in these sequences is conducive to the fact that each performance is not as conspicuous as

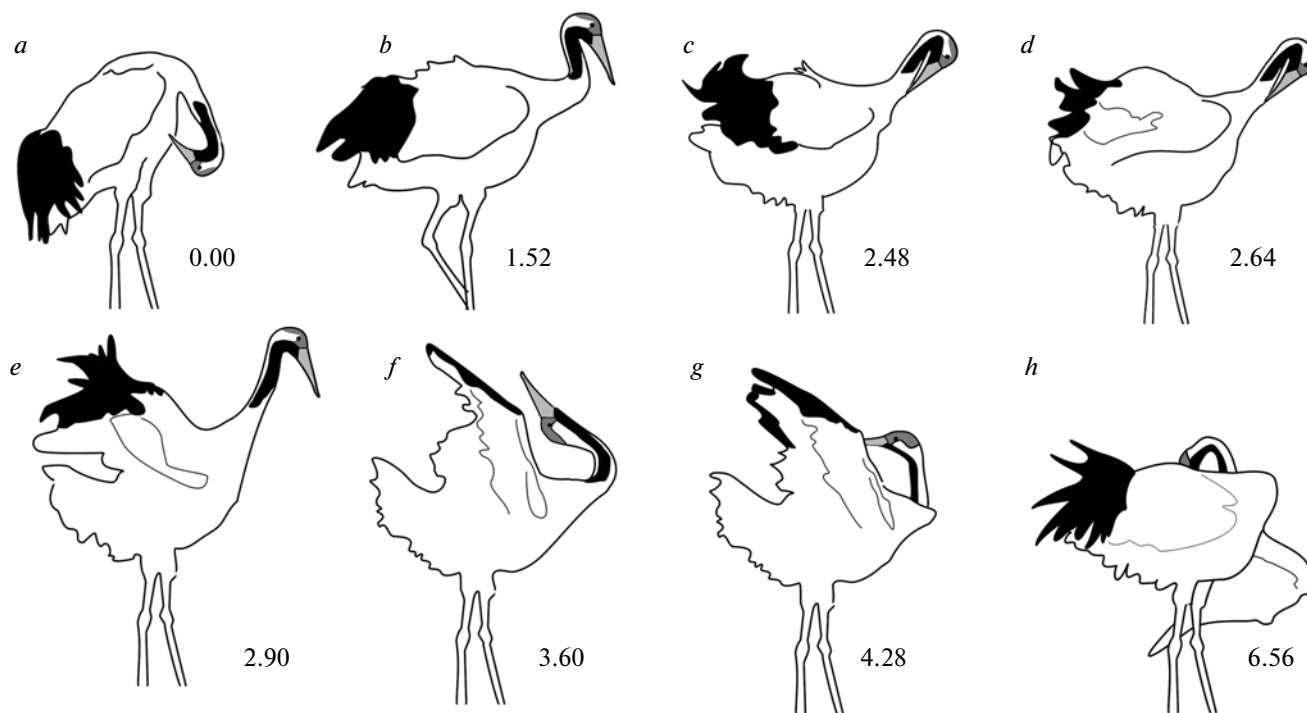


Fig. 16. A fragment of posturing sequence in the Red-crowned Crane in agonistic context. The notation is as in Fig. 3.

in the two other species. To put it differently, the postures are less fixed temporally. This point is supported by comparison of displacement preening durations that are significantly shorter in the Red-crowned Crane than in the Siberian and White-naped Cranes (Table 6).

In summary, it is safe to say that in the terminology of classical ethology the behavioral components of the Red-crowned Crane are 'less ritualized' than those of the other two crane species. This conclusion is very important in the light of our further discussion.

DISCUSSION

The ritualization hypothesis developed by N. Tinbergen over half a century ago has been the cornerstone of classical ethology. Since then it has acquired credibility; however, we are not aware of attempts to

Table 6. Comparison of durations(s) of bill contact with the back and belly in the three crane species

Species	Dorsal preening	Ventral preening
Siberian Crane	8.28 (7.65 ^a)	no
White-naped Crane	5.60 (5.30 ^b)	5.48 (4.10 ^c)
Red-crowned Crane	3.58 (3.05 ^{ab})	2.96 (3.0 ^c)

Note: Mean values are given with the median in parentheses. Medians within a column with identical letter superscripts are significantly different by the Mann-Whitney test ^a $p = 0.0001$, ^b $p = 0.02$, ^c $p = 0.01$.

critically assess on the basis of hard empirical data. The objections put forward by one of the authors earlier (Panov, 1983) were rather speculative like the hypothesis itself.

Features of behavioral actions of cranes that fit the general idea of communicative signals prove to be a perfect material to test the hypothesis by N. Tinbergen. Prior to summarizing in this context the results of our work, it is necessary to briefly focus on the arguments of the hypothesis' author.

Displacement activity as a material for the development of ritualized communicative signals. The point is that some fragments of the so-called daily behavior that initially carried no communication function, under the natural selection pressure gradually acquire conspicuous exaggerated forms and become socially important stimuli (social releasers, displays). This process was termed by N. Tinbergen as emancipation of communicative signals from a flow of daily behavior that not bear any certain information for conspecifics.

According to the hypothesis, these behavioral innovations acquire properties to be understandable by the recipient. Moynihan wrote: "Clarity, precision, and strength of transmission should be useful qualities or characteristics of any signal. They should ensure that the signal cannot pass unnoticed and unrecognized. They can be achieved most easily, or developed most highly, by making the form of the display emphatic (exaggerated), stereotyped, and distinctly different from that of any other behavior pattern. In

other words, they can be obtained by ritualizing the signal, making it a display" (Moynihan, 1970: 86).

This point was similarly put in another study: "A movement can be considered ritualized if ... *its communicative efficiency improved under selection pressure*" (Hazlett, 1972; italics ours). According to this author, ritualization results in increased communicative efficiency through selection of "less equivocal" signals to remove "more equivocal" ones (*ibidem*, p. 97).

In Tinbergen's opinion, the primary components to be ritualized are displacement activities. These activities appear context-irrelevant to the observer. In particular, these are jerky touches of feathers by the bill, like brief preening in situations of conflicts between individuals. They seem to be out-of-context for the behavior, for example, irrelevant preening. Tinbergen wrote: "A displacement activity is an activity belonging to the executive motor pattern of an instinct other than the instinct(s) [in this case not aggression, but comfort behavior — *authors*]. A displacement activity seems to appear when an activated drive is denied discharge [aggressive behavior — *authors*] through its own consummatory action(s)" [attack of an intruder — *authors*] (Tinbergen, 1952: p. 25–26; notes by the authors of this article from here onwards are in square brackets).

We used the ethological terminology applicable to phenomenon of instinctive behavior (entire theory by K. Lorenz, 1937). Following this theory, any behavioral sequence is comprised of a variable part (appetent behavior) and a highly stereotyped final (consummatory) action. The variable appetent behavior is defined as a sum of task-oriented working actions. Its goal itself, however, in this framework is nothing other than the performance of a purely instinctive consummatory actions such. Since the appetent behavior *per se* is not instinctive, the instinctive behavior is not task-oriented (purposive) in the context of this theory.

The process of ritualization of displacement activities consists of the replacement of patterns. As a result, a behavioral innovation, i.e. a "ritualized display", becomes different from the original behavioral act, called "an example". Evolutionary transformations turn into to the following. First, there is exaggeration and simplification, i.e. one movement becomes more intense (e.g. the amplitude rises), whereas others become less intense or may be lost. It results in the second type of transformation, i.e., loss of coordination between parts movements of different of the body (e.g. between the neck with the head and the wings). Each part moves in a spontaneous fashion with no coordination with movements of other parts. All these can be defined as "schematization" of actions, which makes them curious and conspicuous. Tinbergen had no doubt that these changes in motor patterns were accompanied by the acquisition of morphological sig-

nal structures in the body parts that perform exaggerated movements (for instance, of its coloration).

According to this theory, all these events help transform displacement activity into a simple but conspicuous signal that now functions as a sign stimulus. The latter is emancipated and becomes a new behavioral form derived from the original component with a neutral communicative function. Tinbergen wrote: "All these changes seem to aim at one end: adaptation to the responsive capacities of the reacting individual" (Tinbergen, 1952, p. 24). We would like to emphasize that this citation more than other portions of the text unveils the assumption that evolution is aimed at a final goal. It clearly shows the teleological nature of the hypothesis which just because of that looks quite plausible from the standpoint of common sense.

The message content broadcasted through a ritualized signal. So far we have been discussing signal conspicuousness which renders the signal decipherable to the recipient. However, the article in question has no bearing on what particular information "ritualized displays" can deliver. It appears as if the text of the paper discussed should be obvious for a competent reader without further comments. The reader is supposed to be aware that ritualized displays are a commonplace in encounters of between individuals (threat display) and courtship behavior (mating).

Just a single example clarifying the more certain meaning of "displays" is associated with the appeasing signals. As N. Tinbergen wrote, in the Black-headed Gull *Larus ridibundus*, when (prospective) mates meet, they turn the head away from each other by a sudden jerky movement. In Tinbergen's opinion, this is done to conceal the brown face and the weapon (the bill) that these gulls show off to each other in threat postures in aggressive contexts (p. 28).

The author is somewhat self-contradictory in what he warned against the anthropomorphic ("psychological") interpretation of behavior motivations in birds. Page 11 states: "When an aggressive stickleback or a gull makes incipient nest-building movements [displacement activity], one might suppose that they are trying to show to the other of their species that this is the spot where they intend to build a nest" (p. 28) and thus will defend it spot to the last. The author continues: "I consider this anthropomorphic interpretation unsatisfactory."

However, a question arises: if this approach is correct with regard to displacement activities, then why does it fail to apply to "ritualized displays"? It turns out that now birds can be rationally motivated, for example, to appease a social partner. However, this interpretation is completely at odds with Tinbergen's ethological assumption on the lack of directed behavior in the instinctive consummatory action (see above).

This ambivalent point of view of the classic of ethology is responsible for anthropomorphic interpre-

tations frequently occurring in current publications including those that describe signal behavior in cranes (examples of strikingly naive interpretations will be given below).

Signals that fit the definition “highly ritualized signals” in crane behavior. The postures *e* and *b* plus *e* in the Siberian Crane and White-naped Crane, respectively, that were discussed above, completely fit the ritualized displays described by Tinbergen. A slightly less conspicuous “arch posture” of the red-crowned crane also fits this concept.

Following the ritualization hypothesis’s principles, the abovementioned displays actions of the first two species have to be derivatives from displacement preening. However, as we attempted to show, they are somewhat intermediate between spontaneous preening and functional comfort activity. In the former case, they are extremely short, either fully denying the features of actual preening (in the Siberian Crane the bill is simply lying on the back) or preening appears extremely reduced (pecking the breast feathers in the White-naped Crane). In the latter case, these performances are longer and frequently grade into functional preening. In this regard the variant of the *e* posture which is preceded by the *d* posture is particularly indicative (Figs. 2–3). This combination of actions *d*–*e* is performed in the midst of prolonged preening. Therewith these movements are even accompanied by a characteristic call (booming) as it takes place in spontaneous posturing that could be readily interpreted as social signals.

In other words, no evidence of emancipation of these displays from their hypothetical precursor was established either in the Siberian Crane or the White-naped Crane. Similar results were reported by Düttman and Groothuis (Düttman, Groothuis, 1996) for the so-called ritualized behavior of the Shelduck *T. tadorna*.

In the absence of a gap between comfort activity *per se* and displays generally considered (Sauvey, 1985, Ellis et al., 1998) to be ritualized derivatives of comfort behavior, it is easier to assume that both are versions of the same behavioral pattern rather than if to follow the attractive, but completely speculative ritualization hypothesis. We mean that it is more useful to focus on a phenomenon in the context of its proximate causation, rather than to believe blindly in some highly hypothetical ultimate causes.

Are the discussed actions of cranes the signals directed toward a personal social partner? Our numerous video taped observations (collection of the Laboratory of Ethology and Biocommunication, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences) allow us to answer this question rather negatively. To begin with, the most conspicuous posturing (*e* in the Siberian Crane and *b* and *e* in the White-naped Crane) often occur spontaneously in the absence of a potential recipient. When the recipient is present, the mutual orientation of the

communicator and the other individual is frequently such that precludes the possibility for a dialogue. The bird that adopts the posture of interest turns its back to the social partner, frequently being at a significant distance from it. When two mated Siberian cranes are taken up by preening their feathers a short distance away from each other, an unbiased observer has a difficulty assuming that the *e* posture sometimes recorded is directed to the second bird standing motionless. Situations of this kind are more common than those performed nearly synchronously or following one another with some a short delay. However, in this case the movements do not result in any obvious changes in the behavior of the birds, either. White-naped cranes standing a meter or little more apart may nearly simultaneously adopt various postures: one adopts the *b* posture; the other, the *e* posture. It is clearly obvious that this “communication” is meaningless.

For this reason it is interesting to focus on the way signals are exchanged between Siberian cranes in mating plays when there are good reasons to assume that these signals are personalized. The male and female of the pair A in a videotaped 10 min bout twice simultaneously adopted the *e* posture (Fig. 9). It was preceded by joint flights of the partners after which they alighted several meters apart in one line, so that none of them could see the partner’s dropped wing whose black-and-white pattern should theoretically have been a signal. In the other three cases the male in the *e* posture oriented his dropped wing (the left wing twice; the right one, once) to the opposite side of the female. The same is true for another posturing performed by the female close to the male. In the pair B in both cases the female could not see the dropped male’s wing. The fact that displaying a dropped wing is not addressed to an intruder (human–observer) was mentioned during the description of the Siberian Crane behavior.

The finding that the partners perform unison duets in cyclical mode allows us to suggest that the actions of interest are subject to spontaneous endogenous cyclic changes in motivation; i.e., they are independent of the exchange of relevant information.

What message is contained in ritualized signals of cranes? At present the situation in the field of animal behavior is such that many ethologists seek to make a sensational discovery similar to goal-oriented human behavior. In particular, in the field of avian communication efforts are directed towards the identification of its meaning. The aim of searching for the meaning or “semantic content of the signal” was formulated in a short communication in “Animal Behavior” several decades ago (Smith, 1981).

Following the predictions of the ritualization hypothesis, most meaningful should be highly ritualized displays that should be under selection pressure to achieve exactly this objective, as stated earlier. However, precisely these behavioral actions of cranes prove to be the least situation specific ones. We conclude that

they are denied any informative content, i.e. extremely degenerate, semantically void.

To put it differently, if the hypothesis is at least partly true, selection pressure rendered these signals pronounced and conspicuous but failed to endow them with any relevance and suitable for transmission of messages anywhere near meaningful. Obviously, the assumption of the possibility of the evolutionary scenario implicated in the ritualization hypothesis is in the given case nothing more than an eloquent practice.

In crane behavior much more significant for communication are the actions that are not conspicuous in any sense. Among other things, the so-called unison-walking is included. Mating partners show their readiness for duetting by walking side-by-side during one or two minutes, or they may strut following each other. Unison calling starts unexpectedly but nearly simultaneously by both partners, the delay lasts split seconds. To catch "a starting gun shot" is hardly possible. The signal preceding its onset is slow walking of both partners *per se*; occasionally, feather shaking by one of them, described above. To put it differently, communication here occurs through watching each other's behavior performed through daily movements (such as locomotion).

Failure to separate signal displays into well-defined categories. As far as the widely accepted method of dividing communicative signals into agonistic ones, on the one hand, and pair-related behavior (see the extensive study by Ellis et al., 1998) on the other, is concerned, even such rough distinction based on functional relevance turns out to be impossible for most performances. The only exception, as stated above, with certain reservation are precopulatory signals. As regards immediate post-copulatory behavior, the reverse is true. As pointed by Masatomi, "the sequences of these characteristic postcopulatory behaviors are almost identical to the combination of displays evoked in the agonistic situation" (Masatomi, 1983: 69).

For brevity's sake, let us consider as a single example the question of which of the two aforementioned categories the unison duet refers. In the recently mentioned study by Ellis et al. this behavioral action was assigned to the mating behavior category. In contrast, Sauey (Sauey, 1985) insists that in the Siberian Crane the unison behavior is rather a territorial threat. This author wrote that since in this species unison calling is invariably initiated by the male (which is not correct), "...selection pressure could favor those duet components that carry more signs of threat and, simultaneously, reduces the display efficiency in the context of mating behavior". In reality, we could see from the description of signal behavior of the Siberian Crane in this article, duets can be equally attributed to territorial and mating behavior. Like passerine song, the duet could be perceived as a threat to an intruder and a tool to strengthen mating relationships in the behavior of each mate.

Is the communicative behavior of cranes unique in the context of the complexity of its repertoire? Ellis et al. wrote: "Cranes have a tremendously complex repertoire of stereotyped social behavior. The crane social repertoire would tentatively place cranes at the apex of behavioral complexity, at least for stereotyped social behavior. 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" (Ellis et al., 1998:148).

Such an unexpected statement is not surprising if the description methods of these authors are considered. They dissect the continuous fabric of behavioral acts organized into sequences of elementary components (only which, in fact, carry communicative function) into discrete units that, in their opinion, are self-sufficient. For example, in the sequence of actions of the Red-crowned Crane shown in Fig. 16 and lasting for less than 7 s in real time, they recognize at least three discrete "displays" (ventral preen, ruffle-bow-up, and arch). It is no wonder that each crane is assumed to have more than 60 stereotyped social signals termed ethons therein, not counting those associated with nest-building behavior and other activities. Agonistic behavior alone is believed to include 32 discrete "displays" (exact number!) not including vocalizations (Ellis et al., 1998:132).

Without hesitation Ellis et al. assign a well-defined meaning to each discrete display. For example, "Crouch appears to be a form of ritualized incubation and probably signals to an intruder that the performer has made a great investment in the territory" (i.e., chicks; Ellis et al., 1998: 140). Recall the Tinbergen's note on unacceptability of such anthropomorphic interpretations.

Unfortunately, similar interpretations are heavily present in the study by Sauey (Sauey, 1985). For instance, after completing the description of strutting observed in territorial conflicts when the Siberian crane lifts his feet high, the author writes: "Strutting definitely derived from daily walking, however, lifting of tarsometatarsus and toes until the horizontal may be a showing off of the weapon to the opponent since the foot pads with talons may be aggressively used in combats with conspecifics." Meanwhile, our observations suggest that this kind of walking of the Siberian crane occurs not only in territorial conflicts. It normally takes place during nest-building when both partners walk this way at the nest site (Fig. 17). The biological significance here is fairly clear: it is done to ensure eggs are not stepped on. And again, the display has no strict situation specificity, if any.

Comparative aspect. If we had at least some reason to believe that the ritualization hypothesis is plausible, we would have attempted to show results of this process by comparing displays in that, at first glance, both species have much in common. These are the *e* posture of the Siberian Crane and the one following the arch

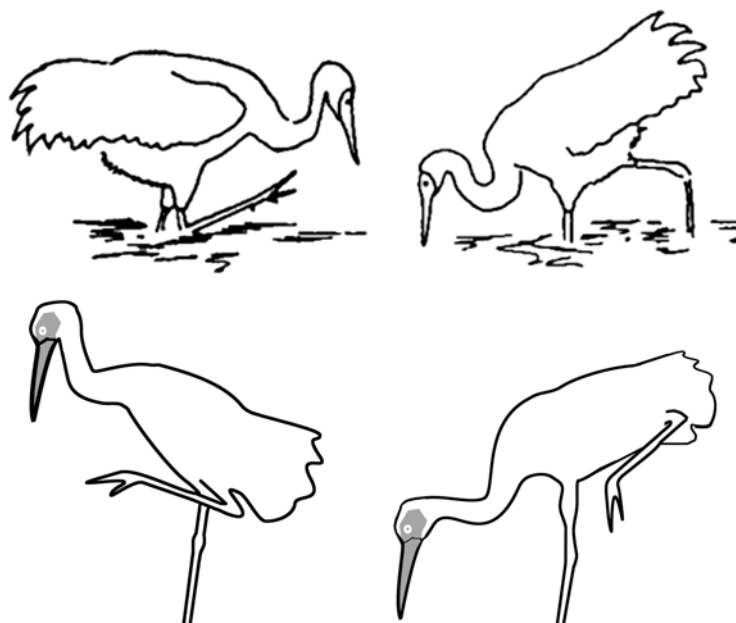


Fig. 17. Motor patterns of a Siberian Crane with lifting feet high. Top, in a territorial conflict (after Sauey, 1976), bottom, nest-building (our recordings).

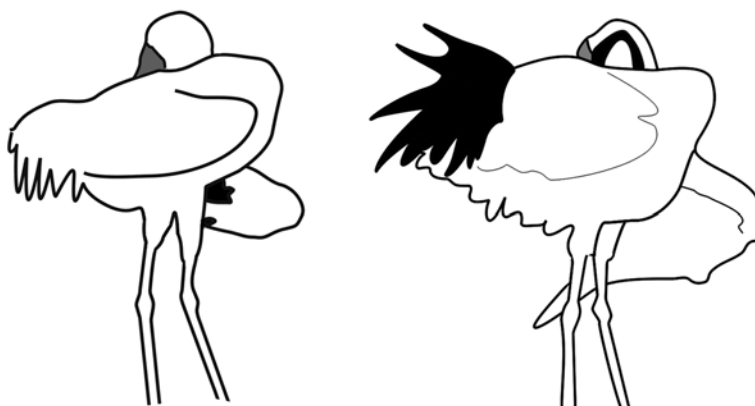


Fig. 18. The *b* posture of the Siberian Crane (left) and arch posture of the Red-crowned Crane (right).

posture of the Red-crowned Crane (Fig. 18). Based on the facts mentioned in the section of the Red-crowned Crane behavior, it was concluded that in terms of classical ethology the corresponding display of the other species is less ritualized than the similar *e* display of the Siberian Crane.

Overall, one might suggest that the posture of the Red-crowned Crane is ancestral, and the derived posture of the Siberian Crane illustrates the next step of ritualization. It should be emphasized that from the standpoint of communicative efficiency such evolution would yield nothing new: the *e* posture of the Siberian Crane is as semantically void as the posture of the Red-crowned Crane. The main point is that the studies of cranes' phylogeny suggest that the Siberian Crane is an archaic species, whereas the Red-crowned

Crane is an evolutionally advanced one (Fig. 1). Therefore, comparative studies similar to the one discussed herein (and widely used in ethology textbooks) do not stand up to scrutiny whatsoever.

Apart from the subject on the ritualization hypothesis, let us develop a comparative approach to describing crane behavior in the context of atomistic (elementaristic) paradigm of describing behavior, on the one hand, and in the context of holistic analysis of crane behavior, on the other. The former methodology is well represented in the study by Ellis et al. cited herein, in which the primary principle was to count the number of "displays" viewed as discrete units. "Descriptive ethology is founded on the premise that discrete behavioral actions 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 tear apart the social alphabet of a species" (Ellis et al., 1998:148). Other methodological drawbacks of this approach were briefly discussed above.

Their comprehensive analysis is given by Panov (1978, 2009), where a fundamentally different, holistic approach to describing and analyzing avian behavior was suggested. It laid the basis for this article showing, in particular, that there is no significant difference between communication behavior of passerines (that were studied in the monograph referred to) and cranes with their ostensible complex repertoire of signals.

The reader can compare the results of the two approaches while examining comparative-ethological aspects of crane behavior. In the present article, really dramatic differences in communication of the three species studied were demonstrated (adhering to the general principles of the organization of their behavior in communication). As far as the atomistic approach by Ellis is concerned, their achievements are listed in Table 7.

CONCLUSION

Suggestion of the evolutionary scenario used as the basis for the ritualization hypothesis originates from inappropriate concepts of early ethologists about what efficient communication is. They thought that it could only occur if a message broadcasted by the sender to the receiving individual is decipherable.

Therefore, the basis of concepts of those days was understanding animal communication as a dialogue based on the exchange of semantically individualized discrete signals like conspicuous, exaggerated "displays".

These viewpoints have become thoroughly out of date. Their weakest link is the notion that most actions by interacting individuals are believed to be no less than a some background neutral in the context of communication. In this interpretation the communicative process is entirely dictated by "inflection points" at which exaggerated "signal displays" come into play.

Tinbergen and his colleagues' point of view was well in agreement with the the scientific climate in time when the incipient ethology was originating. It is then when the synthetic theory of evolution was being formed by merging Darwinism with population genetics. In this period zoologists, field ethologists including, rapidly adopted terminology of early genetics. Without going into details of that not-so-simple novelty, they adopted the paradigm of population genetics as an unassailable, objective confirmation of, until then, purely speculative Darwin's idea of progressive evolution through natural selection. It seemed then that organization of living systems is nothing more than a set of features freely shuffled by evolution.

There was little doubt that the result must necessarily be progressive improvement of living systems through achieving maximum fitness and efficiency of their functions.

The concepts of that time about mechanisms of natural selection were still dictated by bean-bag genetics. It was believed that from the numerous properties of a species selection was able to recognize, single out, catch up, and lock in any, even slightly improving the function associated with it. In other words, the prevailing belief was that any evolutionary process caused by selection always goes until completion, until the fittest form completely replaced the less fit one.

Nowadays the situation looks completely different. From general system theory it is known that a system cannot be simultaneously optimized by more than one parameter. Therefore, optimization of real living systems is only possible by means of finding a compromise between conflicting requirements to optimize various parameters. Notwithstanding that organization of living things is full of various correlations and relationships, a compromise between different adaptive systems should be especially hard to achieve. Therefore, the basis for a species-specific system of interpersonal relationships (social behavior and communication) should be extremely conservative. The reason for this is that the system itself was formed during thousands of years under the circumstances of looking for a compromise between conflicting requirements for maximum optimization of all and every function (Rasnitsyn, 1987).

This includes not only functions immediately associated with communication but also those determining the structure of all other categories of behavior (it is worth noting that this distinction is quite conventional). But the behavior of an organism is nothing other than expression of its morphological structure (the way of organizing psychological processes, sensory physiology, body and extremities constitution etc). Therefore, it is unclear what might be the mechanisms by which natural selection is able to single out and cherish one element of the so-called signal behavior. Restating Meyen's words in a slightly different way (1975: 89), one might say that selection is not able to meticulously take care of each discrete "signal".

At the first glance, the ritualization hypothesis seems quite plausible, for it is built on human common sense. In its turn, it is justifiable only as far as it is developed according to the principles of evolution of human communicative systems. Therefore, the hypothesis discussed, although widely used in the special literature until recently as an explanatory principle, from our point of view is now only of historical interest.

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Table 7. An example of comparative description in the context under the atomistic approach (Ellis et al., 1998)

Signals	Signal number	Siberian Crane	White-naped Crane	Red-crowned Crane
Vocal	1	+	+	+
	2	+	+	+
	3	+	+	+
	4	+	+	+
	5	+	+	+
	6	+	+	+
	7	+	+	+
	8	+	+	+
	9	+	+	+
	10	+	+	+
	11	+	++	++
	12	+	+	+
	13	+	+	+
	14	+	+	+
	15	+	+	+
	16	+	+	+
Visual	1	–	–	+
	2	++	–	–
	3	+	+	+
	4	+	+	++
	5	+	–	+
	6	–	slight form	–
	7	+	+	++
	8	+	++	+
	9	+	+	++
	10	body axis is closer to the vertical	body axis is closer to the horizontal	++
	11	slight form	+	–
	12	+++ wings dropped	+ wings slightly dropped	++ wings dropped
	13	+	+	+
	14	+	+	+
	15	+++	+	+
	16	++	+	+
	17	++	?	+
	18	++	+++	+
	19	+	+	+
	20	probably present	probably present	+
	21	–	++	–
	22	–	–	+++
	23	++	+	+
	24	+++	+	+++
	25	+	+	probably present
	26	probably present	+	+
	27	+	+	+
	28	probably present	+	+
Total	43	yes – 21 no – 4 questionable – 3	yes – 22 no – 4 questionable – 2	yes – 23 no – 4 questionable – 1

Note: Signal numbers are given according to the numbering in the study by Ellis et al., 1998. The number of plusses signs intensity; minus indicates the absence of the display in the repertoire.

organizing and performing our observations in the nursery of cranes of Oka State Nature Reserve.

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SPELL: 1. elementaristic