FACTORS INFLUENCING REPRODUCTIVE BEHAVIOR IN THE CRC CRANE COLLECTION, ESPECIALLY G. *a. antigone,* AND G. *vipio*

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The importance of the information in this article may be lost to a few readers who will read "Crane," and turn the page, but if they can be intrigued to read it through, there is an important message. With more and more fanciers trying to breed birds, it is imperative that they understand the influence of their disturbance in the aviary or bird-room, how to manage it so as to effect the least interference, and how to recognize interference when it occurs.

INTRODUCTION

The captive cranes at the National Zoo's Conservation and Research Center are like those in most zoos and breeding centers. Some years their reproductive activity yields prolific results, while other years, more infertile eggs are produced. One aspect in which the CRC collection differs from many others is that it has been under careful observation for the past three breeding seasons. in order to optimistically look forward to the next breeding season, breeders of exotic species, such as Cranes, have tried consolingly to evaluate the reproductive success of their birds in terms of diet, amount of natural rainfall, and other factors. At CRC, however, steps were taken to insure that each breeding season would provide more than fertility statistics. Hence, the factors which affect successful reproductive behavior were investigated.

While there are many factors which affect the successful completion of the reproductive cycle of the Center's Crane collection, most fall into one of three general categories: intrapair inhibitors, interpair conflicts, and human interaction. While it is obvious that factors which fall into the above categories may bluntly interrupt copulation, the ability of many factors to reduce the likelihood of the initiation of the copulatory sequence is not obvious to the casual observer. Thus, this study was undertaken to evaluate the effects of intrapair inhibitors, interpair conflicts, and human interactions on the interruption, as well as the depressed probability, of the successful completion of the reproductive cycle.

METHOD

This study was conducted during the 1981, 1982 and 1983 breeding seasons at the National Zoological Park's Conservation and Research Center near Front Royal, Virginia. Subjects in each study varied. The 1981 study(6,250 minutes) included two adult pairs of White-Naped Cranes (Grus *vipio*) and three adult pairs of Indian Sarus Cranes (Grus a. *antigone*). The 1982 study (6,000 minutes) included the same White-Naped Cranes and four pairs of Indian Sarus Cranes, two pairs from the 1981 study and two newly formed pairs. The 1983 study (10,800 minutes) included four pairs of Indian Sarus Cranes (from the 1982 study).

Arrangement of Cranes in the twenty-one yard Crane complex differed in the three studies. The individual yards averaged 180 feet by 80 feet, and each contained a nonfreeze waterer, a marsh area, and a heated garden shed where Zeigler Crane Breeder Pellets and whole kernel corn were provided ad libitum. (Cranes supplemented their diets with naturally occurring insects, plant matter, and small veterbrates.)

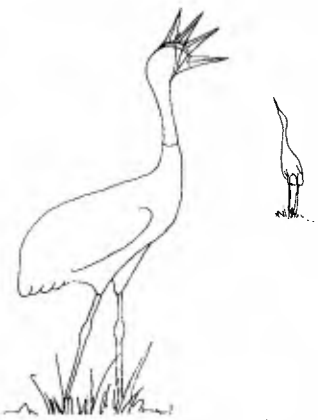
Data from each study was recorded on a prepared data sheet. Although similar data sheets were not used for each study, scan and event sampling techniques were consistently used to record maintenance and social behaviors. Additionally, in the 1983 study, each observed crane yard was marked into nine sections to evaluate yard usage.

INTRAPAIR INHIBITORS: RESULTS AND DISCUSSION

Intrapair inhibitors are those factors, associated with the observed pair, which prevent or reduce the likelihood of the successful completion of the reproductive cycle. Such factors fall into the categories of non-mutual receptivity to initiated reproductive behavior and physical impairment. Intrapair inhibitors terminated 21 (56.8%) of the 37 observed copulations during the three year study, and may have also reduced the likelihood of additional reproductive behavior. While 11 (52.4%) of the copulations terminated by intrapair inhibitors were caused by physical impairments such as pinioned wings (a factor which may be alleviated by pair experience), 10 (47.6%) of the copulatory attempts were terminated by non-mutual receptivity to initiated reproductive behavior. In the category of intrapair inhibitors, the factor of non-mutual receptivity is most responsible for reducing the likelihood of successfully completing the reproductive cycle. Therefore, the observable signs of increasing and decreasing levels of mutual receptivity to reproductive behavior were studied.

An observable sign of increasing receptivity is the bill raising behavior. Described by Masatomi and Kitigawa (1975), the bill raising behavior is rarely seen in non-reproductive Cranes and is likely a physiologically controlled, yet observable, indicator of a Crane's state of receptivity to the reproductive behavior. (It is also the first phase of the copulatory sequence [Masatomi and Kitigawa, 1975].)

Figure 1. Illustration of the bill raising behavior, as it is performed by the Indian Sarus Crane, Grus a. *antigone.*



A bout of bill raising consists of a series (1-20+) of individual bill raises (Figure 1) which may vary from a slight to a ninety degree flexion of the head and bill (the neck remains vertical). The bill may remain raised momentarily, or for an extended period of time. While the duration of this behavior was not recorded, the observed frequencies of bill raising revealed its role as a signal of mutual receptivity.

Distinctive qualities characterize bill raising behavior which is indicative of subsequent reprodutive behavior. To begin with, bill raising bouts which precede copulatory behavior involve mutual participation. Mutual male and female participation, however, is not common, occurring in only 24.0% of the observed bill raising bouts performed by G. *antigone* (1982), and in 11.1% of the observed bill raising bouts performed by G. *vipio* (1982). Of the small percentage which included mutual participation, even fewer resulted in a copulatory attempt. (5.3% of all observed bouts in G. *antigone* (1982) and 2.4% of all observed bouts in G. *vipio* (1982) initiated a copulatory attempt.) Besides mutual participation, bill raising bouts which preceded copulatory attempts consisted of significantly more (2-tailed-P = .01) bill raises per bout (Figure 2).

Figure 2. Comparison of the number of bill raises per bout during precopulatory and non-precopulatory bill raising bouts. Bill raising bouts which precede copulatory attempts consist of significantly more bill raises per bout.

YEAR	SPECIES	SITUATION	X BILL RAISES PER BOUT
1982	G. *antigone*	precopulatory	10
1982	G. *antigone*	non-precopulatory	4
1982	G. *vipio*	precopulatory	6
1982	G. *vipio*	non-precopulatory	2
1983	G. *antigone*	precopulatory	13
1983	G. *antigone*	non-precopulatory	3

While mutual bill raising is an observable sign of increasing receptivity, there are also signs of insufficient levels of receptivity to initiated reproductive behavior. An obvious sign of non-receptivity is the non-mutual performance of the bill raising. Non-mutual performance was the case for 81.5% of the bill raising bouts performed by G. *antigone* (1982) and for 89.0% of the bouts performed by G. *vipio* (1982). In cases of non-mutual performance, the initiator (male or female) of the bill raising bout began. (As an additional note, copulatory sequences initiated in the absence of mutual bill raising were observed to be incomplete and unsuccessful.) Another indicator of non-mutual receptivity to initiated reproductive behavior was the performance of copulation-terminating behaviors, such as feeding, preening, and other maintenance behaviors, during an otherwise appropriate copulatory sequence (Figure 3). A final indicator, which was not common, but which terminated one copulatory attempt in 1983, was intrapair aggression.

Figure 3. According to work conducted on the Red-Crowned Crane, Grus *japonensis, the copulatory sequence consists of eight behavioral phases, deviating from which may or may not prevent successful copulation (Masatomi and Kitigawa 1975). The eight phases are listed in this figure.*

1. bill raising by the male and the female
2. convergence of the male and the female
3. positioning of the male behind the female
4. wing spread by the female
5. mount by the male
6. inclining body by female and balancing by the male
7. copulation
8. dismount

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Thus intrapair compatability and mutual receptivity to initiated reproductive behavior play an important role in the successful completion of the reproductive cycle. While the resolution of intrapair conflicts relies on the Cranes involved, the final two categories (interpair conflicts and human interaction) are more directly the result of captivity and more easily remedied through applied management research.

INTERPAIR CONFLICTS: RESULTS AND DISCUSSION

Interpair conflicts, or agonistic behaviors, are those acts of fighting or escaping performed by an observed Crane(s) and a Crane(s) in an adjacent (chain-link-fence-segregated) enclosure. Agonistic behaviors may be relevant (adornment, arching, bowing, attacking, alerting, escaping) or irrelevant (ground sticking, back preening, leg preening, crouching, wing opening, head shaking) [Masatomi and Kitigawa, 1975]. While the precise message conveyed by these behaviors is not agreed upon [Van Rhijn, 1980], the fact that a message was conveyed, and that the Crane pairs in adjacent yards were interacting, was the point of this investigation.

Figure 4. Total observed frequencies of interpair agonistic behaviors in G. antigone *and* G. vipio. *Data selected from 1982 and 1983.*

YEAR	YARD	SPECIES	MINUTES OF OBSER-VATION	SUB-TOTAL RELEVANT AGONISTIC BEHAVIOR	SUB-TOTAL IRRELEVANT AGNOSTIC BEHAVIOR	TOTAL INTERPAIR AGNOSTIC BEHAVIOR
1982	14	G. *vipio*	1,000	113	249	362
1982	12	G. *vipio*	1,000	293	341	634
1983	7	G. *antigone*	2,700	632	317	949
1983	9	G. *antigone*	2,700	669	524	1193
1982	13	G. *antigone*	1,000	477	755	1232
1982	7	G. *antigone*	1,000	1327	334	1661
1982	9	G. *antigone*	1,000	1039	1289	2328
1983	13	G. *antigone*	2,700	1402	1307	2709
1982	19	G. *antigone*	1,000	2401	817	3218
1983	19	G. *antigone*	2,700	4205	1031	5236

The total observed frequencies of agonistic behavior differed from pair to pair and from year to year within the same pair (Figure 4). The factors which influenced the total amount of interpair behavior were numerous. While many of these factors may be observed in non-captive Cranes [personal communication, Dr. J. Barrow, Hiram College], the state of captivity of the study group may have greatly enhanced the observability of these factors. Important factors in captive collections, species juxtaposition and individual disposition, influence the total observed frequency of agonistic behavior. While many individual differences in aggressive tendencies were observable within a given species, differences were also observable between species. However, individual dispositions to react aggressively or provoke aggression in various situations were the more observable of the two. An individual's tendency (regardless of species) to provoke or react to agonistic behavior was probably most influenced by individual yard designs. The location of feeders, waterers, marsh areas, and nest sites determined the amount of time adjacent Crane pairs spend in close proximity to one another. Due to the nature of the inter-yard barriers, which provided little or no visual isolation, the amount of time adjacent Crane pairs spent in close proximity determined the potential amount of time during which interpair conflicts could occur.

The effects of interpair conflicts were both observable and non-observable. One of the observable effects was the reduction in total yard use, and the concentration of yard use along interpair fence barriers. An observably detrimental effect of interpair conflict was the termination of initiated copulatory sequences. The pursuit of interpair agonistic behaviors, during reproductive behavior, terminated 6 (16.2%) of the total observed copulatory attempts. However, the most interruptive, non-observable quality of interpair conflicts was their ability to reduce the likelihood of subsequent reproductive behavior. Data (from the 1983 study) suggested that a buffer period of at least eight minutes ($x = 8$, Range = 1 − 15+, and a 12+ minute buffer period was observed between a bout of interpair aggression and a successful copulation) was necessary to bridge interpair aggression and intrapair reproductive behavior. If this is the case, then 82.78% ($x =$ 82.78%, Range = 63.20% − 94.70%) of the total observed time was not conducive to reproductive behavior (these percentages omit incubation periods, during which copulatory behavior was not likely to occur and for the finite, twenty-five minute scan period).

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Thus, without the aid of natural plantings which provide dense growth in the spring breeding season or visually isolating fences, the aggressive interaction between adjacent Crane pairs may greatly reduce the amount of time during which copulatory attempts may occur, as well as terminating ongoing reproductive behavior.

HUMAN INTERACTION: RESULTS AND DISCUSSION

Human sources of interaction and disruption of ongoing behaviors consisted of vehicles and pedestrians, utilizing the road parallel to the Crane yard complex. The total number of vehicles, as well as the number of vehicles per scan period differed from year to year(Figure 5), but were ever present as the road provides access to and from areas used by animal keepers, maintenance workers, researchers and residents (Figure 6). Although more vehicles passed the Crane yards during operating hours (0730 - 1600), the observation periods selected for the study were predetermined periods, during which reproductive behavior was likely to occur.

Figure 5. Chart of total number of human interactions (vehicles and pedestrians) and the number of human interactions per scan (25 min.). Data selected from 1981, 1982 and 1983.

YEAR	TOTAL NUMBER OF SCANS	TOTAL HUMAN INTERACTIONS	HUMAN INTERACTIONS PER SCAN
1981	250	322	1.29
1982	240	275	1.10
1983	432	961	2.22

Figure 6. During the 1983 study, 961 human interactions were recorded. The following chart shows to whom the listed percentages of interactions are attributable.

SOURCE	% OF INTERACTIONS ATTRIBUTABLE
CRC Maintenance and Farm Crews	18.42%
Bird Keepers	16.96%
Mountain Residents	12.48%
Mammal Keepers	10.20%
Fence Construction	9.05%
Pere David Deer Research at Rivinus Barn	7.18%
White-tailed Deer Research	6.04%
Radio Tracking Research	4.06%
Misc. Pedestrians	3.02%
Warbler Research	1.98%
Unidentified Vehicles (most probably associated with the fence construction project)	10.61%

Although many of the effects of human interactions were discernible only through data analysis, many were easily observable. A common effect of human interaction was the termination of ongoing behaviors. These behaviors were usually routine maintenance activities, but were occasionally event behaviors such as bill raising and copulatory attempts (Figure 7). The inobvious effect of human interactions, was their ability to reduce the likelihood of subsequent copulatory attempts. Data (1983) suggests

Figure 7. Comparative interruption of activity of the Indian Sarus Crane, G. antigone and the White-Naped Crane, G. vipio by vehicles and pedestrians. Data selected from 1981, 1982 and 1983. (Only Indian Sarus Cranes were observed in 1983.)

	1981	1982	1983
Total Observation Time in Minutes	6250	6000	10800
Total Interruptions	322	275	961
Interruption Yields No Observable Response	82	34	351
Interruption Yields Response Rest Alert	205	171	438
Interruption Yields Response Locomote	61	40	105
Interruption Yields Response Guard Call	4	1	0
Interruption Yields Response Unison Call	5	3	26
Dancing Interrupted and Terminated	5	8	0
Dancing Interrupted and Resumed	1	4	0
Bill Raising Interrupted and Terminated	15	11	32
Bill Raising Interrupted and Resumed	2	2	7
Copulation Interrupted and Terminated	2	1	1
Copulation Terminated and Resumed	0	0	0
Total Observed Bouts of Bill Raising	473	619	605
% Interruption of Bill Raising	3.6	2.1	5.3
Total Observed Copulations	19	10	8
% Interruption of Copulation	10.5	10.0	12.5

Masatomi and Kitigawa, "Bionomics and Sociology of Tancho, or the Japanese Crane, Grus *japonensis*, II. Ethogram." *Jour. Fac. Sci.* Hokkaido Univ. Ser. VI, Zool. 19(4), 1975.

Van Rhijn, Johan, "Communication by agonistic displays: a discussion." *Behavior* (74), 1980.

that a buffer period of at least ten minutes (x = 10, Range = 4 – 25+, and a buffer period of at least 12 minutes was observed between a human interaction and a successful copulation) was necessary to bridge disturbances caused by human interaction and subsequent copulatory attempts.

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If this is the case, then 46.45% ($\bar{x}$ = 46.45%, Range = 41, 40% – 51.80%) of the total observed time was not conducive to reproductive behavior (these percentages account for omitted incubation periods, during which copulatory behavior was not likely, and for the finite, twenty-five minute scan period).

Thus, without limiting the use of adjacent roadways or creating alternate routes of passage for their travelers, human interaction may greatly reduce the amount of time during which a copulatory attempt may be made, as well as interrupt ongoing maintenance, bill raising, and copulatory behaviors.

CONCLUSION

In viewing the disruptive influences of intrapair inhibitors, interpair conflicts, and human interaction, it is evident that there is much overlap, especially in the data dealing with the reduction of the likelihood of subsequent copulatory behavior. The point to be made is that all animals have crucial periods in their reproductive cycles when they are most likely to reproduce successfully and that Cranes are not an exception. Therefore, each interruption reduces the time during which a copulatory ATTEMPT can be made. It is important to note that every copulation is an ATTEMPT to reproduce successfully. A number of successful copulations may be necessary to insure successful reproduction.

As all of the categories of reproductive interference affect the behavioral components, it is difficult to correlate them to the physiological factors which determine egg fertility. Odds against successful reproduction, in captivity, are numerous: arbitrarily bounded territories, restricted movement, disturbances from humans and other animals, aviculturist-determined pairings, unnatural climatic conditions, artificial diets, etc. Every time a captive animal reproduces successfully in captivity, it beats the odds against successful reproduction, stacked by captive situations. Breeders who experience true breeding success are those who have evaluated those captive situations which reduce the likelihood of successful reproduction, and have taken steps to insure that the odds against successful reproduction, faced by their captive animals, are more equal to those in the wild.