Zoo Biology 10:53–63 (1991)

Flamingo Breeding:
The Role of Group Displays

Elizabeth Franke Stevens

National Zoological Park, Washington, D.C.

Group displays in flamingos have been presumed to play a role in stimulating synchronous nesting and in facilitating pair formation. This study compares the group displays and breeding success of a captive flock of Caribbean flamingos *(Phoenicopterus ruber ruber)* at the National Zoological Park between 2 years: the frequency and synchrony of group displays were measured for a flock of 17 in 1988 and then again in 1989 after flock size was increased to 21. In 1989 the rate of occurrence of display activity increased 48%, the synchrony of group displays increased 100%, the frequency of mounts and copulations almost doubled, and for the first time in the flock's history two fertile eggs were produced. The use of sprinklers to simulate rain had no effect on the group displays. The amount of naturally occurring rainfall in 1989 was almost twice that in 1988. The increased frequency and synchrony of group displays could be attributed to increased flock size, change in sex ratio, addition of strange individuals, or increased rainfall. This study, however, provides evidence for a relationship between behavioral stimulation from group displays and components of breeding success in flamingos.

Key words: behavioral stimulation, flock size

INTRODUCTION

Flamingos are among the most social of birds. They are commonly found in very large flocks, which during the breeding season of lesser flamingos can number over 1 million birds. Flamingos seldom breed in flocks smaller than ten pairs [Campbell and Lack, 1985]. Given this propensity to live in flocks of such extraordinary size, it is surprising they breed in captivity at all. Of the 49 captive flocks of Caribbean flamingos *(Phoenicopterus ruber ruber)* listed in the *ISIS Summary for Birds,* only 13 (27%) flocks had successfully produced chicks in the period from 1983 through 1988, and only two (15%) of these successful flocks consisted of 20

Received for publication May 1, 1990; revision accepted August 14, 1990.

Address reprint requests to Dr. Elizabeth Franke Stevens, Conservation and Research Department, Zoo Atlanta, 800 Cherokee Ave., S.E., Atlanta, GA 30315.

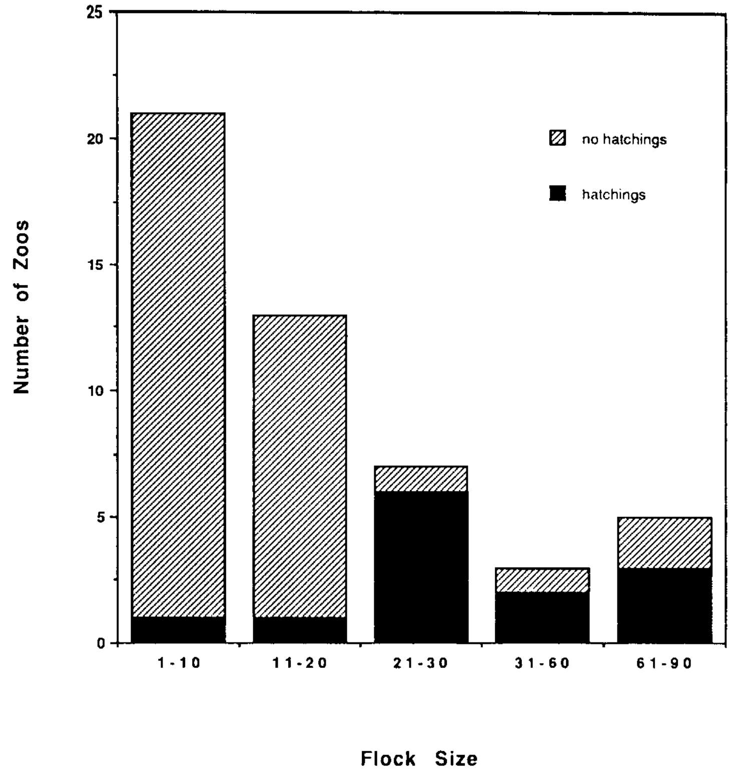


Fig. 1. Flock size and reproductive success. The breakdown of the 49 zoos in the ISIS Bird Summary holding Caribbean flamingos according to flock size and success in producing flamingo chicks from 1983–1988.

individuals or fewer (Fig. 1). Flocks with more than 20 flamingos had a significantly greater chance of successful breeding ($\chi^2 = 20.96$, df $= 1$, $P < 0.001$).

Wild flamingos are adapted to breeding in unpredictable environments with seasonal rains; they are found in salt lakes and brackish coastal lagoons. Factors which initiate breeding are unknown, yet suitable environmental conditions appear to be necessary. At all known nesting sites flamingos breed only if there has been sufficient rainfall [Ogilve and Ogilve, 1986]. Rainfall is considered essential for two reasons: it provides the right conditions for building their mud nests and for the rapid proliferation of their small food items (crustaceans, algae, and unicellular organisms).

Flamingos perform highly ritualized group displays before breeding. Although these displays can occur year-round, their frequency increases dramatically during the breeding season [Studer-Thiersch, 1974] when they appear to stimulate synchronous nesting and to facilitate pair formation [Studer-Thiersch, 1974; Ogilve and Ogilve, 1986]. Large flock size presumably serves to enhance the excitatory effects of group displays.

Group displays have been described in detail [Kear and Duplaix-Hall, 1975; Studer-Thiersch, 1974], yet there has been no attempt to quantify the occurrence of group displays, and no studies have determined the relationship between display behavior and breeding success. The objective of this study was to determine whether an increase in flock size influences group displays and whether group display activity correlates with breeding success. Because rainfall appears to be an important stimulator for breeding behavior, this study also investigated whether "rain" sprinklers could be used to induce group displays.

METHODS

The Study Flock

This study examined the display behavior of a flock of Caribbean flamingos at the National Zoological Park (NZP) in Washington, D.C. This flock had constructed nests, but had only produced one infertile egg in 8 years; the lack of success was presumed to be a consequence of the small flock size. There were 17 flamingos in the flock from 1980 to 1988. Five months prior to the 1989 breeding season flock size was increased by 24%, by adding four young adult captive-bred females. The addition of these four birds balanced the sex ratio (from 10:7 in 1988 to 10:11 in 1989). Throughout this study all of the flamingos were adults; four birds were age 3 to 5 years and the rest ranged in age from 11 to 25 years. All flamingos were sexed by laparotomy and individually marked with high-visibility bands, males on the right leg and females on the left.

The flock was housed in an outdoor exhibit (approx. 14,000 sq. ft.) containing a pool (approx. 3,000 sq. ft.) and a nesting island (approx. 1,000 sq. ft.) which was kept constantly moist. The diet of the flock did not change during the 2 years of this study. The pool was 3 feet deep at its deepest point. The soil on the nesting island was a mixture of topsoil and peat and was loosened and tilled prior to the breeding season (early March) each year. At this time, a net was also erected to exclude the flock from the large grassy area in the exhibit in order to concentrate their activities in the breeding pool. Rain sprinklers consisted of shower heads directed at the central third of the breeding pool. During the study period, these rain sprinklers were activated for 1 to 2 hours at different times each day, except on rainy days.

The Group Displays

The group display of the Caribbean flamingo comprises five ritualized displays: Head-Flag (HF), Wing-Salute (WS), Inverted Wing-Salute (IWS), Twist Preen (TP), and Wing-Leg Stretch (WLS) [see Studer-Thiersch, 1975b; Ogilve and Ogilve, 1986]. This study further distinguished the HF with vocalizations from HF without vocalizations (HF vs. HF + V); thus a total of six displays was recorded.

Observations

To test whether the lack of breeding success was due to insufficient behavioral stimulation, the frequency and intensity of group displays in the flock were examined during the breeding season in 1988 and then again in 1989 after the four birds were added to the flock. Observations were conducted from 0700 to 1900 on April 11 through May 27, 1988, and from 0800 to 1700 on April 18 through May 27, 1989, for a total of 541 hours of observation in 1988 and 364 hours of observation in 1989. Observations occurred in all weather conditions except thunderstorms. The observation time was shortened in 1989 for security reasons.

The observer, equipped with binoculars, checksheet, and a watch sat in front of the exhibit, approximately 10–20 meters from the birds, and sampled the flock during the first 30 seconds of every minute. For each sample, the observer recorded whether or not each display occurred (one–zero sampling [Altmann, 1974]) and the number of flamingos performing each of the six displays. If, for example, four birds were observed to perform both HF and WS during one sampling period, then both displays were given a score of 4. Because all of the displays are conspicuous and unambiguous, and because there were rarely more than three displays performed during one sampling period, the task of recording the number of flamingos performing each display presented no difficulties. In addition, the observer recorded all occurrences of copulations and attempted mounts during the entire observation period, and noted the band numbers of the pair involved. The observer also recorded the times the rain sprinkler was on.

The observers were FONZ (Friends of the National Zoo) volunteers who were experienced in behavioral methodology. They received additional training specific to this study. The same observers participated in the study during both years. During the first week in 1988, I recorded data alongside the observers to ensure that they adhered to the correct methodology. The criterion for inter-observer reliability was 85% agreement over 20-minute sample periods.

Data Summary

The data for each hour of observation were summarized into four measures of display activity: 1) the *frequency of each display:* the number of samples, out of a total of 60 per hour, during which a given display occurred; 2) the *frequency of display activity:* the number of samples during which at least one display occurred. For example, a score of 21 indicated that out of the 60 samples that hour, one or more displays occurred during 21 of those samples; 3) the *synchrony of each display:* the sum of the number of birds recorded to perform a given display divided by the number of samples in that hour during which that display was performed; and 4) the *greatest synchrony of all group displays:* the greatest number of display performances recorded in one sample for that hour (the number of birds performing each display summed over all displays). The score could be a number greater than the number of birds in the flock because one bird could perform more than one display during the sampling period. A score of 15 indicated that during that hour, the greatest synchronous group display activity in one sample consisted of 15 display performances.

RESULTS

Frequency of Each Display

Figure 2 presents the mean number of samples per hour during which each display was observed in 1988 and in 1989. In 1988 WS was observed in significantly more samples than any of the other displays (ANOVA, $F=39.58$, $df=5$, $P<0.0001$; Newman/Keul's range test, $P=0.05$). HF, HF+V, and TP occurred with equal frequency, but significantly more frequently than IWS and WLS ($P=0.05$, Newman/Keul's range test). In 1989, HF, HF+V, and WS were observed with equal frequency and significantly more often than the other three displays (ANOVA, $F=17.97$, $df=5$, $P<0.0001$; Newman/Keul's range test, $P=0.05$). Each display, except for WS and TP, was observed with a significantly higher frequency in 1989 than in 1988 (Fig. 2).

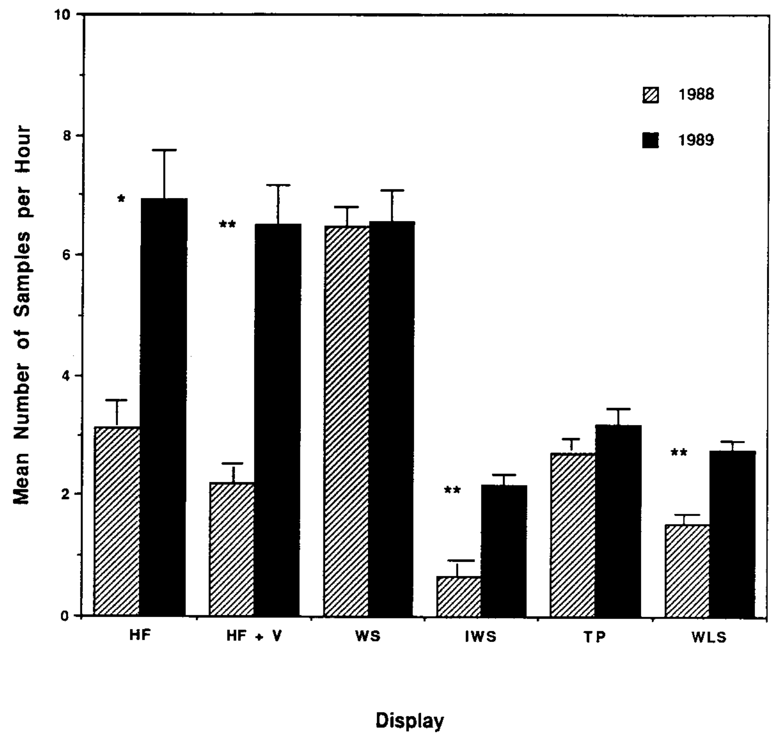


Fig. 2. Mean frequency per hour of each display in 1988 and 1989: the mean number of samples per hour during which each display was observed. HF = Head-Flagging, HF + V = Head-Flagging With Vocalizations, WS = Wing-Salute, IW = Inverted Wing-Salute, TP = Twist-Preen, WL = Wing-Leg Stretch. $*P = 0.0002$, t-test, $n_1 = 47$, $n_2 = 41$. $**P = 0.00$, t-test, $n_1 = 47$, $n_2 = 41$.

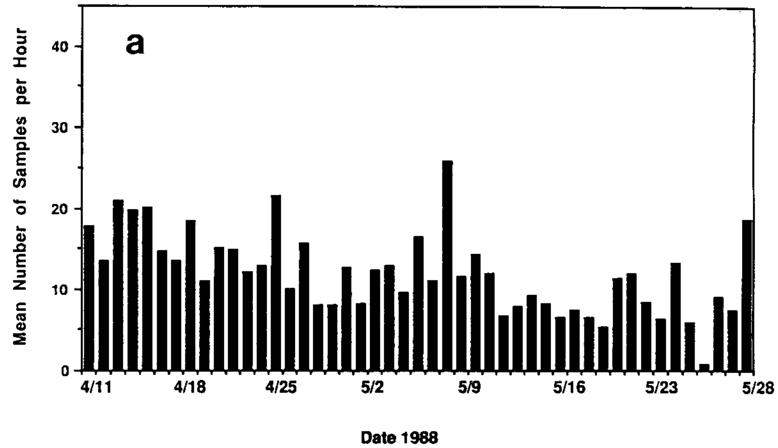
Frequency of Display Activity

Figures 3a and b depict the mean rate of occurrence (frequency per hour) of group displays for each day in both the 1988 and 1989 breeding seasons. Figure 4 shows the mean frequency of group displays by hour of the day in 1988 and 1989.

The mean hourly rate of group displays in 1988 (Fig. 3a) decreased significantly across the 47 days of the study. The rate of group displays in 1989 (Fig. 3b) did not, however, change with time.

The rate of displays in 1988 was not evenly distributed across time of day (Fig. 4; ANOVA, $F = 3.50$, $df = 11$, $P < 0.0001$). Group displays occurred significantly more often between 1700 and 1900 (Newman/Keul's Range test, $P = 0.05$). In 1989, however, there was no significant difference between any of the means for hours of the day (ANOVA, $F = 1.82$, $df = 8$, $P = 0.07$). An analysis of the 1988 data for the same hours sampled during 1989 (0800 to 1700) revealed results similar to those for 1989: there was no effect of time on the frequency of display activity (ANOVA, $F = 1.61$, $df = 8$, $P = 0.12$).

The overall mean frequency ($\pm$ S.E.) of group displays per hour was 12.0 ± 0.74 in 1988 and 17.8 ± 1.21 in 1989. When the mean frequency of group displays per hour was examined by using a student t-test, the mean frequency was significantly greater in 1989 ($t = -4.07$, $P = 0.0001$).



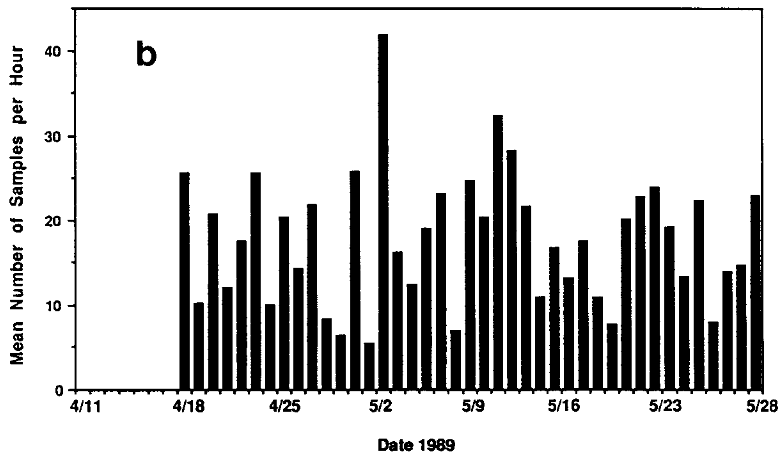


Fig. 3. **a:** Mean frequency per hour of group displays for each day in 1988: the mean number of samples per hour during which at least one group display was observed. The mean frequency per hour decreased significantly across the 47 days of the study period ($R^2 = 0.424$, $n = 47$, $P < 0.01$). **b:** Mean frequency per hour of group displays for each day in 1989: the mean number of samples per hour during which at least one group display was observed. The mean frequency per hour did not show a significant increase or decrease across the 41 days of the study period ($R^2 = 0.002$, $n = 41$, NS).

Synchrony of Each Display

The mean number of synchronous performances of each display per hour in 1988 and 1989 is shown in Figure 5. Every display, except for TP, had a significantly greater number of synchronous performances in 1989 than in 1988 (see Fig. 5).

Greatest Synchrony of All Group Displays

The greatest synchrony of all group displays for 1988 was 19 and this occurred during just 1 hour (out of 541 hours). There were only 12 hours (2% of observation

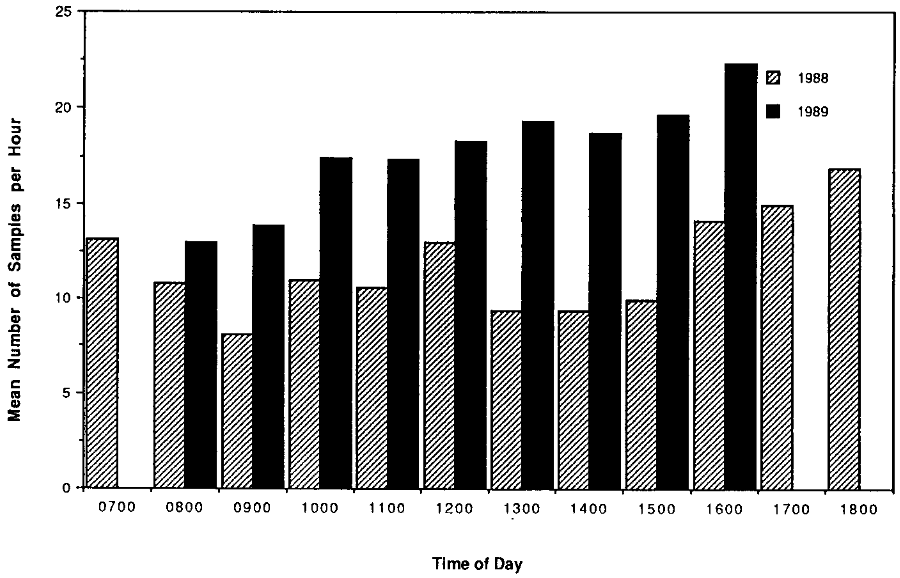


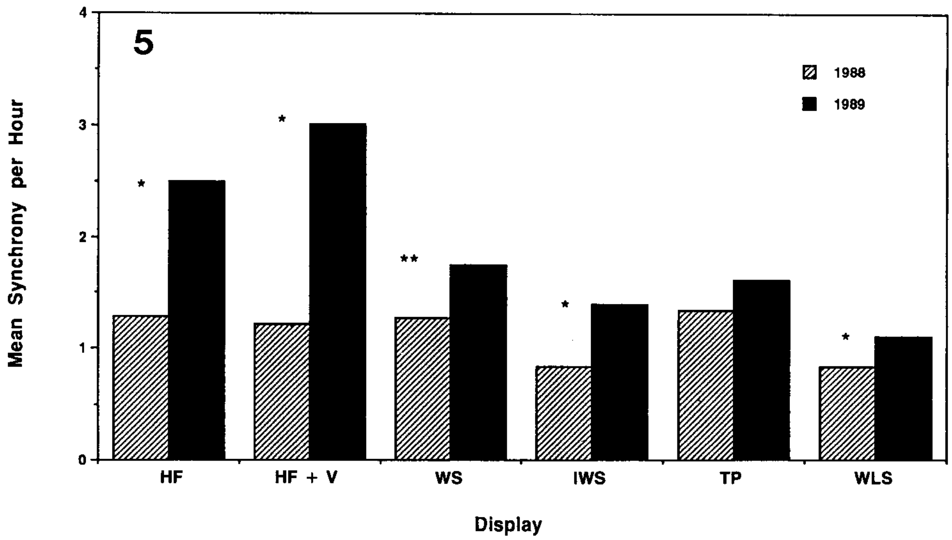
Fig. 4. Mean frequency per hour of group displays by time of day in 1988 and 1989: the mean number of samples per hour during which at least one group display was observed. For both years, between 0800 and 1700, the frequency of group displays was random with respect to time of day (see text).

hours) during which greater than ten displays were performed simultaneously. In contrast, in 1989, the greatest synchrony of all group displays was 27; there were 94 hours (26% of the 364 observation hours) during which greater than ten displays were performed simultaneously, and 44 hours (12% of the observation hours) during which greater than 14 displays were performed simultaneously. The mean for the greatest synchrony of group displays was significantly higher in 1989 than in 1988 ($t = 12.29$, $P = 0.000$, t-test, $n_1 = 541$, $n_2 = 364$; the mean for 1988 was 3.4 ± 0.11; the mean for 1989 was 7.4 ± 0.31).

The greatest synchrony per day is a measure of the *highest* degree of synchrony achieved per day; that is, it is the highest score for greatest synchrony of all group displays for each day. The mean of the greatest synchrony per day was twice as high in 1989 vs. 1988: 15.8 ± 0.31 in 1989 vs. 7.8 ± 0.53 in 1988 (Fig. 6; $t = -7.26$, $P = 0.000$, t-test, $n_1 = 47$, $n_2 = 41$).

The Effect of Rain Sprinklers on Group Displays

To analyze the effect of rain sprinklers on frequency of display activity, the frequency of display activity during the hour prior to the rain sprinkler was compared with the frequency of display activity both during the hour(s) of the rain sprinkler and during the hour following the rain sprinkler (Table 1). Although the frequencies were slightly higher in the hours both during and after the sprinkler, chi-square tests showed that the rain sprinkler had no significant effect on the frequency of group displays either during the hour(s) the rain sprinkler was on, or during the hour after the rain sprinkler (see Table 1).



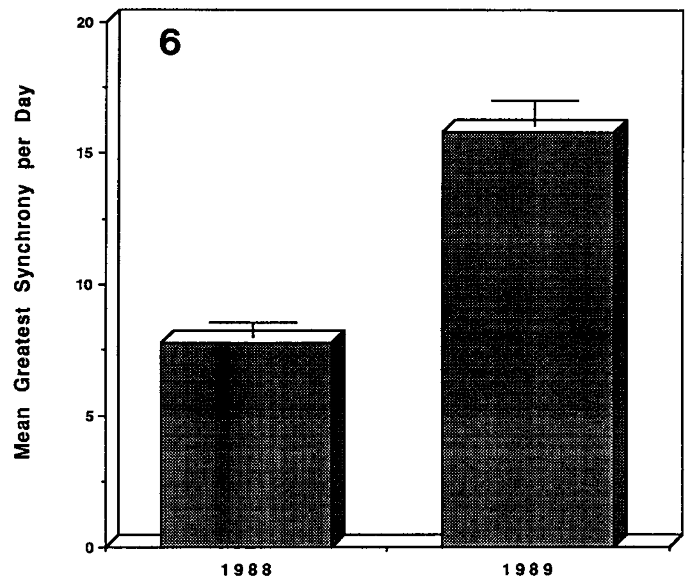


Fig. 5. Mean number of synchronous performances of each display per hour in 1988 and 1989. HF = Head-Flagging, HF + V = Head-Flagging With Vocalizations, WS = Wing-Salute, IWS = Inverted Wing-Salute, TP = Twist-Preen, WL = Wing-Leg Stretch. $*P=0.000$, t-test, $n_1=47$, $n_2=41$. $**P=0.003$, t-test, $n_1=47$, $n_2=41$.

Fig. 6. Mean greatest synchrony of group displays in 1988 and 1989: the mean of the greatest synchrony for each day. $P=0.000$, t-test, $n_1=47$, $n_2=41$.

Frequency of Mounts and Copulations

Mounts and copulations were combined for this analysis as it was sometimes difficult to distinguish between the two. There were significantly more mounts and copulations per day in 1989 than in 1988 ($t=-3.72$, $P=0.0004$, t-test). There were

TABLE 1. The effect of the rain sprinkler on the frequency of group displays: a) before vs. during the hour(s) the rain sprinkler was on, and b) before vs. the hour after the rain sprinkler was on in 1988 and 1989

	1988[a]		1989[b]	
	Frequency increased	Frequency decreased	Frequency increased	Frequency decreased
a) Before vs. During	19	13	11	8
b) Before vs. After	14	15	11	8

[a]1988 a) $\chi^2=1.13$, df=1, $P>0.20$; b) $\chi^2=0.03$, df=1, $P>0.90$.
[b]1989 a) $\chi^2=0.48$, df=1, $P>0.50$; b) $\chi^2=0.03$, df=1, $P>0.50$.

127 total mounts and copulations in 1988 with a mean daily frequency of 2.7 ± 0.4. In 1989, there were 236 total mounts and copulations with a mean daily frequency of 5.5 ± 0.6.

For 16% of the mounts and copulations in 1988, and 22% in 1989, the identity of the birds participating could not be ascertained. (Bands were under water or there was too much activity by other birds in the same area.) There were six pairs and one trio identified in 1988; the trio comprised two males and one female. (This female was the only one to produce an egg in 1988 and her nest was tended by both males). In 1989 there were nine pairs observed during mounts and copulations; only four of these pairs were also identified as pairs in 1988. The other five pairs were new combinations of birds. Only one of the four new females was observed to copulate.

Production of Eggs

In 1988 one egg was laid on May 10, but it never hatched and was determined to be infertile. In 1989 two females laid eggs, on June 6 and June 8; both eggs were determined to be fertile by candling (Tomassoni, pers. comm.), but were destroyed by crows after 25 and 13 days of incubation, respectively. The female who laid the egg in 1988 also laid an egg in 1989. None of the newly acquired females laid an egg during the 1989 season.

DISCUSSION

Both the rate of occurrence of displays and the synchrony of displays were significantly higher in 1989, when the flock size was larger, than in 1988. Concomitantly, in 1989, there were more components of breeding than in 1988: there was a significantly higher frequency of mounts and copulations, and for the first time in the flock's history two fertile eggs were produced.

Not only were the overall frequency and the overall synchrony of group displays significantly greater in 1989 than in 1988, but the majority of each of the six displays was performed with higher frequency (four of six displays) and synchrony (five of six displays). Furthermore, whereas group display frequency showed a significant decrease over the study period in 1988, the overall frequency of group displays was maintained at its significantly higher level throughout the 1989 study period.

The cause of the increased rates and synchrony of behavior in 1989 is not completely clear. The increase in flock size (from 17 to 21) could account for greater display activity; however, three other variables could have played a role: 1) rainfall, which could not be controlled; 2) the more balanced sex ratio, which resulted from the addition of four females to the flock; or 3) the presence of strange individuals in the flock (aside from any effects of group size), individuals who also came from an experienced breeding flock. Rainfall was significantly greater in 1989 than in 1988. During the months March, April, and May, there were 15.6 inches of rainfall in 1989 and only 8.8 inches in 1988. As rainfall is an important environmental cue for reproduction in Caribbean flamingos [Ogilve and Ogilve, 1986], the observed increase in group display activity might have resulted from increased rainfall alone. The present study cannot separate effects of rainfall, sex ratio, introduction of strange individuals, and group size.

The increase in group display activity was greater than the 24% increase in flock size. The mean rate of displays per hour increased 48% in 1989 and the mean greatest synchrony increased 100%. Likewise, the frequency of mounts and copulations in 1989 almost doubled, yet the birds involved in almost all mounts and copulations were the original members of the flock. Of the new flamingos, only one was observed to copulate. Thus, the new birds were not solely responsible for either the increase in display activity or the increase in mounts and copulations.

Other authors have suggested that rain (both natural and artificially generated) stimulates displays [Duplaix-Hall and Kear, 1975; Michael and Pichner, 1989] and that flooding stimulates nesting [Brown et al., 1983]. Although the use of rain sprinklers in this study did not reliably increase display activity in the flock of flamingos at NZP, it is possible that the sprinklers did not "rain" over enough of the exhibit or for a long enough period to have an effect. Perhaps flooding the nesting area and using rain sprinklers could be employed simultaneously to achieve the greatest effect. Clearly, more systematic research is needed to determine exactly which environmental and social factors stimulate group displays and reproduction.

Flamingos in captivity lack an important stimulus which natural flocks experience [Allen, 1956]: the stimulus of thousands of other displaying birds around them. It has been presumed that large flock size on the breeding grounds serves to enhance the function of the group displays: to facilitate pair formation and to stimulate nesting and breeding. This study is the first to show a quantitative relationship between group displays and breeding behavior. The results suggest a positive correlation between the behavioral stimulation provided by the increased frequency and synchrony of the group displays and the occurrence of reproductive behavior: mounts and copulations. The challenge remains to identify the causal relations involved.

ACKNOWLEDGMENTS

This study would not have been possible without the assistance of the FONZ (Friends of the National Zoo) Flamingo Watchers and their organizer, Joanne Grumm. I am grateful to Earl Pinkney, Bryon Shipley, and Linda Moore for their help with the flamingo exhibit and to Charles Pickett for his support in the logistics of the project. Pat Teleska and Debbie Seymour provided hours of assistance with data summary. B. Beck, S. Derrickson, D. Forthman, T. Maple, E. Morton, J. Ogden, L. Perkins, C. Pickett, C. Schmidt, P. Shannon, and R.H. Wiley generously provided thoughtful comments to the manuscript.

REFERENCES

Allen, R.P. The flamingos: their life history and survival. RESEARCH REPORT NO. 5, NATIONAL AUDOBON SOCIETY, 1956.

Altmann, J. Observational study of behaviour: sampling methods. BEHAVIOUR 49:227–267, 1974.

Brown, S.G.; Shannon, P.; Farnell, G. Renesting and Brooding in the Caribbean Flamingo. ZOO BIOLOGY 2:137–141, 1983.

Campbell, B.; Lack, E. A DICTIONARY OF BIRDS. Vermillion, Buteo Books, p. 219, 1985.

Duplaix-Hall, N. and Kear, J. Breeding Requirements in Captivity. Pp. 131–141 in FLAMINGOS. J. Kear; N. Duplaix-Hall, eds., Hertfordshire, England, T. & A.D. Poyser Limited, 1975.

Kear, J.; Duplaix-Hall, N., eds. FLAMINGOS. Hertfordshire, England, T. & A.D. Poyser Limited, 1975.

Michael, G. and Pichner, J. The pink phoenix. MINNESOTA ZOO MAGAZINE Jan/Feb, pp. 6–7, 1989.

Ogilve, M.A.; Ogilve. FLAMINGOS. Great Britain, Alan Sutton Publishing Limited, 1986.

Studer-Thiersch, A. Die Balz der Flamingogattung *Phoenicopteruus,* unter besonderer Beruecksichtigung von *Ph. ruber roseus.* ZEITSCHRIFT FUER TIERPSYCHOLOGIE 36:212–266, 1974.