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EFFECTS OF EXTENDED PHOTOPERIOD ON SANDHILL CRANE REPRODUCTION

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Abstract: Photoperiod studies were conducted with greater sandhill cranes (*Grus canadensis tabida*) from 1969 to 1972 and from 1982 to 1987 at the Patuxent Wildlife Research Center, Maryland. When housed indoors and exposed to long photoperiods, males produced semen during winter. When exposed to artificially extended photoperiods during spring in outdoor pens, females apparently laid earlier in the year and laid more eggs than they would have without the added light. Cranes did not exhibit any signs of photorefractory response to extended photoperiods.

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Rowan first experimentally linked the length of day with reproductive control in birds in a series of studies from 1925 to 1931 (Marshall 1961). In studies since then, every North Temperate Zone bird species tested, and some from equatorial regions, have exhibited photoperiod-influenced reproduction (Immelmann 1971). However, factors other than daylength, such as rainfall, nesting materials and presence of a mate, have also been shown to influence reproduction (Wingfield 1983).

These factors (including photoperiod) can be classified according to whether they start to act early in the reproductive cycle (proximate) or just before the birds lay (ultimate). Ultimate factors (food supply, nesting conditions, competition, predator pressure and inclement weather) can induce or abort the reproductive effort (Immelmann 1971; Wingfield 1983; Deviche 1983; Farner 1986). However, the proximate factors must first physiologically and behaviorally condition the birds if the ultimate factors are to have an effect. Proximate factors act by entraining and strengthening a bird's own endogenous rhythms (Nalbandov 1958; Wada 1983; Scanes et al. 1983). Light is the most effective and universal proximate factor in North Temperate Zone birds (Farner 1986).

In this study we attempted to determine if the greater sandhill crane is a photosensitive species, if they exhibit a photorefractory period and if extended photoperiod can be an effective reproductive stimulant in outdoor pens.

MATERIALS AND METHODS

Three experiments were conducted, (1) spring exposure, (2) winter exposure, and (3) repeated spring exposures to extended photoperiods. Birds received a pelleted diet from gravity flow feeders and water from "van es" type continuous flow waterers (open pans in Experiment 2) ad libitum. Resulting semen volume, egg production and date of first egg were recorded. Birds were manipulated for semen collection and insemination, and live-dead semen smears were made and morphological studies completed to determine semen quality per Gee & Temple (1978). Eggs were removed as laid in the first experiment, and after the second egg of the clutch in the third experiment.

Experiment 1 – Photorefractoriness in Cranes

Ten pairs of cranes that had been productive for 1 or more years were used, 5 pairs in 1969 and 5 in 1970. All were moved during winter (January and February) to 9.1 m^2 pens with established grass surfaces and equipped with clock-controlled incandescent lights (color rendering index [CRI] 90). The supplementary light had intensities of 40 or more lux the first year and 170 or more lux the second and third years. A solid canvas material covered the 2.4 m high, 7.6 cm hexagonal wire mesh fencing to separate the pairs from each other and from other visual disturbances. The birds were handled for semen collection and insemination 3 times per week. During the first 2 years, photoperiod was increased from 11 h (natural photoperiod) to 14 h (3 h of added morning incandescent light) in late February and progressively increased 3% per week to 24 h in late June. In the second year, 3 of 10 pairs were kept in constant light (24 h photoperiod) beginning in late February. In the third year, light was increased from 9.75 h (natural photoperiod) to 12.25 h (added morning light) in mid-January and increased 3% per week to 24 h per day in late June (Table 1). The added light program was discontinued in July. Egg production in lighted pens was compared to production by greater sandhills in other pens and to existing production records.

Experiment 2 – Photosensitivity

Six pairs were moved in September 1971 from lighted pens used in Experiment 1 to smaller pens (3.7 m^2) inside a windowless room maintained at 21°C. They received 10 weeks of short photoperiod (86 lux cool white fluorescent lamps, CRI 70, 6 h per day), followed by continuous light for the duration of the 6 month period. Four inches of crushed sugar cane litter were used as floor covering and small twigs and assorted weeds were provided for nesting material. Changes in physiological and behavioral condition (Gee & Temple 1978) and semen and egg production were measured to determine the effect of the light treatment. The birds were returned to their original pens in February.

Experiment 3 – Extended Photoperiod on Date of First Egg

Nine pairs were moved in fall from 12.2 m X 18.3 m unlighted pens to 9.1 m X 24.4 m lighted pens. Each pair was in visual contact with adjacent pairs but always separated from them by an empty pen or some greater distance. Above the 2.4 m Page Wire fencing, mercury high intensity discharge lamps Fluomeric[R], CRI 55[1], mounted at 3.7 m, delivered 170 lux or more throughout the pen. Photoperiod was increased from 10.75 h to 15.5 h in mid-February and increased 3% per week to 24 h per day in early June (Table 2). The added light was discontinued each season after the birds completed incubation and the procedure was repeated each spring for the next 4 years. Annual pen rotation was used to reduce parasitism; each pair was moved from the occupied pen to an adjacent pen 1 year and back again the next year. Only the onset of laying (date of first egg) was recorded because other important criteria (rate of laying, total egg production, and length of season) were disrupted by constraints imposed by other propagation objectives.

From 1983-1987, 21 pairs of Florida sandhill cranes (*G.c. pratensis*) were maintained as a control group in similar pens but without added light. Onset of laying was also recorded for birds in this group.

Mean onset of laying was compared among years with extended photoperiod using 2-way analysis of variance (ANOVA) with pairs of cranes as a blocking factor. For a subset of 5 greaters with established reproductive histories, mean onset of laying during years with and without added light were compared using 3-way ANOVA. Procedures appropriate for ANOVA with empty cells were used (SAS Type IV analysis)(SAS Institute 1985; Milliken & Johnson 1984) because some pairs did not lay every year. These tests do not provide unique results because of the imbalance in the data, but they do use all of the available data in a correct manner. Tukey's multiple comparisons were used to compare year means subsequent to ANOVA.

RESULTS AND DISCUSSION

Experiment 1 – Photorefractoriness

In this experiment, we wanted to demonstrate the presence or absence of a photorefractory period in the greater sandhill crane. The photorefractory response in photosensitive species causes termination of the breeding period (gonadal regression, unresponsiveness to stimulatory light periods). In nature, photorefractoriness insures adequate time for birds to raise chicks, molt and gain weight for migration (Lofts & Murton 1973).

In addition to the extended photoperiods in this study, 3 of the 10 pairs were exposed to 24 h light for an entire reproductive season. No signs of interruption in the reproductive cycle were noted, nor were any signs of photorefractory response to the extended photoperiods exhibited.

This study was not designed to determine the effect of extended photoperiod on egg production and uncontrolled factors may be confounded with the photoperiod manipulation. However, moving cranes (10 pairs) to lighted pens in late winter may have increased egg production (6.7 eggs per pair per year compared to 4.5 per year for the 6 of 10 pairs with comparable reproductive histories)(Table 3). A larger sample size and a control group would be needed to conclusively determine effects of increased photoperiod on egg production. We expected decreased egg production in

[1] *Fluormeric[R], self-ballasted mercury 450 watt lamps, Duro-test Corporation, 2321 Kennedy Blvd., N. Bergen, NJ 07407. Mention of commercial items does not constitute endorsement by the authors or by the U.S. Fish and Wildlife Service.*

these pairs due to disturbance from the move, the small pen size and handling stress. A new semen collection and insemination technique being developed concurrently in the lighted pens required extensive handling of the birds (Gee & Temple 1978).

In most North Temperate Zone birds, reproductive development (date of first egg and initiation of semen production) is accelerated by long photoperiods in late winter and early spring (Immelmann 1971). The rate of acceleration for a given stimulatory photoperiod is light-intensitydependent with the maximum response generally observed between 110 to 180 lux (Farner 1959). However, the effect of light has not been studied with most nondomestic birds, including cranes, and species react differently to light intensity. For example, eastern bobwhite (*Colinus virqinianus*) exposed to long photoperiods at intensities from 1 to 1100 lux lay eggs 31 to 33 days after exposure, but 17 days after exposure to 3200 lux (van Tienhoven & Planck 1973).

Experiment 2 – Photosensitivity

Males from 6 pairs of experienced breeders produced semen in winter, but the females failed to lay eggs (Table 4). The first male produced semen after 21 days of photostimulation and the last after 39 days. Semen quality was less than expected based on the peak of other reproductive seasons; only 19 of 35 samples contained an adequate number of live, motile and morphologically normal sperm. Females showed obvious physiological signs associated with the onset of egg production (pubic expansion and cloacal enlargement) and 5 were near enough to laying to be inseminated. Also, courtship behavior and abortive attempts at nest construction were observed. The experiment, terminated after 14 weeks of photostimulation, may have been too brief to obtain eggs. Males usually begin semen production 1 month or more before the first egg is laid. However, we believe the small pen size, low relative humidity, inadequate nesting materials and possibly other factors interfered with egg production. In other male nondomestic birds, extended photoperiod induces semen production even though the females require factors in addition to extended photoperiod to lay eggs (Farner 1986). The most important finding from Experiment 2 was that long photoperiod and a minimal number of other stimuli induced reproductive cycling in cranes.

Experiment 3 – Extended Photoperiod on Date of First Egg

Because of the extremely late laying dates and high variability in 1986, the analysis of data from years with added light was separated into 2 parts, 1983-1985 and 1985-1987. In the first 3 years, mean onset of laying was significantly later ($F_{2,14}$=6.33 p=0.011) in spring in 1983 than in 1985 (Table 5, Fig. 1). In 1986, the reproductive cycle was disrupted by unknown causes. The mean date of the first egg was later ($F_{2,16}$=18.66 p<0.001) in 1986 than 1985 or 1987, which did not differ from each other. However, in the analysis of data from 5 pairs with reproductive histories from 1979 to 1987, no difference in mean onset of laying from years with and without added light could be attributed to the extended photoperiod ($F_{1,4}$=0.01 p=O.909). The pattern of mean onset of laying did not change dramatically with extended photoperiod, although it was earlier for 2 consecutive years (1984-85) following addition of light in 1983 (Fig. 2).

Even in 1983, the date of first egg should have been earlier than in a year without extended photoperiod. Nestling American kestrels (*Falco sparverius*) from the northeast and passage birds captured in Florida (wintering birds from the larger northern race) were brought into captivity at Patuxent in 1964-1966, which is south of the natural breeding area for both populations. The northern race laid nearly a month later than the northeastern population, but both may have been a little earlier than the wild populations in their native habitats. Females from both populations laid progressively earlier each year, with those from the northern race making a greater shift toward earlier laying (Porter & Wiemeyer 1972).

In 17 pairs of Florida sandhill cranes (those that laid in more than 4 of the 5 years), mean onset of laying was earlier ($F_{4,60}$=7.50 p<0.001) in 1983, 1985 and 1986 than in 1984, and earlier in 1985 than in 1987 (Table 6). However, the Florida sandhills were not an adequate control group for the greater sandhill cranes because they normally lay a month earlier than greater sandhill cranes (Fig. 3), and they may not be influenced by the same weather patterns or other factors that increase or decrease date of lay. The pattern of change in onset of laying does not seem to be the same for Florida sandhills and greater sandhills in the years 1983-1985. Although cranes may respond to photostimulation, the effectiveness of extended photoperiod in changing the onset of laying in outdoor pens is difficult to demonstrate. In addition to control groups to compensate for annual variations, a study to determine the effectiveness of extended photoperiod should measure intensity and duration of reproductive activity in addition to date of first egg.

An extended photoperiod in the spring has been used with most productive whooping cranes (*Grus americana*) since 1974. The lighting system used was designed to mimic the environmental conditions found at Wood Buffalo National Park in Canada during the breeding season. The 17-18 h of light found on arrival at the breeding grounds is scheduled to occur at Patuxent in March when the temperature and rainfall are similar to the temperature and rainfall at Wood Buffalo. We assumed that whooping cranes that begin to lay in environments similar to the natural one are more likely to lay in captivity, and to lay more eggs than in one that is less similar. In addition, we continued to increase photoperiod from March until June at the rate of 3% per week in an effort to provide additional stimulation (King 1959).

We need to know more about the effect of extended photoperiod on crane reproduction. Although the greater sandhill crane is a photosensitive species that is not photorefractory, the effect of extended photoperiod on production in outdoor pens has not been demonstrated. Light is an effective proximate reproductive factor in most birds, but ultimate factors, such as weather, can terminate or otherwise condition the reproductive effort (Immelmann 1971). Light effects on crane reproduction may be subject to modification by a broad spectrum of ultimate factors. The next study of extended photoperiod should include a sufficient number of animals and provide control over covariate factors to reduce variance and increase our ability to detect a treatment effect. Control and treatment groups should include at least 15 animals each. The variables measured should include total egg production, onset and intensity of egg production, onset and intensity of semen production, reproductive condition of the female, and egg fertility. Also, the experiment should continue for 3 to 5 years to determine if extended photoperiod has cumulative effects.

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Table 1. Extended photoperiod used on greater sandhill cranes, 1969-1971 (experiment 1).

Date	Lamps Activated (EST)	Natural Hours	Light* Hours
18 Jan	0448	9.75	12.25
25 Jan	0441	9.95	12.50
01 Feb	0434	10.18	12.75
08 Feb	0412	10.38	13.25
15 Feb	0351	10.72	13.75
22 Feb	0338	10.97	14.08
01 Mar	0321	11.27	14.50
08 Mar	0258	11.57	15.00
15 Mar	0236	11.88	15.50
22 Mar	0218	12.17	15.92
29 Mar	0200	12.48	16.33
05 Apr	0137	12.78	16.83
12 Apr	0118	13.05	17.25
19 Apr	0051	13.38	17.83
26 Apr	0022	13.63	18.42
03 May	2359	13.54	18.92
10 May	2331	14.15	19.50
17 May	2302	14.35	20.08
24 May	2234	14.57	20.67
31 May	2159	14.72	21.33
07 Jun	2124	14.85	22.00
14 Jun	2058	14.93	22.50
21 Jun	2025	14.95	23.08
28 Jun	1946	14.93	23.75
05 Jul	**	14.88	24.00
12 Jul	**	14.77	24.00

* Light hours do not include twilight.
** Continuous light

Table 2. Crane light regimen (experiment 3).

Date	Lamps Activated (EST)	Natural Hours	Light* Hours
16 Feb	0206	10.72	15.50
23 Feb	0148	10.92	15.92
02 Mar	0131	11.27	16.33
09 Mar	0108	11.57	16.83
16 Mar	0051	11.88	17.25
23 Mar	0023	12.17	17.83
30 Mar	2355	12.48	18.42
06 Apr	2332	12.78	18.92
13 Apr	2303	13.05	19.50
20 Apr	2236	13.38	20.08
27 Apr	2207	13.63	20.67
04 May	2134	13.54	21.33
11 May	2101	14.15	22.00
18 May	2037	14.35	22.50
25 May	2009	14.57	23.08
01 Jun	1934	14.72	23.75

* Light hours do not include twilight.

Table 3. Effect of extended photoperiod on egg production from 6 greater sandhill cranes (experiment 1).

	With Extended Photoperiod			Without Extended Photoperiod	
	Years			Years	
Pair	1	2	3	1	2
1	-	8	6	11	9
2	4	7	6	3	0
3	5	9	6	-	4
4	-	3	3	4	5
5	-	4	7	-	3
6	-	13	13	2	4
		Mean=6.7 Std. Dev.=3.2		Mean=4.5 Std. Dev.=3.7	

Table 4. Reproductive responses of 6 crane pairs during winter to 24-hour light and a 17°C environment (experiment 2).

Period[a]	Average no.[b] semen samoles	Average cloacal[c] condition	Body wt.(kg) M	Body wt.(kg) F	Body temp.(°C) M	Body temp.(°C) F
10/4/71						
to 11/29/71	0	1	5.7	4.2	41.2	41.4
to 12/13/71	0	1	5.6	4.3	41.2	41.6
to 12/27/71	0	1.2	5.6	4.2	40.9	41.1
to 1/10/72	1.5	1.7	5.7	4.3	41.1	41.4
to 1/24/72	2.8	2.2	5.6	4.2	41.2	41.4
to 2/7/72	4.0	2.4	5.5	4.2	-	-
to 2/21/72	4.2	2.2	5.5	4.1	-	-
to 3/6/72	2.0	2.4	5.5	4.1	-	-
to 3/20/72	1.0	2.3	5.5	4.0	40.9	41.6

[a]Birds received 6-hour light 10/4/71 to 12/13/71 and 24-hour light thereafter.
[b]Number of semen samples collected per attempt from 6 males.
[c]Cloacal score: l=small (regressed state), 2=medium (some enlargement), 3=large (nearly ready to lay), 4=extra large (laying female). Average for 6 females, none of which had laid.

Table 5. Tukey multiple comparisons comparing mean onset of laying* of 9 pairs of greater sandhill cranes among years 1983-1985 and 1985-1987.

1983-1985

Tukey Grouping**		Mean	S.D.	N	Year
	A	123.5	12.44	8	83
	A				
B	A	114.6	14.24	8	84
B					
B		103.4	13.93	9	85

1985-1987

Tukey Grouping**	Mean	S.D.	N	Year
A	133.4	21.71	9	86
B	110.8	7.24	9	87
B				
B	103.4	13.93	9	85

* Mean date of first egg, calendar days.
** Means with the same letter are not significantly different ($p > 0.05$).

Table 6. Tukey multiple comparisons comparing mean onset of laying* of 17 Florida sandhill cranes.

Tukey Grouping**		Mean	1983-1987 S.D.	N	Year
	A	93.8	20.01	17	84
	A				
B	A	90.5	8.29	16	87
B					
B	C	79.8	10.98	17	86
B	C				
B	C	79.7	12.93	14	83
	C				
	C	75.6	11.70	17	85

* Mean date of first egg, calendar days.
** Means with the same letter are not significantly different ($p > 0.05$).

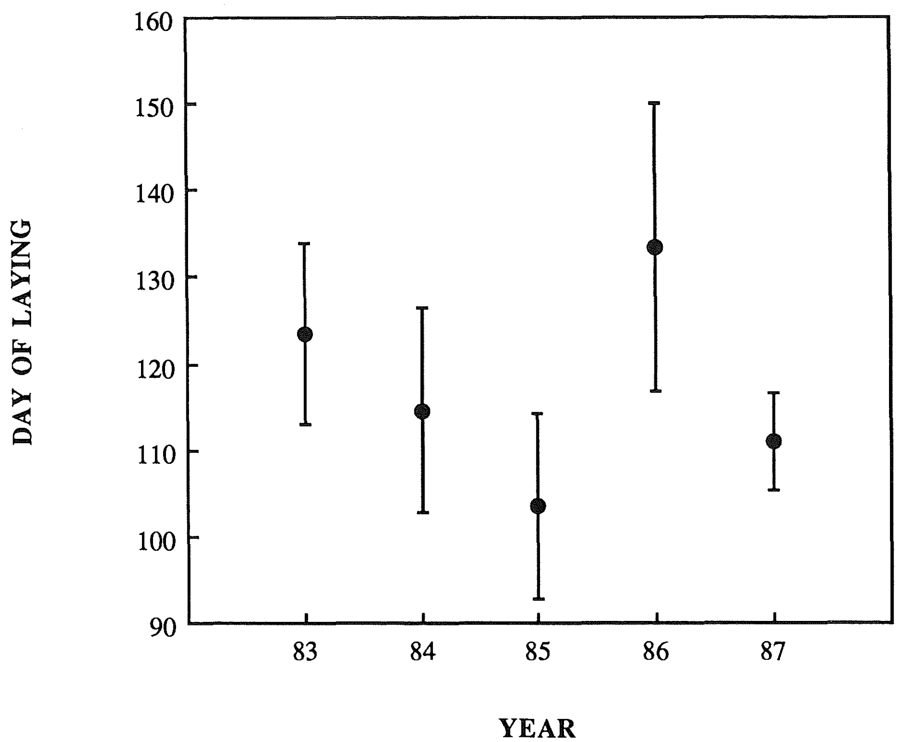

Figure 1. Means and approximate 95 confidence intervals for day of laying for 9 pairs of greater sandhill cranes exposed to extended photoperiod.

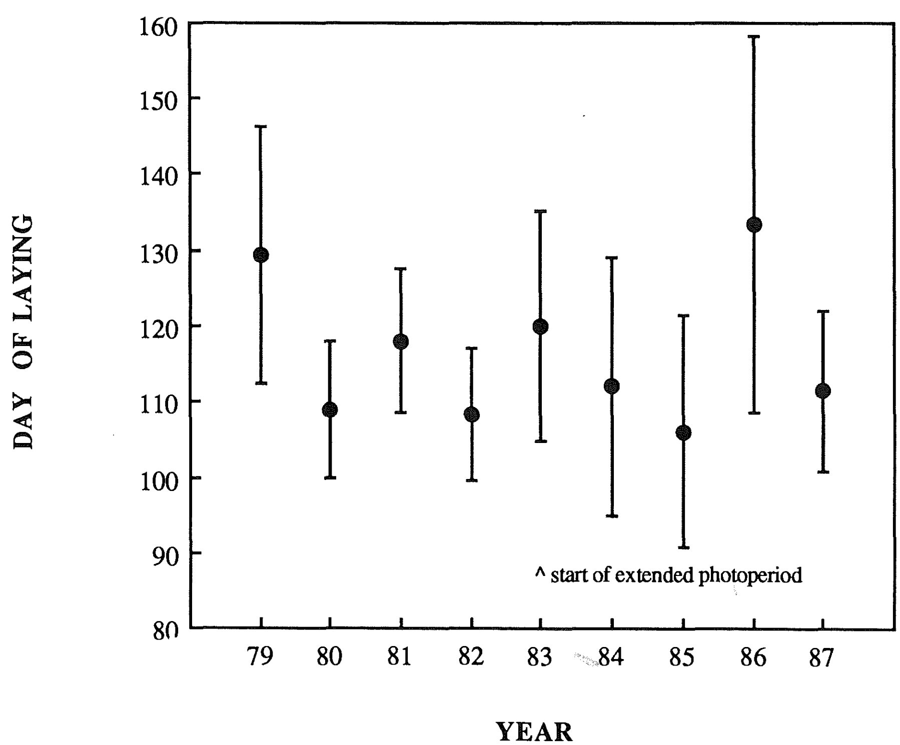

Figure 2. Means and approximate 95% confidence intervals for day of laying for 5 pairs of greater sandhill cranes before (79-82) and after exposure to extended photoperiod (83-87).

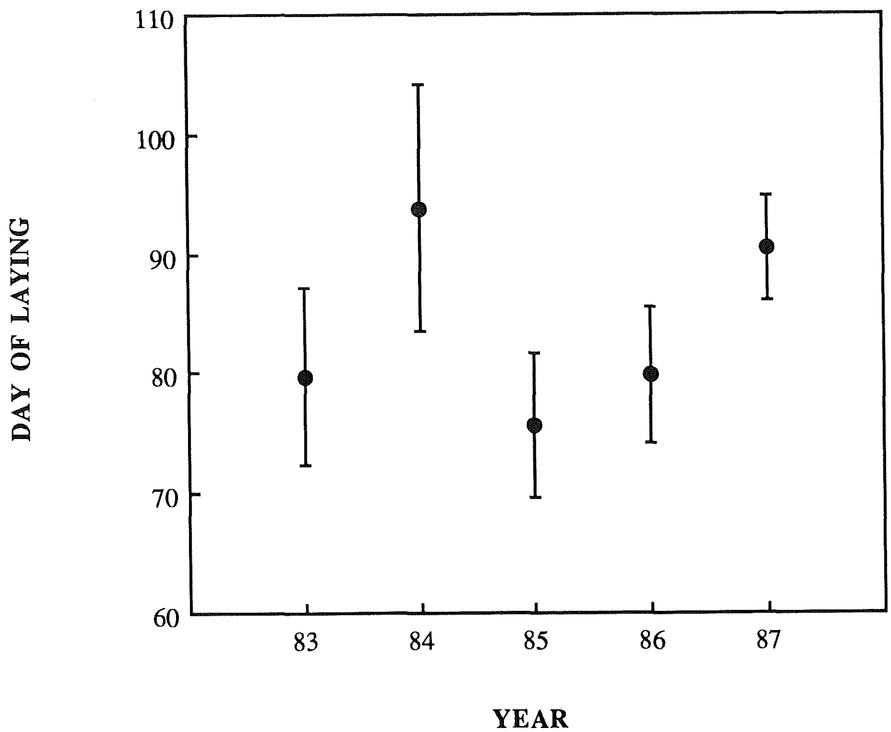

Figure 3. *Means and approximate 95% confidence intervals for day of laying for 17 pairs of Florida sandhill cranes with natural photoperiod (Laurel, MD).*