

# Trumpeter Swan nesting behaviour

JAMES A. COOPER<sup>1</sup>

## Introduction

A knowledge of the normal progression of nest construction, laying, incubation and hatching, permits identification of aberrant behaviour and correlation of this behaviour with certain environmental conditions which can be controlled. This is particularly significant for rarer species that need to be managed for maximum productivity and, yet, popular with the viewing public. The Trumpeter Swans *Cygnus cygnus buccinator* breeding in the Yellowstone-Grand Teton area of Wyoming, the Hennepin County Park Reserves of the Twin Cities of Minnesota and elsewhere are excellent examples. Without a firm grasp of normal behavior, assessment of the impact of human disturbance including research is difficult, and this absence of information may lead to unnecessarily restrictive or permissive control of access.

Previous studies of captive Trumpeter Swans (DeVos 1964; Johnsgard 1965; Tillery 1969) and of wild Trumpeters (Banko 1960; Hansen *et al.* 1971) have elucidated general aspects of breeding behaviour. Haapanen *et al.* (1977) recorded incubation time budgets and described postures of the closely related Whooper Swan *Cygnus cygnus cygnus* in the wild. Evans (1975) studied the nesting behaviour of captive Bewick's Swans *Cygnus columbianus bewickii*, and captive Whistling Swans *Cygnus columbianus columbianus* (Evans 1977), while Scott (1977) studied the nesting behavior of wild Whistling Swans. This paper describes a quantitative investigation of the breeding ethology of captive Trumpeter Swans.

## Study areas and birds

The investigation was centered at the Morris T. Baker Park Reserve located in Medina, Minnesota, 24 km west of Minneapolis. Further monitoring was done at the Lake Rebecca Park Reserve in Independence, Minnesota, 40 km northwest of Minneapolis. A single breeding pair of captive swans was studied at each location. The Baker pair, hatched in the wild at the Red Rocks

National Wildlife Refuge, Montana in 1970, and transferred to Minnesota as cygnets, were maintained in a 1 hectare, 5-sided, wire pen containing a 3 m by 10 m island. Water covered all but 5% of the enclosure to an average depth of 1 metre. Aquatic vegetation, primarily narrow leaf pondweed *Potamogeton* sp. and lesser duckweed, *Lemna minor*, was abundant while upland plants consisted of nettles *Stachys* sp. and burdock *Arctium minus* on the 2 meter-wide, north pen shoreline. The Rebecca swans were of the same age and origin as the Baker pair, but their pen differed by shape (rectangular) and the presence of a floating nest platform, instead of an island.

## Methods

The third and fourth nestings of the Baker swans were monitored and observed in 1975 and 1976, and their fifth nesting observed in 1977. The third nesting of the Rebecca pair was filmed during the hatching and departure phases in 1976. Monitoring was by remote sensing, time-lapse photography and remote control filming. Observations of the Baker swans were made from a car parked in a grove of trees, 50 m from the nest, using a 20× spotting scope.

The remote infra-red/thermistor monitor, used in 1975, consisted of a small (15 × 15 × 40 mm) photoelectric relay placed at the nest and a thermistor temperature probe positioned under the eggs. Both sensors were connected, via wire cable, to a strip-chart recorder powered by a 12 V DC battery and housed in a wooden shelter, 30 m north of the nest. The system recorded the presence of the bird at the nest by recording interruptions of the infra-red beam projected across the nest and nest temperature changes.

A time-lapse, super-8 movie camera (Minolta XL400) was employed in 1975 and 1976 to record daylight activities at the nest. The camera, enclosed in a protective case, was placed on the shoreline, 30 m from the nest, and a battery-powered clock positioned within the field of view. Single frames were exposed every 15 seconds on day 1, 7, 10, 18, 25, and 32 of incubation in 1975. When

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it was established from infra-red recordings that the female was not off the nest at night during incubation, that the male visited the nest during the absence of the female, and that the latter was inadequately recorded by the infra-red/thermistor recorder, the time-lapse camera was used exclusively in 1976. The frame interval was lengthened to 60 seconds, making a film change necessary only every 3 days.

To document specific displays, postures and nest maintenance behaviours, the Baker pair was filmed, using two remote-controlled super-8 cameras were placed on a tripod, 10 m from the nest. After an observation period, the exposed film was retrieved and the cameras reloaded. These films, and time lapse footage, were analyzed in the laboratory and from these, postures and display drawings prepared.

The phenology of laying was established each year by short (< 5 minute) visits to the nest site. Disturbances were held to a minimum and public access to the swan pens and their immediate surroundings prohibited. Wind speed, air temperature, rainfall and solar radiation at Baker were recorded continuously during 1975 and 1976. Statistical procedures described by Draper and Smith (1968) were used in regression analysis.

## Results

The 4 nesting attempts studied were successful. The Baker pair laid 7, 9, and 7 eggs in 1975, 1976, and 1977 respectively, while the Rebecca birds had 7 eggs in 1976. The weather conditions varied dramatically between 1975 and 1976 (Table 1), and the dates of nest establishment reflected these environmental differences. The Baker female laid the first egg on 1 May and departed with young on 14 June in the wet, cold spring of 1975. In the dry, warm spring of 1976, the first egg appeared on 14 April and nest departure was on 31 May.

The nesting period of the swans was divided into five phases: prelaying, laying, incubation, hatching, and nest departure. The prelaying phase extended from the release of

the pair into the breeding pen to the laying of the first egg, the laying period from the laying of the first to the deposition of the last egg and the incubation phase from the laying of the last egg until the initiation of embryo sounds. The hatching phase spans the period from first embryo sounds until the drying of the last cygnet, and the departure phase from this point until the first exit of the young from the nest cup. The 5 phases constituted approximately 20, 20, 55, 4, and 1% of the nesting period.

### *Prelaying phase*

Prelaying behaviour of the Baker swans was studied in 1976. The phase began with transfer of the pair from the winter pen, shared with their young from the previous year, to the breeding pen on 31 March. On 14 April the first egg was laid (Figure 1).

One minute-interval photographs of the island revealed that the pair initiated nest construction the day following release. Choosing the site used the previous year, nest construction progressed rapidly the first day after release then declined in intensity (Fig. 2). Construction was done primarily by the female with minor assistance from the male. Typically the female swam and then walked to the site, then stood and grasped nest material, straw which had been placed on the island, by extending her neck forward and dropping the material at her feet (Figure 3A). The male, accompanying the female to the nest site, stood a metre or 2 from his mate and gathered material in the same manner, transferring straw towards the base of the mound being built by the female. While he accompanied the female to the nest site constantly during the prelaying phase, he gathered nest material in only 1 of every 5 visits, with no apparent pattern to such bouts.

Initially, the pen restricted her activities to standing at the nest site, but in the afternoon of the first day after release, she performed nest settling; this behaviour, observed repeatedly in the prelaying, laying and incubation phases formed and maintained the nest cup. The sequence of settling

**Table 1. Weather conditions measured at the M. T. Baker Park Reserve, Medina, Minnesota, during the incubation phase.**

Parameter	1975	1976
Total rainfall	14.3 cm	1.8 cm
Days with rain	12.0	5.0
Mean daily temperature	16.5°C	13.3°C
Mean daily solar energy	7.43 GmCal/Cm <sup>2</sup> /Min	8.54 GmCal/Cm <sup>2</sup> /Min

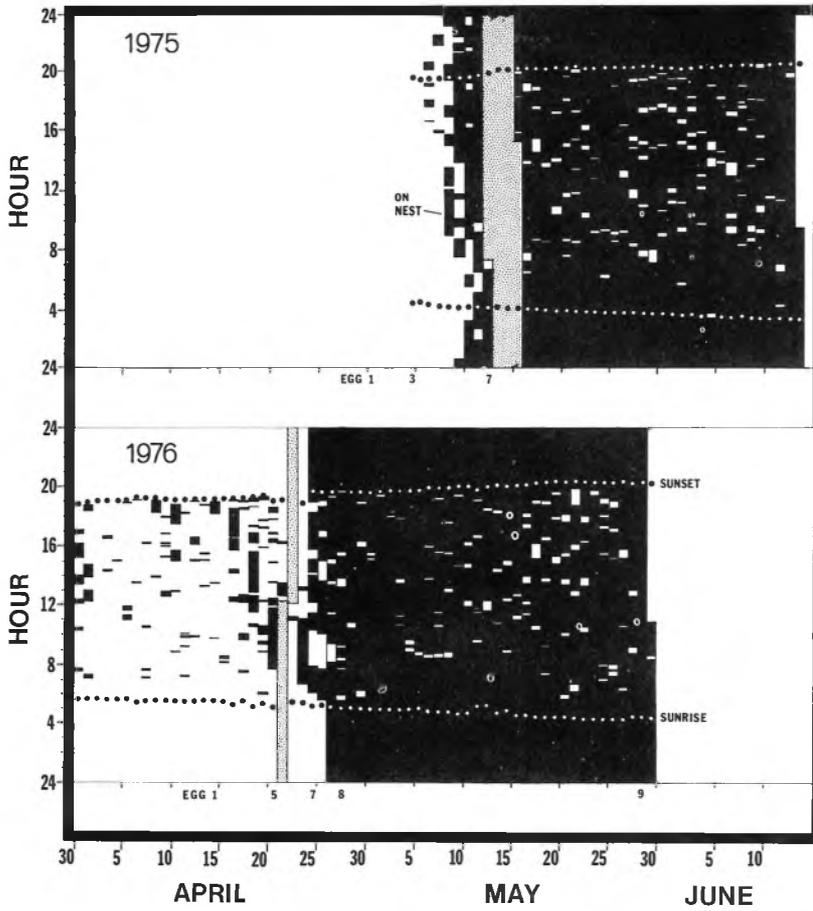


Figure 1. Nest attentiveness of a Trumpeter Swan female, M. T. Baker Park Reserve, Medina, Minnesota, 1975 and 1976. Black areas represent periods when the female was on nest, stippled areas periods when no data were recorded, egg numbers indicate clutch size on that date.

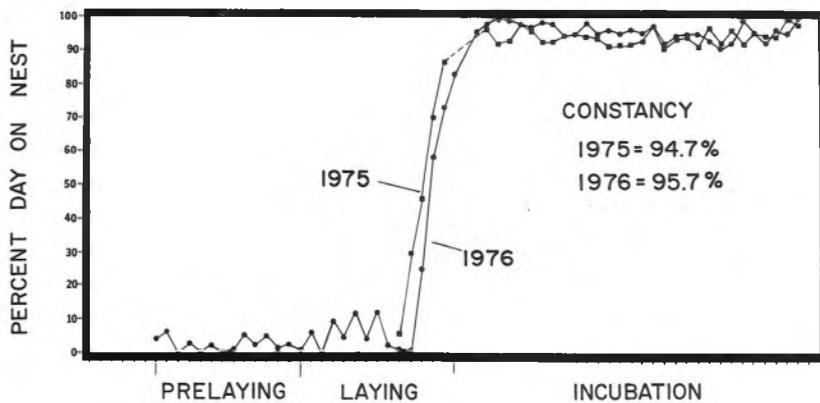
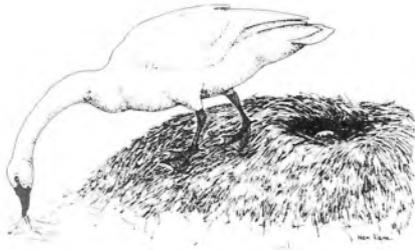


Figure 2. Percentage of the day spent on the nest by a female Trumpeter Swan, M. T. Baker Park Reserve, Medina, Minnesota, 1975 and 1976.



A



B

**Figure 3. Trumpeter Swan nest material gathering behaviours: A—off the nest; B—on the nest.**

movements comprised: (1) lowering of the breast as the body was shifted forward while simultaneously paddling the feet and extending the wings downward partially to support the weight (Figure 4A), (2) lowering of the body to a sitting position accompanied by a side to side rocking of the body and a shuffling of the feet (Figure 4B), and (3) redistribution and packing of the material pushed forward against breast and flanks by a patting motion (Figure 4C). This sequence was repeated several times with intervening changes in orientation until the nest cup was completed. In general, sitting was in the afternoon and evening and, thus, the longest prelaying visits to the nest mound occurred at these times (Figure 1).

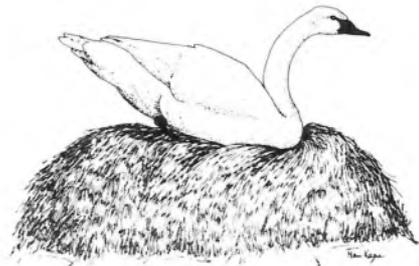
Copulation was not observed during the prelaying phase but undoubtedly occurred. Coitus, however, was seen on the 14th day of incubation in 1975 when the female left the nest briefly. The pre-copulatory, copulatory and post-copulatory behaviours agreed with the descriptions of DeVos (1964).

#### *Laying phase*

In 1976, the Baker pair spent 15 days

constructing the nest prior to laying while the Rebecca birds spent 35 days. Tillery (1969) reported a 19 day nest construction period for a captive pair of Trumpeters at the Great Bend Zoo, Kansas.

Egg laying rates could not be ascertained from the infrared or film recordings, but were estimated from the finding of new eggs in the nest. The maximum laying rate was calculated by assuming that the last egg was found on the day it was laid, and the first egg two days after it was laid. The minimum rate assumed that the first egg and the last egg were laid on the days they were found. The maximum laying rate for 1975 was 45 hours



A



B



C

**Figure 4. Trumpeter Swan nest settling behaviours: A—forward thrust with foot paddling, B—shuffle, C—patting.**

per egg, the minimum 39 hours. Based on the dates of discovery of the first 8 of the 9 egg clutch laid in 1976, the maximum laying rate was 48 hours per egg, the minimum 40 hours. DeVos (1964) and Hansen *et al.* (1971) reported a 48 hour per egg rate while Tillery's (1969) data indicated a rate of 50 hours per egg.

The nest construction behaviours continued and intensified during the laying phase as the female spent more and more time at the nest. However, four new behaviours not seen during prelaying were first observed. These were: (1) the *raised-wings* display, (2) the *quivering-wings* display, (3) breast down pulling and (4) incubation.

The *raised-wings* display was encountered during inspection visits and its onset coincided with the appearance of the first egg. The display was mutual but normally initiated by the disturbed female, whose calling attracted the male. An erect stance was assumed with wings spread but bent slightly at the wrist, neck and body feather

ruffed, and head oriented toward the intruder (Figure 5A). A *threat* display consisting of trumpeting in unison and vertical head bobbing, accompanied the *raised-wings* display. The birds can give the intruder rapid pecks or wing blows while standing directly over the eggs. Scott (1977) reported similar behaviour employed against an arctic fox *Alopex lapopus* by an incubating Whistling Swan. Hanson *et al.* (1971: Frontispiece) presented an excellent photograph of the display, and the behaviour appears to be similar in the Mute Swan *Cygnus olor* (Scott *et al.* 1972: Plate 6).

The most dramatic and vocal display was the mutual *quivering-wings*, during which the wings are partially extended and held parallel to the ground (Figure 5B) and rapidly moved from the wrist. The female initiated the display, commonly standing at the nest (21 of 30 observations). The display was always stimulated by approaching Canada Geese *Branta canadensis* and nearly always (29 of 30 observations) by geese flying directly over

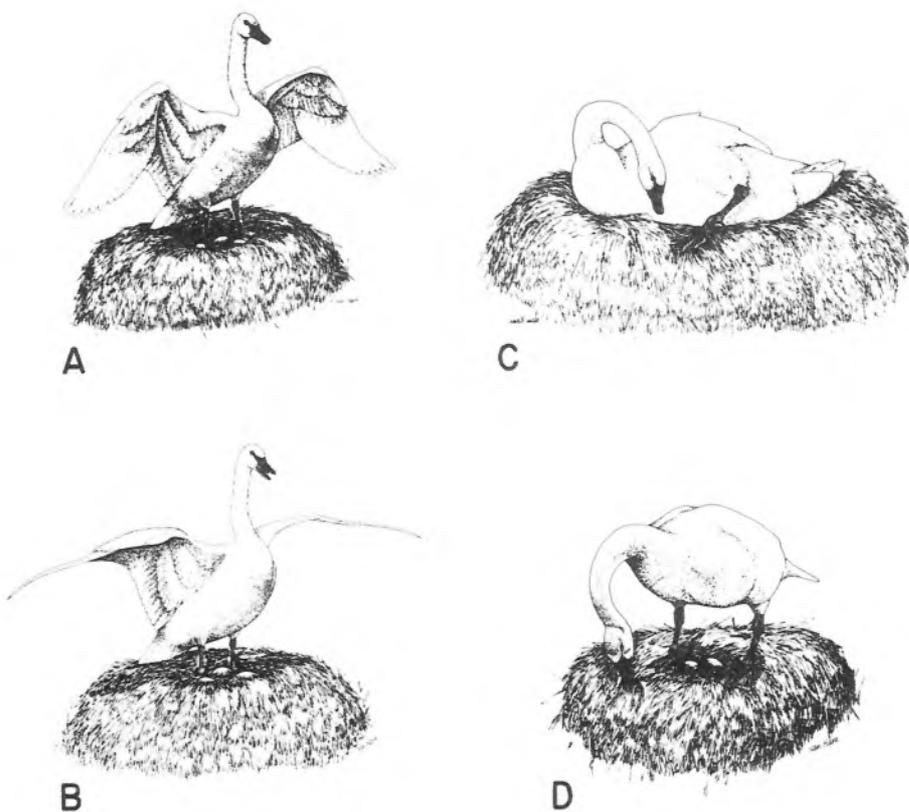


Figure 5. Trumpeter Swan nesting behaviours: A—*Raised-wings* display, B—*Quivering-wings* display, C—roll down pulling posture, D—egg covering.

the swan pen. Twelve displays occurred between 1500 and 1800 hours, and 7 between 0700 and 0900 hours, times when the Canada geese were most active. All *quivering-wings* displays were brief 15 to 30 sec displays in 29 of the observations. A display began when the female sighted geese flying towards her, extending her head to an alert posture (Figure 12C), stood, elevated her wings, and initiated the wing-quivering and calling. The male invariably began displaying within seconds and the pair continued until the intruders had passed. The swans followed the progress of the birds overhead by partial turning of their bodies.

The female pulled down from her lower breast and incorporated it into the nest. This was accomplished by either a partial roll of the body to one side and the extension of the bill to the breast (Figure 5C), or while in a posture similar to the egg lift stance (Figure 10B). Down appeared in the nest when the clutch was about half complete, with the third egg in 1975 and the fifth in 1976. A rapid increase in the time spent on the nest then occurred and it appears that the onset of incubation accompanied down pulling. The occurrence of pulling bouts by time of day was random, but the behaviour declined rapidly by the tenth day of incubation and terminated before the twenty-fifth day. An average of 1 pulling bout per hour was recorded on day 1, 0.5 bouts per hour on day 7, while only 1 bout was recorded on day 10 and on day 18. The down pulling bouts averaged 48 sec (SD = 6.0,  $n = 23$ ) and ranged from 15 to 120 sec.

The quantity of down deposited in the nest cup was approximately 10% of that in nearby Canada Goose nests (Cooper 1978), and at no time was the down quantity sufficient to form such a blanket as that with which the goose eggs could be covered. The feather removal did not result in the visible brood patch reported by Hanson (1959) for geese.

#### *Incubation phase*

Incubation was by the female. The onset of incubation was progressive, with a rise in attentiveness, during the latter half of the laying phase and reaching a plateau 2 days after the last egg was laid (Figure 2). This transition presents a difficulty in designating the first day of incubation. Following Cooper (1978), the incubation phase was defined as being from the laying of the last egg to the beginning of embryo vocalization.

A slightly modified version of Skutch's (1962) terminology was used to describe the incubation phase. Incubation constancy is the percentage of the day spent on the nest, periods off the nest being termed recesses, and periods on the nest sessions. The latter are subdivided into times spent sitting on the eggs, the sitting spells, and breaks, when the female stands to rearrange the eggs or nest materials, or reposition herself.

#### Constancy

The Baker female had a 30 day incubation phase in both years with an average incubation constancy of 94.7% in 1975 and 95.7% in 1976, the difference being non-significant. Within a single season, the time spent on the nest varied little (Figure 2). Multiple regression analysis of daily constancy in relation to day of incubation, to mean daily air temperature, to total daily solar radiation and to rainfall yielded no significant fits. The best regression explained only 10% of the variation in daily constancy.

#### Recess

Three types of nest absences were observed. A normal recess was one where the female stood and covered the eggs (Figure 5D) prior to departure. A defence recess was denoted by lack of egg covering, a rapid exit from the nest mound after having assumed an alert posture (Figure 12C), given a *quivering-wings* display (Figure 5B) or done both, and by defence of the territory. Material gathering recesses were brief absences (< 5 min) when the female left the nest while grasping materials and moving them toward the nest (Figs. 3A and 3B). Only 3 gathering recesses were observed, in the first 2 days of incubation. These recesses were considered remnants of laying phase behaviour and were eliminated from the recess analysis.

Sixty percent of recesses were normal, 40% defence. Recess frequency but not length varied by recess type. Normal recesses were taken most often from 1500 to 1900 hours, whereas defence recesses were common in both morning and evening (Figure 6), when the Canada Geese were most active. Normal recesses averaged 21 min (SD = 12.4,  $n = 32$ ) and defence recesses 18 min (SD = 13.0,  $n = 31$ ), the difference being non-significant. Normal recesses occurred daily throughout incubation, but defence recesses were more

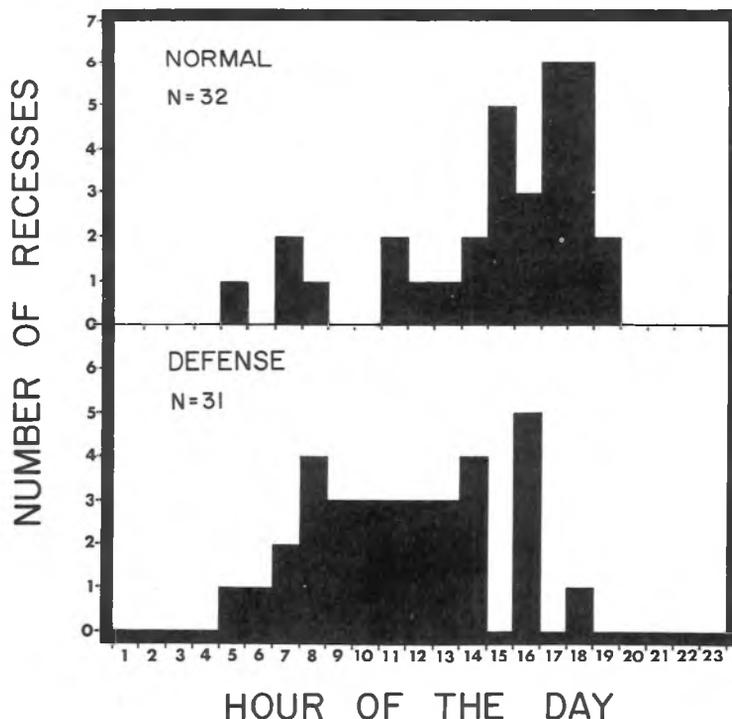


Figure 6. Trumpeter Swan incubation recesses by type and time of day, Morris T. Baker Park Reserve, Medina, Minnesota, 1976.

frequent in early incubation, 50% recorded in the first 12 days, and were clustered, i.e., more than 1 per day.

Regression analysis of factors that may have affected normal recess length was made. Independent variables were the same as those used in analysis of incubation constancy, together with recess type and time of day. The best fit explained 11% of the variability in length and was not significant. Overall, recesses taken varied little between years, an average of 4 per day in 1975 and 3 per day in 1976 (Figure 7). Recess length, however, did vary significantly ( $p > 0.05$ ) between years. In 1975, recesses ranged from 4 to 62 min, with a mode of 10 and the median of 17 min. Recesses in 1976 varied from 1 to 150 min with a mode of 19 and a median of 18 min. The more but shorter recesses in 1975 and fewer but longer recesses in 1976 resulted in no significant difference in total time off.

Recess activities were recorded during 11 normal, 4 defence and 2 mixed recesses. Recess activities were classified as: (1) Feeding and locomotion associated with feeding, (2) comfort movements devoted to bathing and preening, (3) displaying with the male and defending the territory, and (4)

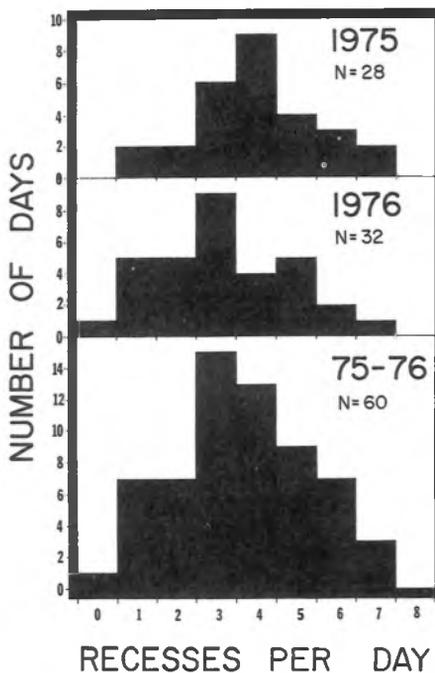


Figure 7. Trumpeter Swan incubation recesses per day, Morris T. Baker Park Reserve, Medina, Minnesota, 1975-1976.

locomotion not associated with the foregoing behaviour.

On a normal recess, after having covered her eggs, the female walked to the water using one of two routes, drank, bathed and preened; at this point, the male usually joined her and accompanied her during the remainder of the recess. Feeding normally followed the first bathing bout, and was terminated by a longer, more vigorous bathing and preening period, including oil preening just prior to the return to the nest. Standing over the eggs, the female spent a minute or two preening (Figure 10A), followed by settling behaviour. The settling was repeated an average of 6 times (range 3 to 10) with a counterclockwise shift in orientation each time, resulting in at least one complete rotation during the 2 to 5 min settling period. Patting, unlike in nest construction, was restricted to the final settling.

During a defence recess, the female first

joined the male in defending against intruding Canada Geese. Defence consisted of the pair swimming toward the intruders while trumpeting loudly and pumping their heads. Typically, this *threat* behaviour was sufficient to force the geese from the pen, but on 2 occasions when the intruders did not retreat, the pair rushed over the water toward the geese while simultaneously giving the *quivering-wings* display. Defence was followed by a *triumph* display, a brief bout of preening, and a return to the nest.

On three occasions, Canada Geese flew above the pen while the female was taking a normal recess. This resulted in a *quivering-wings* display, a *triumph* display, and preening followed by a return to the nest. Such recesses were termed mixed.

The relative times spent on each activity during the recesses observed are given in Table 2.

**Table 2. Trumpeter Swan incubation recess activities, Morris T. Baker Park Reserve, Medina, Minnesota, 1975-1977.**

Day of incubation	Recess length (Min)	Percentage of time spent in			
		Feeding	Comfort movements	Locomotion	Displays
NORMAL RECESSES					
9	19.9	20	56	24	0
11	23.2	29	54	17	0
11	16.2	23	40	12	20
18	13.2	24	27	43	6
19	12.0	46	31	12	10
19	15.4	28	52	20	0
22	26.2	29	66	1	0
22	19.2	71	5	19	0
29	19.7	51	17	31	0
Total/Mean	165.0	38	41	17	5
DEFENCE RECESSES					
17	22.9	0	33	3	64
17	6.5	0	24	4	72
19	20.8	19	6	24	47
24	15.6	24	8	11	56
24	15.1	1	8	0	92
Total/Mean	80.9	10	16	9	64
MIXED RECESSES					
18	15.8	29	24	6	41
18	9.0	10	5	50	36
23	19.5	2	58	19	22
Total/Mean	44.3	13	35	21	32

## Sessions

Time spent at the nest between recesses varied from 3 to 1664 min. Session distribution was bimodal, a peak occurring at 2-hour intervals and another at 15-hour intervals (Figure 8). The longer sessions were a result of the female's steadfastness to the nest at night. Nearly all (99%) of the sessions longer than 10 hours began after 1200 and terminated the following day. Analysis of the effects of environmental factors and day of incubation on session length yielded no significant relationships. Breaks when the female stood while at the nest divided a session into a series of sitting spells. An average of 2.6 breaks occurred per hour (range = 0 to 9, SD = 1.46,  $n = 416$ ) with 2 breaks per

hour most common. Regression analysis of break frequency in relation to environmental conditions, hour of the day and day of incubation produced no significant fits. Breaks varied in length from 15 sec to 15 min, the former being typical (Figure 9). The longer breaks usually included either egg moving behaviour, *quivering-wings* display, or shading of the eggs. Certain behaviours preceded a break and were signals for its initiation. These were down pulling, oil preening, a *quivering-wings* display (sitting) and nest material gathering. Such activities were invariably followed by a break within 5 min. During a break, the female invariably shifted her orientation relative to her previous position on the eggs, occasionally moved the eggs and always performed the

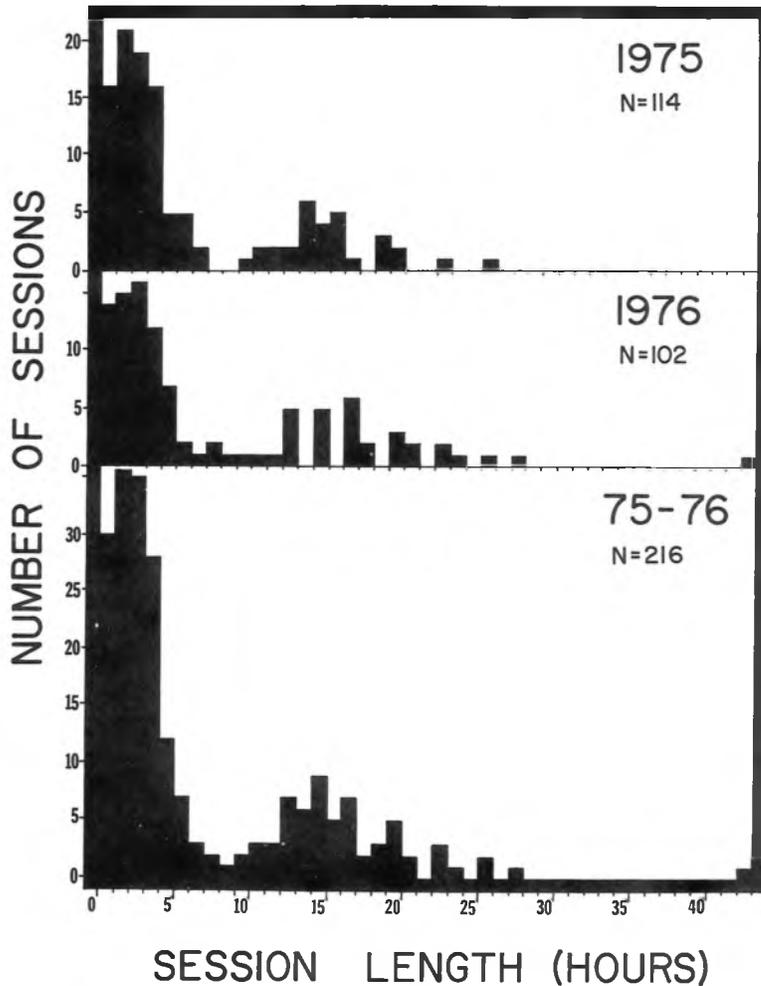


Figure 8. Trumpeter Swan incubation session lengths, Morris T. Baker Park Reserve, Medina, Minnesota, 1975-1976.

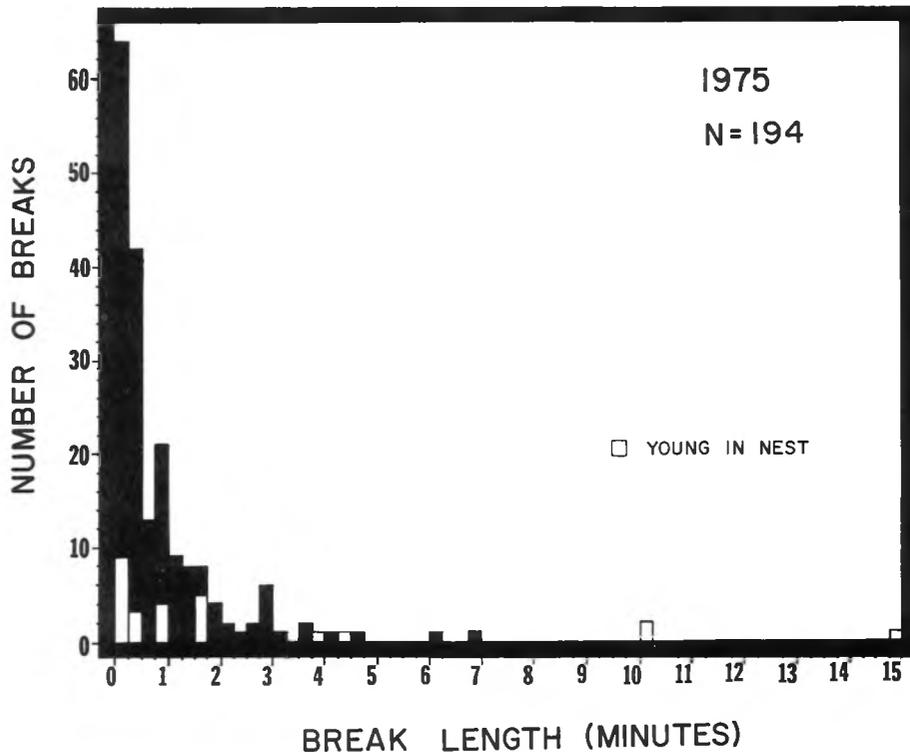


Figure 9. Trumpeter Swan incubation break lengths, Morris T. Baker Park Reserve, Medina, Minnesota, 1975.

settling sequence. Egg moving occurred during 40% of the breaks, without significant relationship to time of day or stage of incubation. Egg movements were accomplished by (1) a backwards extension of the head below the breast and the lifting of an individual egg with underside of the bill (Figure 10B), (2) wedging the bill between the egg and the surrounding nest materials and pushing or pulling the egg (Figure 10C), or (3), rarely, lifting a foot on which an egg rested. Normally both bill lift and wedge movements were used in the same egg turning bout. Because Trumpeter Swan eggs are usually separated by nest material, an egg shift left a pocket which the female filled by a patting motion immediately after moving an egg. Each moving bout was followed by a settling, and 2 or 3 bouts were typical for a break with egg turning, 7 being the maximum observed.

*Quivering-wings* displays while standing produced breaks similar in length to those where egg turning occurred, ranging from 30 to 180 sec with a mean of 68 sec (SD = 49.3, n = 54). The longer breaks

resulted from shading behaviour when the female stood over the eggs in the middle of the day. This behaviour probably reduced the female's thermal stress for panting always accompanied these breaks.

Sitting spells were brief, ranging from 1 to 173 min, those less than 5 min being most frequent (Figure 11). Regression analysis of spell length in relation to environmental conditions, time of day and stage of incubation, explained only 5% of the variation in spell length, a non-significant level. The female's sitting postures were: (1) normal, (2) alert, and (3) sleep. In normal incubation posture (Figure 12B), she sat with neck slightly curved and head level. She frequently turned her head from side to side, watching her surroundings. When disturbed, the neck was erected (Figure 12C) and, depending on the disturbance, the female either gave a *quivering-wing* display, left the nest, or both, or resumed normal posture. Resumption of normal posture was frequently followed by nest material gathering (Figure 3B) and patting (Figure 4C). Sleeping, with lengthy closure of the eyes, was observed when the

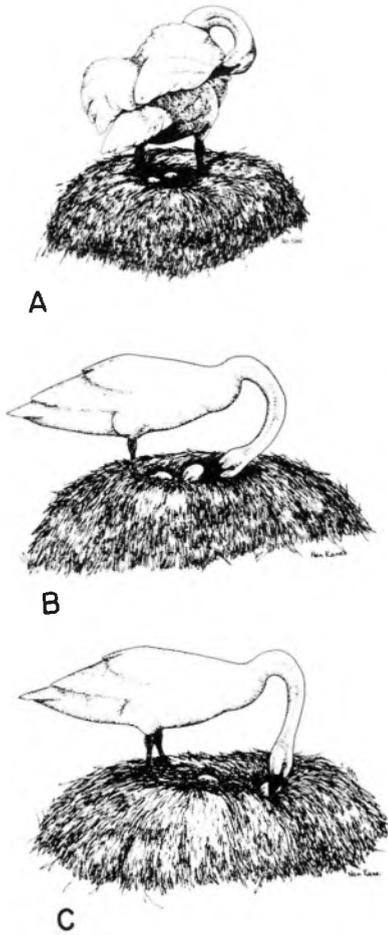


Figure 10. Trumpeter Swan nesting behaviours: A—Preening at the termination of a recess, B—Left egg turning, C—Wedge egg turning.

female rested her head on the middle of her back with tip of the bill beneath the scapulars (Figure 12D). However, based on eye closure, only 70% of the time spent in this posture was considered sleep. Sleep posture bouts were extremely brief, varying from 1 to 41 min, with 2 min bouts comprising 20% and half of the bouts being less than 6 min. The number of sleeping posture bouts recorded on day 1, 10, 18, and 25 of incubation were 27, 10, 22, and 36, or 2.1, 0.7, 1.7 and 2.8 per hour, respectively. Analysis of bout length by time of day and day of incubation gave no significant relationships. However, sleeping bout length during showers averaged 18.3 min ( $n = 10$ ) whereas dry period bouts averaged 7.8 min ( $n = 85$ );

the difference was significant ( $p > 0.05$ ). Cloud cover also appeared to stimulate sleep. On two of the days filmed in 1975, partly cloudy conditions prevailed, and during a sitting spell, intervals of sleep coincided closely with blockage of the sunlight.

Preening bouts while sitting on the nest, primarily oil-preening (Figure 12A) ranged from 15 to 75 sec, 30 sec being average ( $SD = 15.6$ ,  $n = 39$ ), and, like sleeping posture bouts, most common on rainy days.

#### Hatching and departure phases

Hatching terminated incubation behaviour, and like incubation, the onset of the phase was indistinct. The most obvious clues to hatching were an increase in attentiveness (Figure 2) and the cessation of settling and egg turning behaviours. The failure of the female to perform the settling sequence was first recorded on day 30, a time when no eggs had pipped but when embryo vocalizations were heard. By day 31, no settling behaviour and egg turning were seen; the female simply lowered herself on the nest, and as the cygnets emerged, she accommodated them by a partial spreading of the wings. Emergence of the cygnets spanned days 31 and 32 or approximately 48 hours, agreeing with the observations of Kear (1972). Preening bouts, *quivering-wings* displays, and breaks continued at the same frequency as during incubation, but breaks and preening bouts were longer. Breaks ranged from 15 to 900 sec, the average being 160 sec ( $SD = 222.6$ ,  $n = 30$ ), preening bouts averaged 45 sec ( $SD = 36.1$ ,  $n = 18$ ), with a range of 15 to 180 sec on day 32 of incubation.

In all cases, initial exodus from the nest was in the morning of day 33, at 0922, 1053, and 0832, for the Baker birds in 1975 and 1976, and for the Rebecca swans in 1976, respectively. Morning brood departures have also been recorded for the Mallard *Anas platyrhynchos* (Caldwell 1971) and the Canada Goose (Cooper 1978).

The cygnets did not immediately follow the female when she left the nest, but were enticed by her repeated returns and departures. Cygnets typically left singly and those off the nest were attended by the male while the female returned to the nest. The departure phase lasted from 5 to 20 min. Once off, the pen and cygnets returned to the nest within 30 min, and then made repeated departures and returns throughout the day.

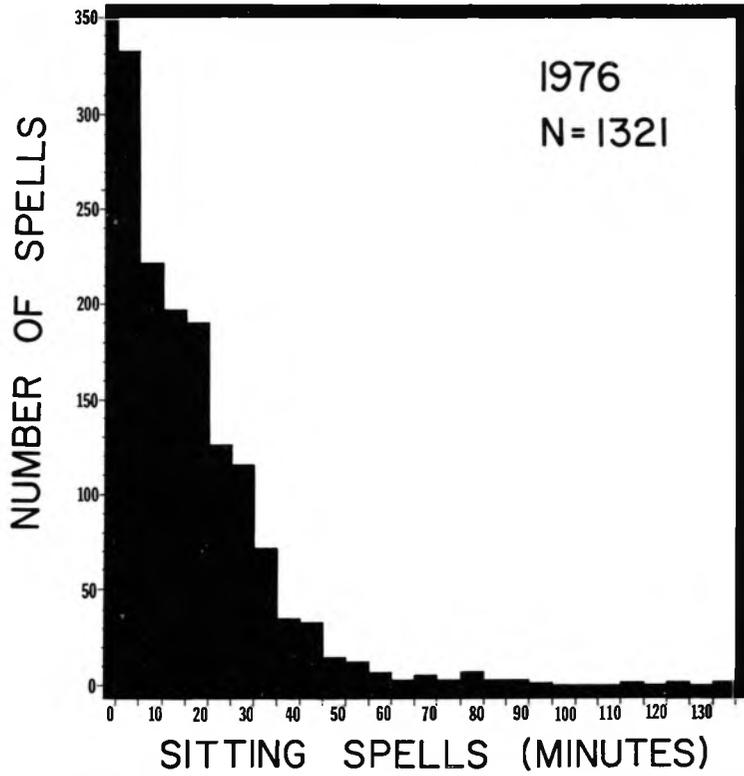


Figure 11. Trumpeter Swan incubation sitting spell lengths, Morris T. Baker Park Reserve, Medina, Minnesota, 1976.

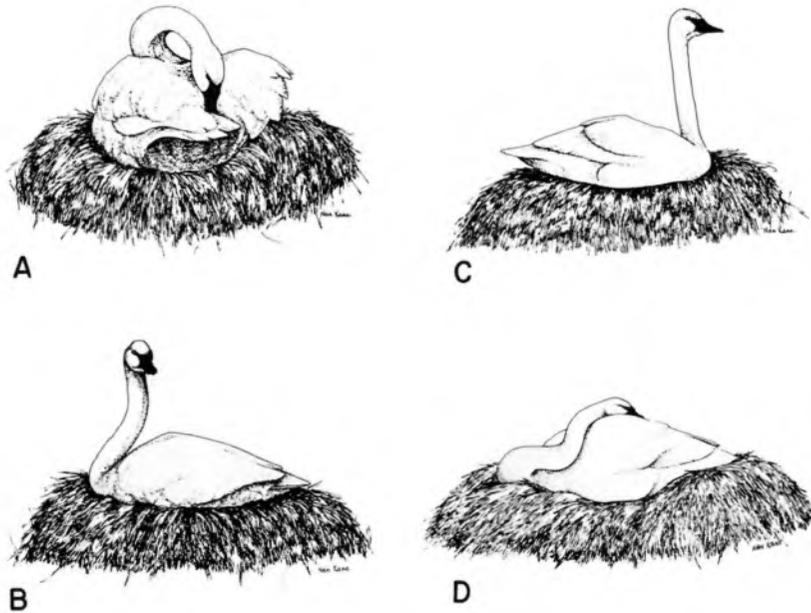


Figure 12. Trumpeter Swan nesting behaviours: A—Oil preening on nest, B—Normal Incubation posture, C—Alert posture, D—Sleep posture.

### Male's behaviour

In addition to the male's participation in the nest construction, display, defence, and nest departure behaviours, the male also frequented the nest during some normal incubation recesses. Because manipulations of nest materials and eggs resulted in feather staining and because the female devoted much of her time to these activities, her dark head and neck was easily distinguished from the male's by the beginning of incubation.

Twenty nest visits by the male were recorded during the study. In all cases, he first joined his mate while she bathed or fed, accompanied her for a varying length of time, then swam to the nest mound, ascended via 1 of the entrance/exit paths gathering material. Once at the nest, the male stood, but never sat, manipulating nest material and transporting material from the mound to the cup. After having been at the nest from 1 to 23 min, averaging 5 (SD = 4.7,  $n = 20$ ), the male departed, usually using a different route and gathering materials and transporting them toward the mound exactly as the female did during nest construction (Fig. 3A). The male's exit from the nest coincided with the return of the female.

Visits to the nest by the male were not randomly distributed by either time of day or day of incubation. In 1975, the male was not seen at the nest after day 18. In 1976, during the first 25 days of incubation, the male visited the nest twice on 1 day, once on 13 days and not at all on 11 days, nor after day 25. Of 20 male visits, 6 (30%) occurred before 1200, 10 (50%) between 1200 and 1800, and 4 (20%) after 1800.

### Discussion

The Trumpeter Swan's breeding strategy includes the maintenance of a territory from prelaying in early spring to near the time of fledging in late summer (Banko 1960), a lengthy prelaying period (Tillery 1969; this study), a highly attentive, single-sex intermittent incubation (this study) and a prolonged preflight brood rearing period during which many (50–85%) offspring succumb (Banko 1960; Page 1976). Because reproductive success is the ultimate test of the fitness of a strategy, the extremely high cygnet loss during rearing may be assumed to have a significant affect on some behaviours preceding this period.

The lengthy prelaying phase, when relatively little time is devoted to the nest mound (Figure 2), may be necessary for the female to build up internal energy reserves for laying and incubation. Page (1976) reported a significant increase in nests, clutch size, and cygnet survival when the food provided the Trumpeters wintering at the Red Rocks National Wildlife Refuge was doubled. Reynolds (1972) found that breeding Mute Swans spent most of the daylight hours feeding during the prelaying and laying periods, and hypothesized that body condition was a determinate of the timing of breeding and clutch size in this species. Banko (1960) suggested that the Trumpeter Swan territory size was related to the quantity of food available at a given distance from the nest site. Thus, the prelaying phase is devoted primarily to feeding and the extent of the territory may be partially a function of the distribution of the food. The continued defence of this area presumably would also ensure an undiminished food resource for the adults and young after hatch. In addition, establishment of the territory prior to incubation would also reduce the defence recesses of the sitting female.

The progressive rise in nest attentiveness in the latter half of the egg laying phase (Figure 2) is similar to that found for Canada Geese (Cooper 1978), the Mallard (Caldwell and Cornwell 1975) and the Shoveler *Anas clypeata* (Afton 1977), and may be typical for many waterfowl. Frith (1967) and Meirs and Williams (1969) reported that the Black Swan *Cygnus atratus* initiates incubation prior to laying the last egg. Banko (1960) cited egg failure as a major factor in reducing Trumpeter Swan productivity and, based on the fact that most dead embryos were well developed, hypothesized that incubation during laying may be the cause.

Trumpeter Swan incubation period lengths, measured from the laying of the last egg to departure of the young, have been reported as 33–37 days (Banko 1960), 32–33 days (Banko and MacKay 1964), 33 days (Johnstone 1965) and 33–35 days (Sheppard 1962). During this study a 33-day incubation period was recorded, composed of a 30-day incubation phase, a 2-day hatching phase and a less than 1-day departure phase. I believe that a 33-day period is probably the minimum incubation length. A shorter period would require more heat input (higher attentiveness) and I doubt that the pen can increase her attentiveness much beyond the 95–96% level. Conversely, it is

likely that disturbance, causing the female to leave the nest more often, would lengthen the incubation period as was reported by Breckenridge (1956) for the Wood Duck *Aix sponsa*. The high attentiveness and limited time spent feeding are indicative of fasting by the female during incubation. If the Trumpeter Swan's strategy is similar to fasting strategies hypothesized by Ryder (1970) for the Ross' Goose *Anser rossii* and for the Canada Goose by Cooper (1978), where the internal reserves are limited, then extension of the incubation period much beyond the norm would not be expected. This may explain the relative narrow range of observed Trumpeter incubation lengths.

The involvement of the incubating female in defence emphasizes the significance of territoriality in the Trumpeter's strategy, and the low probability of egg predation. If the female is relatively independent of food resources during incubation, then her behaviour maintains the integrity of the territory and may, as Kear (1972) stated, ensure that food is available to the cygnets. Her rapid return to the nest after defending, however, may lessen egg predation. The few recorded instances where Trumpeter Swan eggs have been lost to predators occurred when the female was off the nest (Dixon 1931; Page 1976). The highly vocal and visual displaying prior to and during the defence recess certainly could serve as signals of an unattended nest to potential egg predators.

The postures and displays observed in this study with the exception of the *Triumph* display conform to the general descriptions for the Trumpeter by Banko (1960), DeVos (1964), Johnsgard (1965) and others. The *Triumph* display according to Banko (1960) and Johnsgard (1965) involves a mutual display of quivering-wings, bobbing head and staccato trumpeting, ending in reclining neck and wings and wailing notes. My observations suggest that the quivering-wings component may be the final portion of the defence display and that the mutual head bobbing and trumpeting constitute the *Triumph* display. On numerous occasions, disturbances which put the female in the alert posture, were followed by mutual head bobbing and calling without quivering of the wings. It may be that the captive birds studied were atypical and that the *Triumph* display includes both quivering-wings and mutual head bobbing.

The fact that components of the incubation rhythm (constancy, recess length, session length, sitting spell length and break

frequency) show no significant relation to day of incubation, time of day or weather conditions, indicate that the Trumpeter Swan has a relatively rigid pattern of incubation, and supports the suggestion that the bird is fasting, and, therefore relatively independent of the environment. Cooper (1978) reported a similar lack of correlation between environmental conditions and incubation rhythm in the Canada Goose. However, Afton (1977) found that much of the variation in incubation rhythm in the Shoveler could be explained by variation in the weather and stage of incubation. Furthermore he concluded that the Shoveler was highly dependent on breeding ground resources, whereas Cooper felt the Canada Goose was independent of breeding ground foods. Certainly the relative large Trumpeter Swan egg with its slow cooling rate, and the potential for internal reserves in this large bird, would permit the development of a pattern independent of short term variations in the weather.

The role of the male's behaviour during nesting appears to be primarily defence of territory. This is accomplished by highly vocal and visible displays with a minimum of physical contact (Banko 1960) and, perhaps, by continuous advertisement via the conspicuous white plumage (Wynne-Edwards 1962). The function of the male's involvement with the nest is unclear. In contrast to DeVos' (1964) observation that the male Trumpeter did not assist positively in nest building, the Baker male contributed to construction of the nest, yet his efforts were minor compared to his mate's. Similarly, the male's visits to the nest while the female took a normal recess may be interpreted as egg protection (Kear 1972). But, these visits were infrequent and confined to the early portion of incubation phase. Discounting protection, one may speculate that these visits are vestigial, reflecting an earlier strategy where the male participated in incubation similar to that observed in the Black Swan (Miers and Williams 1969), in the Bewick's Swan (Evans 1975), and in the Whistling Swan (Scott 1977).

Haapanen *et al.* (1977) measured incubation time budgets and described nest construction behaviour and incubation postures of the Whooper Swan. Similarities with the Trumpeter include a minor male involvement in nest construction, nest visitation without sitting by the male during an incubation recess, the participation of the female in defence of the territory and the *quivering-wings* display, and bimodal, daylight incubation recesses that occur most

frequently between 1600 and 2000. The Trumpeter and Whooper Swans differed in the length of the normal recess, the time spent feeding by the female while on a recess, and the degree of sleeping on the nest. Normal recess length was longer for the Whooper, averaging 25 minutes for day 6 to 19 of incubation and 48 min from day 20 to 32. The Trumpeter recesses average 21 min and were not correlated with the day of incubation. Recess activities also differed between the two subspecies. The Whoopers devoted from 64 to 72% of the normal recess to feeding while the Trumpeter female at Baker spent only 38%. Sleep posture was observed so frequently during the Whooper incubation phase, 60% of the daylight hours (0600 to 2200) and 80% of the night hours (2200 to 0600), that it was deemed the 'normal' incubation posture. In contrast, the Trumpeter female at Baker spent an average of 10% of the daylight hours in sleep posture and 75% in normal incubation posture. Overall, the Whooper devoted 85% of the day to the nest compared to the 95 to 96% of the Trumpeter. Whether these differences reflect subspecific variation or are the result of individual variation cannot be ascertained without additional study.

Comparison of the nesting behaviour of the Trumpeter (this study) and Whooper Swans (Haapanen *et al.* 1977) with that of the Bewick's (Evans 1975) and Whistling Swans (Evans 1977; Scott 1977) revealed few similarities and some striking differences. Similarities include a predominance of nest building by the female, mutual participation in the *quivering-wings* display and territorial defence (reported for Whistling), and a high nest attentiveness during the hatching phase. Unlike their larger relatives, the male Bewick's and Whistling Swans incubate. Evans (1975) found that captive Bewick's males spent from 2 to 42% of the day sitting on the nest, and Scott (1977) observed Whistling Swan cobs incubating from 10 to 27% of the day. Moreover, the smaller northern swans are more attentive to the nest. With both sexes sharing incubation, Scott (1977) computed a 97 to 99% incubation for the Whistling Swan. Evans (1975) did not report constancy data, however from her descriptions of the Bewick's activities patterns, it is evident that the nest was seldom left unattended. No sleeping postures were observed for the Bewick's or Whistling swan, while the latter when disturbed assumed a hiding posture similar to that of the Canada Goose (Cooper 1978).

Based on these limited studies, it appears

that the Trumpeter and Whooper Swans have nearly identical nesting behaviours, and that Bewick's and Whistling Swan nesting behaviours while similar, differ significantly from their larger relatives. These data support Delacour and Mayr's (1945) classification of the northern swans, where the larger, more southerly breeding birds and the smaller, tundra breeding swans are grouped into 2 species with 2 subspecies each. I believe that the bisexual incubation of the Whistling and Bewick's Swans and its absence in the reproductive strategies of the Whooper and Trumpeter Swans is significant enough to make Johnsgard's (1974) lumping of all 4 northern swans as one species and Palmer's (1976) separation of Trumpeter and Whooper Swans into 2 species, doubtful.

Several tentative hypotheses may be advanced to explain the differences in nesting behaviours of the smaller and larger northern swans. The bisexual incubation of the smaller, tundra breeding birds, resulting in a higher incubation constancy, permits, (1) a minimum incubation period, (2) an increase in the protection of the eggs from predators and (3) a higher level of feeding by the female during laying and incubation. Nesting in northern latitudes, the Bewick's and Whistling Swans are subjected to critically short breeding seasons. Lensink (1974) stated that the timing of breeding and fledging were the most significant factors influencing Whistling Swan reproduction. By maintaining a higher incubation constancy, the smaller swans have a minimum incubation period. Reported incubation period lengths support this concept. With nearly constant egg heating, Bewick's Swan young leave the nest in 29–30 days after the last egg is laid (Johnstone 1957), and Whistling Swan cygnets depart in 31 days (Bellrose 1976), whereas the Trumpeter Swan has a 33-day incubation period (this study) and the Whooper Swan a 34-day period (Haapanen *et al.* 1973). Cooper (1978) found that predation of Canada Goose nests was significantly influenced by the size of the predator relative to size of the goose and the degree of dry, upland access afforded the predators at the nest site. While egg predation is not considered a significant factor in swan reproductive success (Kear 1972), Cooper's findings imply that the potential for egg loss to predators should be greater for the smaller swans which tend to nest in the upland (Kear 1972). Furthermore, the presence of a hiding posture of the Whistling Swan (Scott 1977) suggests that predation has been a factor in the evolution of the nesting behaviour of this

bird. Scott (1977) hypothesized indirectly that territorial defence was more important to Trumpeter and Whooper Swans and that Bewick's and Whistling males could spend more time on the eggs as a result of the lower involvement in defence. It appears (this study) that territorial defence is a major component of the Trumpeter Swan breeding strategy and has resulted from the critical food requirements of the young and the limited nesting habitat. In contrast, with a great expanse of suitable habitat in the far north but a short breeding season, the smaller swans may have evolved a strategy that permits the female to feed more during laying and incubation and thus enable her to devote additional time to assisting the feeding young (trampling) during the short brood rearing period.

The most striking difference between the incubation pattern of the Trumpeter and that of other intensively studied waterfowl is the short sitting spells. Cooper (1978) found that the Canada Goose had an average sitting spell length of 68 min while Caldwell and Cornwell (1975) reported the Mallard took 1.6 to 2.0 nest breaks per hour, equivalent to 30 to 38 min sitting spells. The frequent shifting at the nest may be a heat distribution mechanism. Heat may be distributed evenly by changing the orientation of the body relative to the eggs rather than shifting the eggs relative to the body. The absence of predator pressure would permit such behaviour. In the smaller species where motion at the nest may attract predators, egg movement would be more advantageous. The position of the eggs relative to the feet may also be important. The Trumpeter has a poorly developed brood patch and much of the heat provided to the eggs may come from the feet. The final motion of the settling where the body is rocked from side to side and feet shuffled appears to result in positioning of the feet under the eggs. Waterfowl have a well developed mechanism for thermoregulation of the feet (Kilgore and Schmidt-Nielsen 1975), and thus a potentially efficient mechanism for heat transfer.

Page (1976) suggested that human activities near Trumpeter Swan nests could be detrimental. The results of this study provide several guidelines for assessing disturbances. Human activities that result in normal recesses longer than 150 min, in more than 7 recesses per day or in incubation periods consistently longer than 33 days may be deemed significant. Similarly, the failure of the female to initiate incubation once breast down is plucked or the presence of cold eggs

in the nest after clutch completion should be considered abnormal.

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### Summary

Captive Trumpeter Swan *Cygnus cygnus buccinator* breeding behaviour was observed, photographed and electronically monitored in the Hennepin County Park Reserves near Minneapolis, Minnesota from 1975 to 1977.

The nesting period was divided into 5 phases: prelaying, laying, incubation, hatching and departure. The female constructed the nest with minor assistance from the male and incubated the eggs. Egg laying intervals were estimated at 39 to 48 hours. The female spent 94.7% of the day on the nest in 1975 and 95.7% in 1976. Times off the nest (recesses) were restricted to the daylight hours and were classified as nest material gathering, normal or defence recesses. Normal and defence recesses did not differ significantly in length, averaging 21 and 18 min respectively. Normal recesses occurred primarily from 1500 to 1900, whereas defence recesses were observed in both morning and evening when intruding Canada Geese *Branta canadensis* were most active. Hatching began 30 days after the last egg was laid, was complete by day 32 and the cygnets left the nest on the morning of day 33. Postures and displays were described for all phases of nesting.

The involvement of the pair and particularly the incubating female in territorial defence, combined with apparent fasting of the female during this phase, suggests that protection of food resources for the cygnets is significant. The nesting behaviour of the northern swans were compared and, based on striking differences in the behaviours of the larger (Trumpeter and Whooper *C. cygnus cygnus*) and the smaller (Bewick's *C. columbianus bewickii* and Whistling *C. columbianus columbianus*) members of the group, Delacour and Mayr's (1945) classification of these birds supported.

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**Prof. James A. Cooper.** Dept. of Entomology, Fisheries and Wildlife, University of Minnesota, 219 Hodson Hall, 1980 Folwell Avenue, St. Paul, Minnesota 55108, USA.