

# Nesting behaviour of male and female Whistling Swans and implications of male incubation

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## Introduction

Among waterfowl (family Anatidae), female ducks and geese are responsible for nest construction and incubation, though males sometimes perform nest-building movements (McKinney 1968) and sit on eggs (Balham 1954; Dane *et al.* 1973). Incubation by male waterfowl is rare and has been reported in Magpie Geese *Anseranas semipalmata*, whistling ducks, *Dendrocygna* sp. and *Thalassornis leucotis*, and Black Swans *Cygnus atratus* (Kear 1970). Male Whistling and Bewick's Swans *C. columbianus columbianus* and *C. c. bewicki* sit on eggs in captivity (Evans 1975, 1977), as do wild male Whistling Swans (Scott 1977). These males are believed incapable of true incubation, i.e. "applying the heat necessary for embryonic development to an egg after it has been laid" (Beer 1964), but the nature of female and male nest attendance and implications of male "incubation" for pair and young are poorly understood. This study was undertaken to: 1. quantify nesting behaviour of male and female Whistling Swans and identify factors influencing their involvement in incubation, 2. compare male and female ability to heat eggs, and 3. determine the effect of nest attendance on male and female daily activity budgets.

## Study birds and areas

Wild swans were studied in the Colville River Delta, Alaska (70°N, 151°W). The flat terrain is covered with numerous wetlands and low-growing vegetation; soils are saturated and underlain with continuous permafrost. Summers are cool and brief. Temperatures may rise to the low-mid 20°s C, but snow may fall during any month. Weather is characterised by overcast skies, frequent fog, persistent winds and low precipitation. Thawing begins in late May and proceeds quickly, but surface water freezes by late September.

I studied a captive pair in Juneau, Alaska (King & King 1978), which is outside the

natural breeding range, but has the same photoperiod as the southern breeding range of Whistling Swans (Bellrose 1976). Male and female were obtained as cygnets in 1971; the female was captured from breeding grounds in western Alaska, and the male was found in southeastern Alaska during the autumn, apparently too thin and weak to continue migration. Male and female paired by 1976 and were isolated in their breeding pen that spring. The female laid in 1979, incubated full term but no eggs hatched. At least one egg hatched from nestings in 1980, 1981, and 1982. A grassy dike with scattered bushes surrounded the largely unvegetated and freshwater pond that filled 70% of the pair's 0.15 ha pen. Cracked corn and commercial feed for laying poultry were provided *ad lib*.

## Methods

Colville River Delta field camps were established between 13 to 20 May in 1981–83, before peak swan arrival. Prelaying behaviour was observed from hides and filmed. Nests were located on foot and selected for study based on accessibility (2.3–6.2 km from camp) and how well personnel could conceal themselves during maintenance of monitoring equipment. Pairs were assigned a number indicating pair and year, e.g. 1–81 represents pair 1 whose behaviour was studied in 1981.

The breeding season was separated into six periods:

(a) *prelaying*: day of the first territorial visit until the day before laying of the first egg.

(b) *laying*: day the first egg was laid until the day before laying of the last egg.

(c) *early incubation*: day of laying of the last egg (day 1 of incubation) to day 10 of incubation in the wild, and day 12 in captivity.

(d) *middle incubation*: days 11–20 of incubation in the wild, and 13–24 in captivity.

(e) *late incubation*: days 21–30 of incubation in the wild, and 25–36 in captivity.

(f) *hatching*: days 31–32 of incubation in

the wild, and 37–38 in captivity.

Incubation terminology of Cooper (1979) was adapted for biparental involvement. *Male* and *female constancy* are the percent of day (24 h) each sex sits on the clutch, and *pair constancy* their sum. *Sessions* are periods when a bird, of either sex, sits on the eggs. A session consists of a series of *sitting spells* separated by *breaks*, when the bird stands to reposition nest materials, eggs, or itself. A sitting spell usually contains one or more *sleeping spells*, which begin when a bird lays its head on its back and end when the head is raised. During a *nest visit* a swan returns to the nest but departs without initiating a session. *Recesses*, or periods spent off the nest, were grouped into six types:

(a) *normal*: female covers the eggs before leaving; male may or may not cover the eggs.

(b) *defence*: bird departs, without covering the eggs, to defend against a territorial intruder, and resumes incubation after defence.

(c) *mixed*: similar to defence recess except the swan continues to recess following defence and its mate initiates the next session.

(d) *hiding*: bird leaves eggs without covering them, and stands or sits inconspicuously at or near the nest base.

(e) *brief*: bird walks about and away from the nest, then resumes incubation.

(f) *disturbance*: bird leaves nest due to human disturbance.

#### *Nest monitoring and observation*

Super-8 movie cameras (Minolta XL401 or XL601) were used to film activities (Cooper & Afton 1981) at six wild nests. Twenty-four hour daylight allowed cameras to record data continuously. Day of incubation at camera installation was estimated by back-dating from nest departure assuming 32 days for incubation and hatching (this study). Cameras were placed 55–85 m from the nest. Filming began at one nest (used successfully the previous year) a day after peak swan arrival in the delta, on day 2 of incubation at two nests, and days 3, 4 and 5 at the others. Filming continued 35–73 hr after nest departure. Ten days of coverage were lost in 1983 to lens condensation or camera failure. Film was exposed at one frame/min and usually changed every 2–2.5 days.

The captive nest was monitored with a multi-sensor system (Cooper & Afton 1981). A Super-8 movie camera (Minolta XL401), set 15 m from the nest in a hide, recorded activity during daylight hours. Filming began one week before laying and film was exposed at one frame/15 sec on days 1, 4, 6, 9, 14, 19, 24, 29, and 34 of incubation, and one frame/min at other times. A plastic-shelled, glycerin-filled egg (110 x 68 mm), with a thermistor medical probe, Rustrak 1331, inserted in its centre, was placed in the clutch the day following laying of the second egg. Glycerin and a fresh egg have similar densities (glycerin 1.246 g/ml, fresh egg 1.035 g/ml (Romanoff & Romanoff 1949)), so the artificial egg heated and cooled at rates similar to a fresh egg. Egg temperature was continuously recorded with a strip chart thermistor-event recorder, Rustrak 2133, and later read at 10-min intervals and when sessions began and ended. At night (6–10 hr/day), presence, but not the sex, of an incubating bird was detected with an infrared photo-electric relay, so I made six all-night watches, and briefly illuminated the breeding pen with a spotlight at 15 min intervals to identify the incubating bird. The male was not observed incubating during all-night watches so I assumed the female incubated at night.

I used time-lapse photography to approximate sitting spell lengths for two wild pairs, and the captive pair during daylight hours. Film could not be used to obtain sitting spell data for other wild pairs because cameras were too distant to enable consistent detection of position shifts. Defence and mixed recesses were identified by an abrupt departure without covering the eggs, preceded by an alert posture and/or *raised* or *quivering-wings displays* (Cooper 1979). Nest visit lengths were estimated by time in the camera's field-of-view.

In addition to filming, four wild pairs and the captive pair were observed from hides 350–1100 m (wild) or 15 m (captive) from their nests. Observation bouts usually lasted 6 hr (wild) or 4 hr (captive), and were limited to daylight hours in captivity. Pre-laying and incubation recess behaviour were noted every 30 sec. Incubation behaviour (sitting [head up or head on back], and break) was noted every 60 sec. Sleeping spell lengths and break activities were timed by stopwatch and counted, respectively. I observed egg-laying from inside the King's

home, which was 70 m from the captive nest. Laying was detected from female movement, posture, and sight of the emerging egg.

Sex of a given bird was determined by neckband for the captive pair, and body size (Scott 1981) and/or behaviour, particularly during nest exchanges (Scott 1977) for wild pairs. To evaluate my ability to sex wild swans on film, I compared identifications made during direct observation with those made during film review. All identifications ( $n=120$ ) during direct observation (pre-laying through to termination of nesting) agreed with those made during film review, so I assumed swans could be sexed from film with satisfactory accuracy. Other clues used to identify specific wild pair members during direct observation included position during copulation, pattern of yellow on bills, feather staining on head and neck, bill profile, and head shape.

#### Weather

Extreme daily temperatures were measured with max-min thermometer (Colville River Delta camp) or thermograph (King's home) and averaged to estimate mean daily temperature. Wind speed was estimated daily in the Colville River Delta using classes of 0–8, 8–16, 16–24, 24–32, and 32–40 kmph, and the midpoint of each class provided an estimate of mean daily wind speed. In Juneau, 3-hourly wind speeds (NOAA 1983) were averaged to estimate mean daily wind speed. I calculated mean daily wind chill indices (Munn 1970) from daily estimates of mean air temperature and wind speed. Occurrence of precipitation was noted daily (Colville River Delta camp) or obtained for 3 hr intervals (Juneau airport) (NOAA 1983).

#### Statistical analysis

I used multiple regression analyses (Neter & Wasserman 1974) to identify factors influencing incubation rhythms. Models were developed to explain maximal variation in the dependent variable, with independent variables usually contributing at  $p<0.05$ .  $R^2$  values were adjusted for number of variables in the model and sample size. Hatching days were deleted from regression analysis because females became highly attentive; film change days

were omitted from pair constancy analysis after preliminary work indicated they were a significant disruption. Regression techniques were used to examine incubation rhythms even though data were sequential observations from the same individuals and lacked independence. As a result, models should be interpreted cautiously because standard errors of the regression coefficients were underestimated. Although statistical rigour is lost, valuable insight can be gained from sequential sampling (Myers 1974).

## Results

### Pre-laying period

Wild and captive pairs visited the future nest more than once before laying began. Pair 4–82 were filmed at their nest nine days before laying began. They walked and stood near the nest, preened, poked in the bowl and performed *sideways-building*, gathering and setting materials to the side with the bill. Pair 4–82 subsequently made 0–5 nest visits (mode=2) a day before laying. Visits were during all periods of the day and averaged 18.9 min (range 3–64,  $n=12$ ). The female gathered materials and excavated the bowl with her bill, while the male set clumps of sod and vegetation on and near the nest. The female was first observed scraping a bowl 4 days before she laid. The captive female made 1–2 nest-building bouts/day at the future nest during the week preceding laying, with afternoon bouts most common. Bouts averaged 10.0 min ( $se=2.01$ ,  $n=11$ ) and lengthened as laying neared, but significant nest construction did not begin until the session when laying began. The captive male accompanied the female during all nest-building bouts, performed *sideways-building* for  $\leq 3$  min, and left before the female about 40% of the time.

Film records suggested that swans, especially males, sometimes visited the nest during territorial defence. Pair 4–82 frequently stood erect on the tall nest mound and the male was once filmed in a *raised-wings display* (Cooper 1979). During the two days preceding laying, male 4–82 made three visits of less than 3 min each, apparently alone, when he stood on the nest and poked into the bowl. At least twice the

captive male made short (<4 min), solitary evening trips to the future nest where he stood and poked into the bowl. These visits coincided with peaks of agonistic display with other captive swans.

Swans engaged in copulatory behaviour during prelaying. Pair 4-82 was not observed copulating, but pair 3-82 was on five occasions during prelaying, each on separate days on the lake occupying most of their territory. The captive pair copulated the day they were released into their breeding pen (J. G. King, pers. comm.) and 1-2 times daily during the nine days preceding laying. Copulation continued during laying with similar frequency, and seven copulations were observed after laying ceased, the last on day 15 of incubation. Wild pairs were not observed copulating during laying or incubation.

#### *Laying period*

Female 4-82 and the captive female began laying in the afternoon. I believe laying at nest 4-82 began between 14.13-17.30 hrs because there was an egg in the nest when it was visited at 17.33, and the session, initiated at 14.13, was the first of significant length. The captive female began laying in the late afternoon (17.40) and her mean egg-laying interval was 41.9 hr (se=0.51, range=40.1-43.2, n=5). Constancy of female 4-82 rose quickly as laying progressed. In captivity, female constancy rose sharply the day the first egg was laid, then increased slowly as laying proceeded with drops on non-laying days (Figure 1).

Male behaviour during the laying period differed sharply between the wild and captive pairs. During the session when female 4-82 laid her first egg, her mate fed nearby, visited the nest twice, and sat on the egg when she left. Constancy of pair 4-82 would have been almost 100% from day 2 of laying on, were it not for film change disturbances, because the male continued to incubate during female recesses (Figure 1). The captive male did not sit on the clutch during the laying period, but frequently remained at the nest during female recesses after half the clutch was laid, poked into the bowl, and set materials on the nest mound and over the eggs.

Wild and captive females *pulled down* (Cooper 1979), but males did not. Female 4-82 *pulled down* during her first laying

session and continued to, though less frequently, through early incubation. The captive female began 90 min after laying the fifth of a six egg clutch, and continued through mid-incubation. Both wild and captive females added little down to the bowl, and in captivity close observation indicated the female lacked a readily visible brood patch (Hanson 1959). However, her breast feathers looked ruffled and uneven for the remainder of nesting, and were erected and separated into clumps by deep clefts when she incubated, apparently enabling close contact between skin and eggs.

During the laying period, females began performing a series of actions collectively called *settling* (Beer 1961; Drent 1970; Cooper 1979) when initiating a session. The same behavioural sequence is termed *re-settling* when it occurs during a break. The female lowered herself and shoved down and forward with her breast by alternately pushing with her feet against the sides of the bowl. Her wings were dropped slightly and planted against the nest rim for balance and support. Then she sat, humped her back, braced her wings and tail against the nest, and rocked from side to side while rapidly *shuffling* the feet into the bowl. Lastly, she packed nest materials about breast and sides with the bill. *Settling* was usually repeated several times within a few minutes with intervening shifts in orientation; *shuffling* and packing nest materials did not always terminate *settling*. *Egg-moving*, a backward extension of the head below the breast and lifting of individual eggs with the underside of the bill, or wedging the bill between the egg and surrounding nest materials and pushing or pulling the egg (Cooper 1979), occurred during the laying period but was not quantified.

#### *Incubation rhythms*

At two wild nests where date of laying of the last egg could be determined within 1-2 days, incubation and hatching required 31-32 days. In captivity, 38 days were required. Incubation was primarily by the female in both cases, and varied over a wide range (Table 1, Figures 2 and 3). Constancy of wild pairs consistently approached 100% because males usually sat on the eggs soon after females left and remained until they returned. A wild swan rarely left the nest

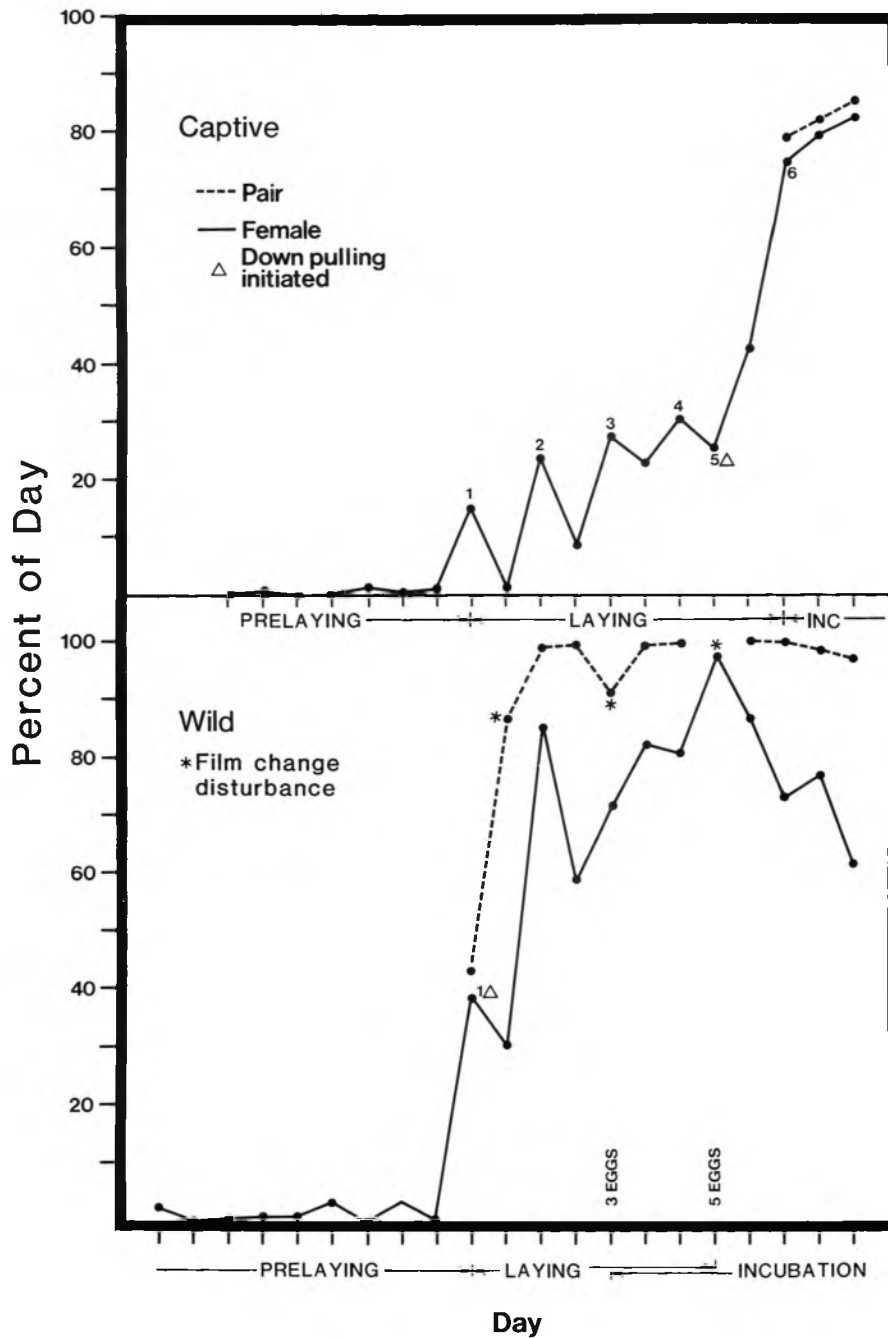
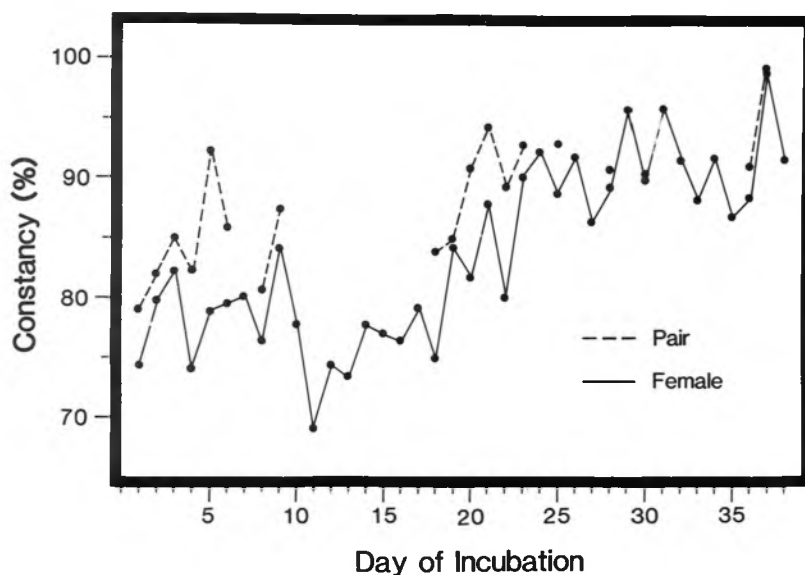


Figure 1. Percent of day (24 hr) a captive and a wild (4-82) Whistling Swan pair sat on the nest bowl from prelaying through early incubation, Juneau, 1983, and Colville River Delta, Alaska, 1982, respectively. Numbers indicate known days when eggs were laid.

**Table 1.** Mean incubation constancies at a captive and five wild Whistling Swan nests, Juneau, 1983, and Colville River Delta, Alaska, 1981–83, respectively. Hatching days omitted. Standard errors of means in parentheses. Means within a column lacking one similar superscript differ significantly ( $p < 0.05$ ).

Nest	Female	n	Mean constancy (%)		Pair	n <sup>d</sup>
			Male	n		
1–81	79.1 <sup>a,b</sup> (1.79)	29	19.6 <sup>a</sup> (1.65)	29	98.1 <sup>a</sup> (0.58)	16
range	61.2–94.5		5.4–36.5		91.9–99.9	
2–82	74.7 <sup>a,b</sup> (1.74)	26	20.6 <sup>a</sup> (1.68)	26	96.6 <sup>b</sup> (0.77)	12
range	61.1–91.2		4.9–37.6		92.7–99.6	
2–83	79.2 <sup>b</sup> (1.58)	23	19.6 <sup>a</sup> (1.62)	23	99.3 <sup>a</sup> (0.18)	14
range	62.0–93.5		5.0–37.6		97.5–99.9	
3–82	62.0 <sup>c</sup> (1.95)	28	35.8 <sup>b</sup> (1.71)	28	99.1 <sup>a</sup> (0.23)	16
range	45.1–81.1		18.7–49.8		97.0–100	
3–83	60.4 <sup>c</sup> (1.79)	23	38.1 <sup>b</sup> (1.92)	23	99.2 <sup>a</sup> (0.16)	13
range	45.3–76.6		22.3–54.6		97.8–99.9	
captive	83.0 <sup>a</sup> (1.18)	36	2.5 <sup>c</sup> (0.60)	36	85.5 <sup>c</sup> (1.17)	36
range	69.1–95.8		0–13.6		69.1–95.8	

<sup>d</sup>days with film changes omitted for wild pairs.

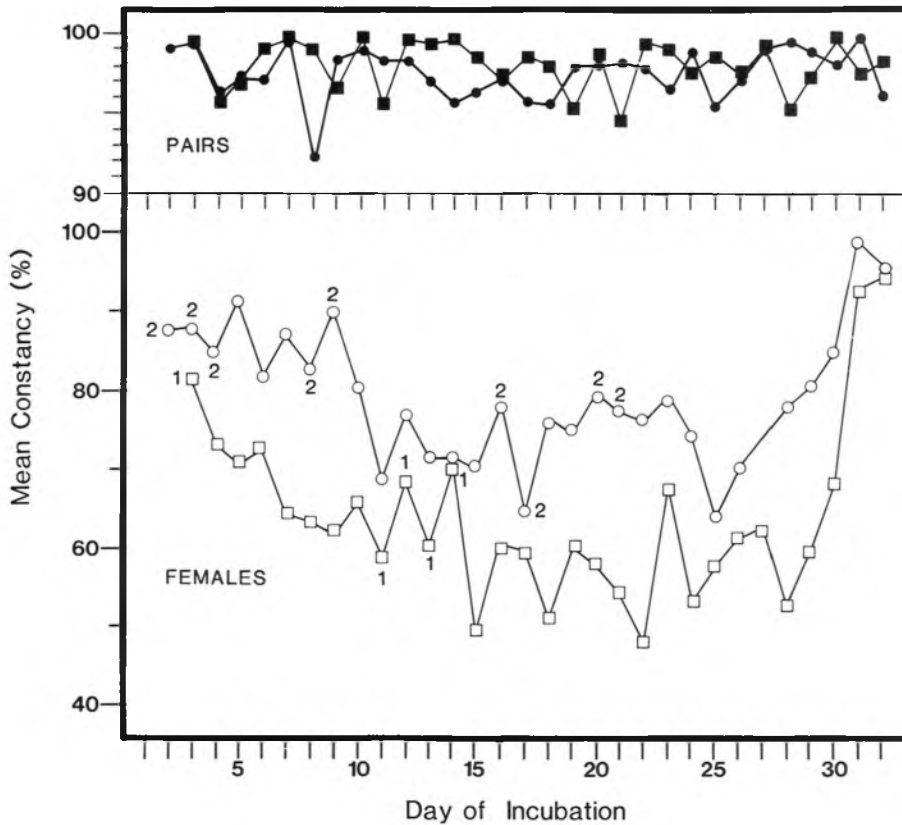


**Figure 2.** Pair and female constancy by day of incubation for a captive Whistling Swan pair, Juneau, Alaska, 1983.

area unless its mate was in the immediate vicinity except to engage in territorial defence or avoid humans. On the two occasions when defence and human disturbance were not involved and the nest was left unattended, it was a female that left, and her mate flew to the nest in under 5 min. The captive male sat on the clutch on half of the days during incubation (Figure 2), and his mean constancy was less than 3%, so

pair constancy in captivity averaged about 15% less than for wild pairs (Table 1). However, the captive male “stood guard” at the nest during female recesses an average 4.9%/day ( $se = 0.48$ ,  $range = 1.3–12.6$ ,  $n = 36$ ).

The percent of the day which wild females recessed was influenced by day of incubation and weather, and differed among individuals (Table 2). Female constancy



**Figure 3.** Mean female and pair constancies by day of incubation at two sets of wild Whistling Swan nests, Colville River Delta, Alaska, 1981-83. Circles = pairs 1-81, 2-82, 2-83. Squares = pairs 3-82, 3-83. The full set of pairs was used to calculate both daily means unless female constancy line is numbered otherwise.

**Table 2.** Regression models to predict female absence (percent of day) during incubation at five wild Whistling Swan nests, Colville River Delta, Alaska, 1981-83. Hatching days omitted. Standard errors of regression coefficients significant at  $p < 0.01$ . A-constants lacking a similar superscript differ significantly ( $p < 0.01$ ).

Variable	Nest	Regression coefficient
a-constant	1-81	19.32 <sup>a</sup> (4.91)
	2-82	21.78 <sup>a</sup> (4.96)
	2-83	20.44 <sup>a</sup> (5.03)
	3-82	35.81 <sup>b</sup> (4.95)
	3-83	38.35 <sup>b</sup> (5.24)
day of incubation		1.99 (0.38)
(day of incubation) <sup>2c</sup>		-0.05 (0.01)
mean wind chill (kcal/m <sup>2</sup> )		-0.017 (0.004)
rain and/or snow fell during day <sup>d</sup>		-3.26 (1.35)

$R^2 = 0.66$ ,  $s_{y.x} = 7.07$ ,  $n = 129$ .

<sup>c</sup>enables a curvilinear relationship between day of incubation and percent absence.

<sup>d</sup>equal to 1 if true, 0 if false.

dropped for the first 10–15 days of incubation, then stabilised until sharply increasing to the highest level during hatching (Figure 3). Female attentiveness rose with mean daily wind chill and when it rained or snowed (Table 2). Female constancy at nests 3–82 and 3–83 were similar ( $t=1.54$ ,  $df=120$ ,  $0.10 > p > 0.05$ ), and lower than at the other nests ( $t \geq 7.75$ ,  $df=120$ ,  $p < 0.001$ ) (Tables 1, 2, and Figure 3). Despite individual variation, females adjusted constancy similarly in response to day of incubation, wind chill and precipitation ( $F=0.94$ ,  $df=16, 104$ ,  $p > 0.50$ ).

Wild swans usually flew (>90%) to and from feeding sites on their territory during recesses. Incubating swans apparently lacked specialised calls or displays to signal nest relief. Males made themselves available for nest duty through trips to the nest. Males made almost twice as many daily trips to the nest as females (males:  $\bar{x}=4.84$  trips,

$se=0.18$ ,  $n=136$ ; females:  $\bar{x}=2.88$  trips,  $se=0.11$ ,  $n=136$ ). However, males initiated sessions during 52.0% ( $n=688$ ) and females 91.3% of trips to the nest ( $n=414$ ). Swans frequently (55%) returned to the nest after territorial defence ( $n=20$ ) and this often led to a nest exchange. Of a sampled 82 nest exchanges, 15% were preceded by defence.

Wild females initiated recesses throughout the day but avoided late evening and early morning hours (Figure 4). Normal recesses made up 84.8% of female recesses ( $n=369$ ) followed by mixed (6.5%), defence (6.0%), and disturbance (2.7%) recesses. Female normal and mixed recesses did not differ significantly in length ( $F=1.04$ ,  $df=1, 323$ ,  $p > 0.10$ ; normal:  $\bar{x}=159.2$  min,  $se=4.86$ ,  $n=313$ ; mixed:  $\bar{x}=175.8$  min,  $se=19.07$ ,  $n=24$ ), and were combined for analysis of recess frequency and length. Daily recess frequency did not differ among females ( $F=0.28$ ,  $df=4, 6, 5$ ,

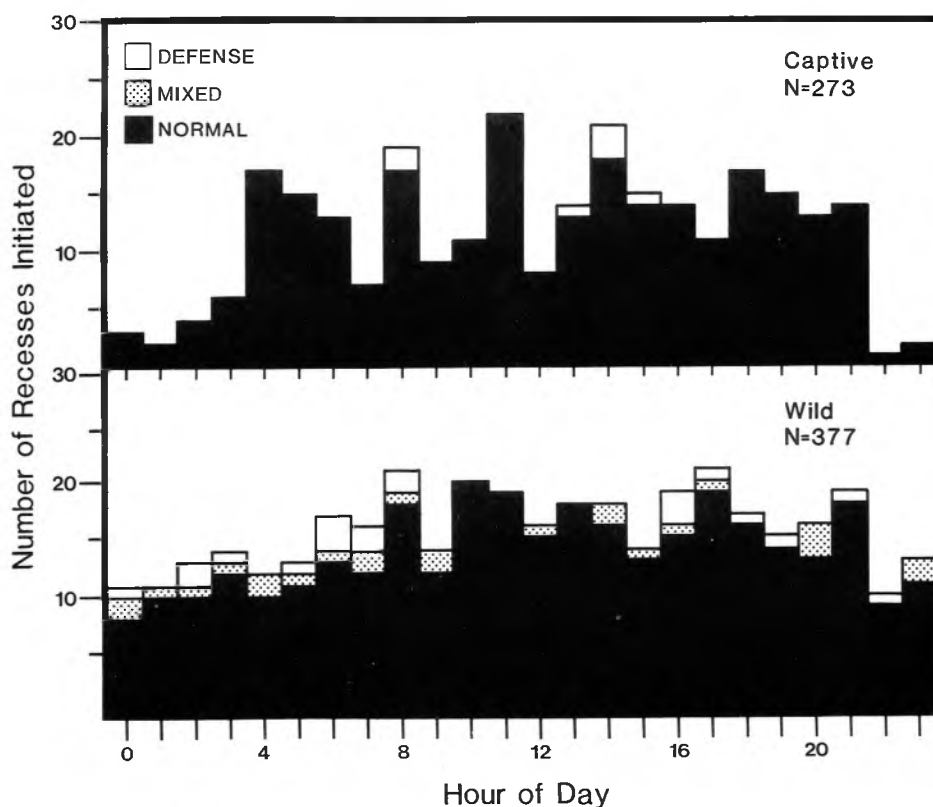


Figure 4. Distribution of normal, mixed and defence female recess initiation times during incubation and hatching at one captive and five wild Whistling Swan nests, Juneau, and Colville River Delta, Alaska, 1983, respectively.



$p > 0.50$ ); females averaged 2.6 recesses (normal and mixed) a day ( $se = 0.08$ ,  $n = 127$ ) and most commonly took three (range = 1–7). Female recesses at nests 3–82 and 3–83 averaged longer than at other nests ( $F = 31.33$ ,  $df = 4, 332$ ,  $p < 0.001$ ) (Table 3). Recess frequency and length (Figure 5) of all females generally increased up to day 10 of incubation, stabilised, then declined during hatching.

Similar proportions of female ( $n = 369$ ) and male recesses ( $n = 423$ ) were defence-initiated (mixed and defence), 12.5 and 9.0%, respectively, and the departing bird or its mate initiated the next session with similar likelihood. Defence recesses averaged 17.3 min ( $se = 5.24$ ,  $n = 22$ ) and 7.1 min ( $se = 1.65$ ,  $n = 18$ ) for females and males, respectively. Frequency of defence-initiated recesses differed as much as five fold between pairs (Table 4) and appeared related in part to proximity of other nesting swans and a pair's social status. They were least frequent at nest 1–81, 1.4 km from the nearest swan nest and the most isolated nest studied. Frequency of defence-initiated recesses at nest 2 declined from 1982 to

1983, when distance between nests 2 and 3 increased from 300 m to 400 m. Defence-initiated recesses at nest 3 dropped only slightly during 1983, however, and observation indicated that when pair 3 engaged in territorial defence pair 2 did not become involved.

In the wild, females did not initiate brief or hiding recesses, but they comprised 4.3% and 11.1% of male recesses ( $n = 423$ ). Mean length for brief recesses was 7.9 min ( $se = 1.60$ , and 12.7 min ( $se = 2.19$ ), for hiding recesses. Brief recesses usually con-

**Table 4. Frequency of defence-initiated recesses (mixed and defence) during incubation and hatching at five wild Whistling Swan nests, Colville River Delta, Alaska, 1981–83.**

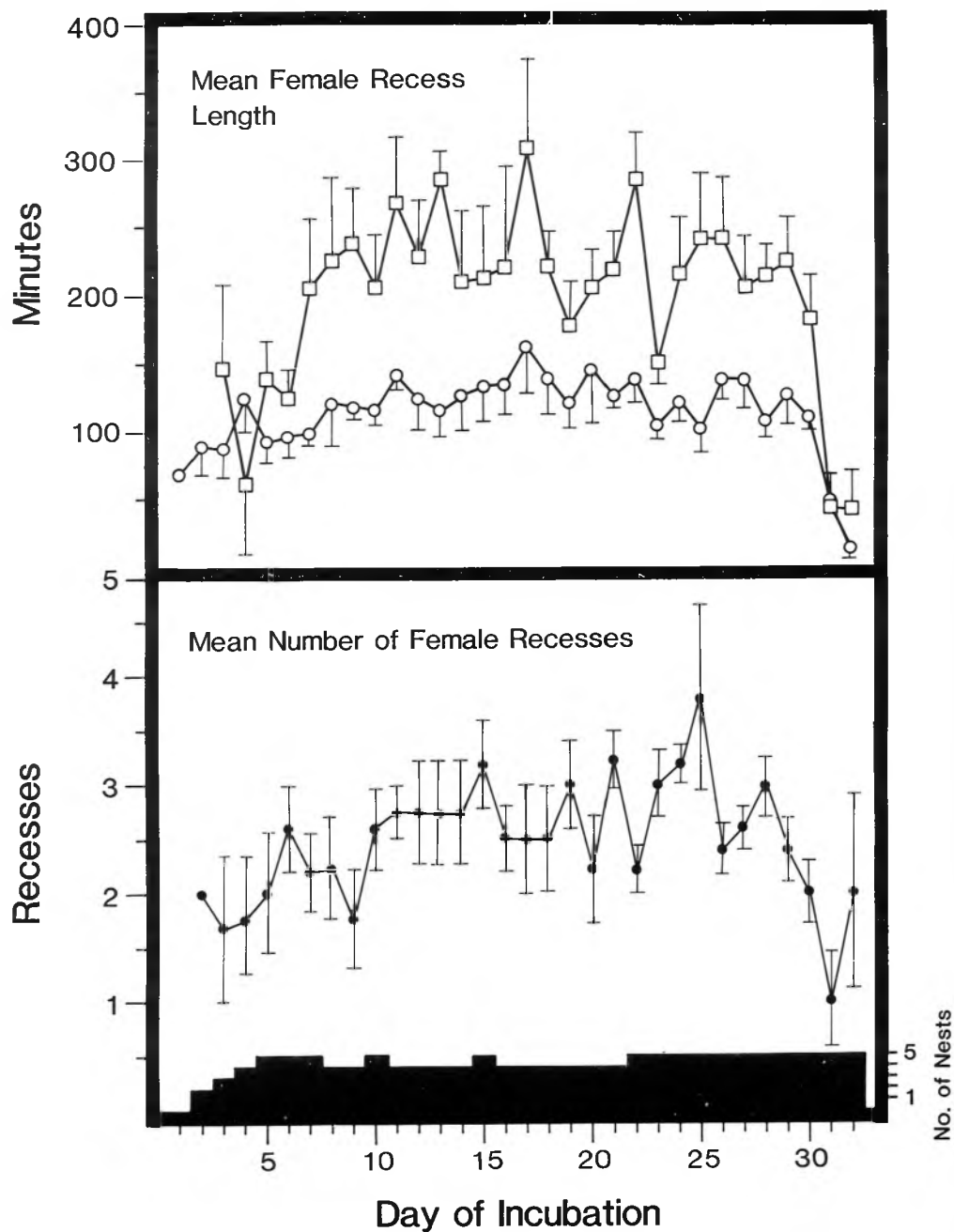
Nest	Days observed	Defence-initiated recesses/day
1–81	31.1	0.22
2–82	28.1	0.53
2–83	26.5	0.23
3–82	30.1	1.13
3–83	26.0	0.96

**Table 3. Female recess and session lengths, and male session lengths (min) during incubation and hatching at a captive and five wild Whistling Swan nests, Juneau, 1983 and Colville River Delta, Alaska, 1981–83, respectively.** Recesses include normal and mixed recesses. Standard errors of means in parentheses. Means within a column lacking one similar superscript differ significantly ( $p < 0.05$ ).

Nest	Session <sup>a</sup>	Female			Male	
		n	Recess <sup>a,b</sup>	n	Session <sup>a</sup>	n
1–81						
mean	489.5 <sup>c</sup> (46.58)	73	117.3 <sup>c</sup> (8.12)	73	116.3 <sup>c</sup> (7.31)	68
range	37–1744		7–354		19–310	
2–82						
mean	357.3 <sup>c,d</sup> (37.69)	79	115.9 <sup>c</sup> (5.52)	73	71.3 <sup>d</sup> (4.66)	105
range	2–2781		4–240		0.5–178	
2–83						
mean	482.0 <sup>c</sup> (53.32)	56	117.9 <sup>c</sup> (4.92)	58	94.3 <sup>c,d</sup> (5.50)	70
range	75–2817		40–247		1–240	
3–82						
mean	363.0 <sup>c,d</sup> (27.73)	67	228.6 <sup>d</sup> (11.98)	63	160.6 <sup>e</sup> (8.70)	88
range	25–1462		22–493		5–450	
3–83						
mean	240.6 <sup>d</sup> (14.60)	83	184.8 <sup>e</sup> (11.99)	70	174.9 <sup>e</sup> (11.59)	76
range	5–680		10–473		2–467	
captive						
median	102	267	25.5	273	31.0	35
range	9–812		2–186		1–120	

<sup>a</sup>sessions and recesses preceded or terminated by film changes omitted for wild pairs.

<sup>b</sup>defence recesses omitted.



**Figure 5.** Mean number and length of female recesses (normal and mixed) by day of incubation at five wild Whistling Swan nests, Colville River Delta, Alaska, 1981-83. For recess length plot, circles = females 1-81, 2-82, 2-83 and squares = females 3-82, 3-83. Vertical bars represent +1 SE.

tained *sideways-building*, and seemed to reflect conflicting tendencies to leave and remain on the nest. Hiding recesses appeared to be a submissive response to other swans. Male 2-82 was responsible for 70% of hiding recesses. Nests 2-82 and 3-82 were 300 m apart, and when his mate recessed, he responded to displays and movements of pair 3-83 by hiding in a trough behind the nest a mean of 23 min/day ( $se=8.6$ , range=0-76,  $n=12$ ). The following year 400 m separated nests 2 and 3, and frequency of hiding recesses by male 2 declined by almost two-thirds.

Incubation rhythm of the captive pair differed from that of wild pairs. Day of incubation and weather influenced percent of day the captive female recessed (Table 5), but in contrast to wild swans, female constancy increased with day of incubation (Figure 2). Whether a male session occurred during the day (MSES), or male constancy (MCON) did not explain further variation in her daily recess time (MSES:  $t=-1.11$ ,  $df=30$ ,  $p>0.10$ , MCON:  $t=0.03$ ,  $df=30$ ,  $p>0.50$ ). On average the female initiated 6.9 ( $se=0.47$ ,  $n=36$ ) normal recesses/day and their mean length was much less than those of wild females (Table 3). She preferred to initiate recesses during daylight hours (Figure 4) and when the male approached, or was sitting nearby. The male remained beside the nest for all or a portion of 65% of female recesses ( $n=221$ ). He usually went to the nest and began *sideways-building* less than 5 min after she left, but on occasion departed with the female instead of remaining at the nest.

When the male did sit on the eggs ( $n=28$ ), he usually ended his session before the female returned (75%), and often left the nest area (46%). Frequency and length of the captive female's recesses were related to male behaviour. Female recess frequency dropped an average 0.74 recesses/day for every recess during which the male sat on the eggs (Table 6), and female recesses averaged 7.2 min longer if the male guarded the nest, and 35.0 min longer if the male sat on the eggs during the female's recess (Table 7). Male constancy declined as incubation progressed (Figure 2) and with rain (Table 8). The male responded protectively to human and Common Raven *Corvus corax* nest visits by being more attentive (Table 8), and once sat on the eggs as a helicopter flew overhead.

#### Nest exchange behaviour of wild pairs

Nest exchange behaviour in the wild followed a flexible pattern and was similar during laying and incubation. As their mate returned, the attending swan moved nest materials about with the bill. Display was most common and vigorous during early nesting, following territorial defence, or when the wind was  $<5$  kmph (usually evening and early morning). Though unquantified, pairs displayed with different frequency and intensity, and some exchanges lacked display.

Females relieving males stopped to preen, particularly the breast, while walking to the nest. When the female climbed onto the nest the male stood, poked into the

**Table 5.** Regression models to predict recess time (percent of day) during incubation for a captive female Whistling Swan, Juneau, Alaska, 1983. Mean wind chill and hours of rain were correlated ( $r=0.6483$ ) and could not be included in the same model. Hatching days omitted. Standard errors of regression coefficients in parentheses. Regression coefficients significant at  $p<0.05$ .

Variable	Regression coefficient			
	Rain model		Wind chill model	
a-constant	17.10	(2.77)	22.27	(4.00)
day of incubation	2.04	(0.64)	2.07	(0.64)
(day of incubation <sup>2</sup> ) <sup>a</sup>	-0.15	(0.04)	-0.15	(0.04)
(day of incubation <sup>3</sup> ) <sup>a</sup>	0.0025	(0.0007)	0.0024	(0.0007)
mean wind chill (kcal/m <sup>2</sup> )	-		-0.0098	(0.0050)
hours in day with rain	-0.204	(0.098)	-	
rain model:	$R^2=0.72$ , $s_{y.x}=3.72$ , $n=36$ .			
wind chill model:	$R^2=0.72$ , $s_{y.x}=3.75$ , $n=36$ .			

<sup>a</sup>enables a curvilinear relationship between day of incubation and percent absence.

**Table 6.** Regression model to predict number of normal incubation recesses per day for a captive female Whistling Swan, Juneau, Alaska, 1983. Hatching days omitted. Standard errors of regression coefficients in parentheses. Regression coefficients significant at  $p < 0.05$ .

Variable	Regression coefficient	
day of incubation	1.79	(0.26)
(day of incubation <sup>2</sup> ) <sup>a</sup>	-0.10	(0.02)
(day of incubation <sup>3</sup> ) <sup>a</sup>	0.0016	(0.0003)
hours in day with rain	-0.10	(0.04)
number of female recesses during which male sat on eggs	-0.74	(0.26)
a-constant=1.89 (1.16); $R^2=0.72$ , $s_{y.x}=1.48$ , $n=36$ .		

<sup>a</sup>enables a curvilinear relationship between day of incubation and recess frequency.

**Table 7.** Regression model to predict length (min) of normal incubation recess for a captive female Whistling Swan, Juneau, Alaska, 1983. Hatching days omitted. Standard error of regression coefficients in parentheses. Regression coefficients significant at  $p < 0.05$ .

Variable	Regression coefficient	
day of incubation	-0.73	(0.17)
number of recesses initiated in last 24 hr	-1.20	(0.57)
recess initiated from 18.00-23.59 hr <sup>a</sup>	-7.19	(3.35)
male guarded nest <sup>a</sup>	7.18	(3.23)
male sat on eggs <sup>a</sup>	35.05	(4.56)
a-constant=48.64 (6.89); $R^2=0.32$ , $s_{y.x}=21.58$ , $n=221$ .		

<sup>a</sup>equal to 1 if true, 0 if false.

**Table 8.** Regression model to predict constancy (percent of day) during incubation for a captive male Whistling Swan, Juneau, Alaska, 1983. Hatching days omitted. Standard errors of regression coefficients in parentheses.

Variable	Regression coefficient	
day of incubation	-0.080 <sup>a</sup>	(0.054)
hours in day with rain	-0.13 <sup>a</sup>	(0.08)
human or raven nest visits <sup>b</sup>	2.86 <sup>c</sup>	(1.02)
a-constant=3.60 (1.09); $R^2=0.31$ , $s_{y.x}=2.98$ , $n=36$ .		

<sup>a</sup> $p < 0.10$ .

<sup>b</sup>equal to 1 if true, 0 if false.

<sup>c</sup> $p < 0.05$ .

bowl, and covered the eggs or performed *sideways-building*. Males covered eggs by poking and tugging materials over them with the bill. About half the time females prevented males from covering eggs by nudging males aside or *settling* immediately after they moved aside. Females preened the breast once again while standing over the bowl and *settled*. Males did *sideways-building* while leaving the nest. Male 3, in 1982 and 1983, was reluctant to be relieved during 60% of exchanges ( $n=17$ ), but his mate persisted in attempts to resume incubation. The male nipped the female from

1-9 times, and less often butted her with his head, shoved her with his breast, or did not rise from the eggs. The female did not nip, but did shove him. Once after being repelled by his nips, she backed up the nest and forced the male to rise from the eggs by nearly stepping on him. On another occasion, the female returned to the nest but departed 3 min later when he did not rise. She returned after 50 min, and preened and walked about until he rose 10 min later.

Wild males relieving females might preen while walking to the nest, but did not concentrate on the breast. Females usually

(>85%) stood and covered the eggs less than 5 min after males arrived if an exchange was to occur. Males did not force females from the nest and females showed no aggression toward mates. Females covered the eggs by standing over the bowl, and circling once while rapidly pulling nest materials over the clutch with the bill. In contrast to egg covering by males, the behaviour followed a rigid pattern and was never interrupted or prevented by males. Females did less *sideways-building* than males after being relieved and often did none. *Sideways-building* was filmed on 33% of female (n=308) and 85% of male departures (n=303). Females left the camera's field-of-view, and most likely had taken flight, within 2 min of rising (maximum=8 min) over 90% of the time. However, in 90% of cases, males were still in the field-of-view 2 min (maximum=90 min) after being relieved, usually because they engaged in *sideways-building*.

#### Incubation behaviour

Behaviour of incubating males and females differed, and this difference was most striking in captivity (Table 9). Upon initiating a session, females repeated *settling* more often than males and always performed *settling* at least once. Thirteen percent of the time wild males merely sat on the eggs when initiating a session; this was always the case for the captive male.

Median sitting spell length of wild males was less than for wild females, and transformed means ( $l/min^2$ ) differed significantly ( $t=6.18$ ,  $df=2710$ ,  $p<0.001$ ), primarily because wild females lengthened sitting spells initiated between 00.00–05.59 and males did not (Figure 6). Means of the transformed sitting spell lengths ( $l/min^2$ ) of captive female and male did not differ significantly ( $t=0.38$ ,  $df=1193$ ,  $p>0.35$ ). Captive and wild females, and wild males performed *resettling* with similar frequency during breaks. However, females appeared to exert greater forward movement, and wild males greater vertical movement of the feet during *shuffling*, and wild males did less patting of materials about breast and sides following *shuffling* than females. During breaks, the captive male poked into the bowl, moved materials about with his bill, sat without *resettling*, and did not pack materials about himself with his bill. *Egg-moving* in the wild occurred during a greater proportion of female than male breaks, but because males took breaks more frequently than females, both apparently moved eggs at similar rates. Observer distance prevented determining whether wild males moved eggs as effectively as females. The captive male did not perform *egg-moving*; nudging with the bill while poking in the bowl apparently did not result in major egg movement. Wild swans usually incubated with head on back (pair 2–83: female: 50.9%, male: 66.8%; pair 3–83: female: 66.0%, male: 72.4%).

**Table 9.** Characteristics of incubation behaviour for a captive and two wild Whistling Swan pairs (2–83, 3–83), Juneau, and Colville River Delta, Alaska, respectively, 1983.

Behaviour	Captive				Wild			
	Female	n	Male	n	Female	n	Male	n
mean times repeated settling/initiation	4.0 (0.23)	45	0 (0)	2	2.7 (6.17)	26	1.6 (0.18)	31
range	1–8		0		1–4		0–3	
median sitting spell length (min)	19.0	1076	22.5	50	27.0	1853	23.0	859
mean times repeated resettling/break	1.3 (0.05)	173	0 (0)	8	1.0 (0.02)	317	1.1 (0.03)	187
range	0–4		0		0–3		0–3	
breaks with egg-moving behaviour (%)	39.9	173	0	8	70.6	309	53.6	179
frequency of egg-moving/hr	1.3		0		1.6		1.4	
hr observation <sup>a</sup>	111.4		21.4		164.8		75.5	

<sup>a</sup>observation limited to daylight hours for captive birds.

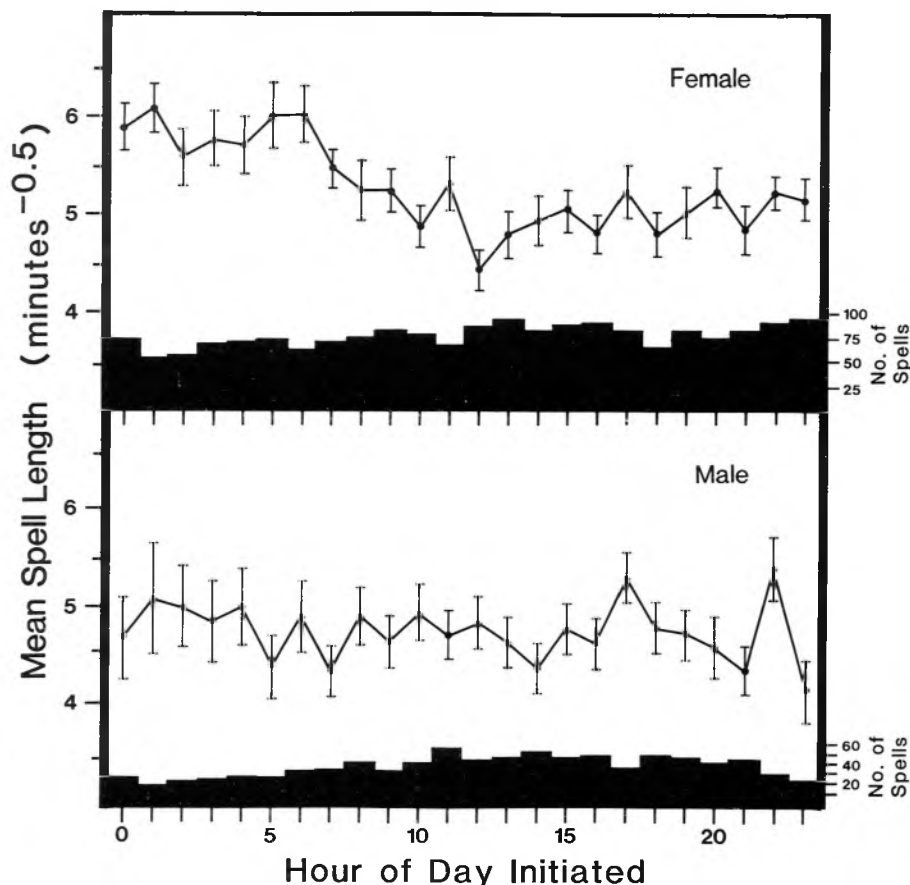


Figure 6. Mean male and female sitting spell lengths ( $l/min^2$ ) ( $\pm 1$  SE) by initiation hour during incubation at three wild Whistling Swan nests (1-81, 2-83, 3-83), Colville River Delta, Alaska, 1981 and 1983.

#### Artificial egg temperatures

Data from days 1-9 and 21-24 of incubation were analysed, when the egg's temperatures, and its rapid response to the onset of female sessions and recesses, indicated it was positioned in the clutch. On average, the egg cooled  $2.4^{\circ}\text{C}$  ( $se=2.71$ , range=0-12.5), from  $34.3^{\circ}$  to  $31.9^{\circ}\text{C}$ , during female recesses and rose that amount during female sessions. The egg remained at the same temperature or cooled during male sessions. A multiple regression model was developed to identify factors influencing the egg's cooling rate during female recesses (Table 10). The egg cooled more the longer the female's recess, the cooler the air relative to the egg, or during rain. In addition, comparison of length coefficients

for unattended periods ( $-0.059$ ) and male sessions ( $-0.059 + 0.037 = -0.023$ ) (Table 10, Figure 7) indicated the temperature drop averaged 2.5 times less for periods of equal length when the male sat. Male ability to slow egg cooling was probably a result of heat and insulation provided by his body. No rain fell during male sessions so his effect under rainy conditions could not be evaluated.

#### Recess and daily activity budgets of a wild pair

Onset of incubation sharply influenced female 3-82's daily activity budget (Table 11). Most dramatic was a drop in foraging during early incubation to about 25% the prelaying level. However, because she

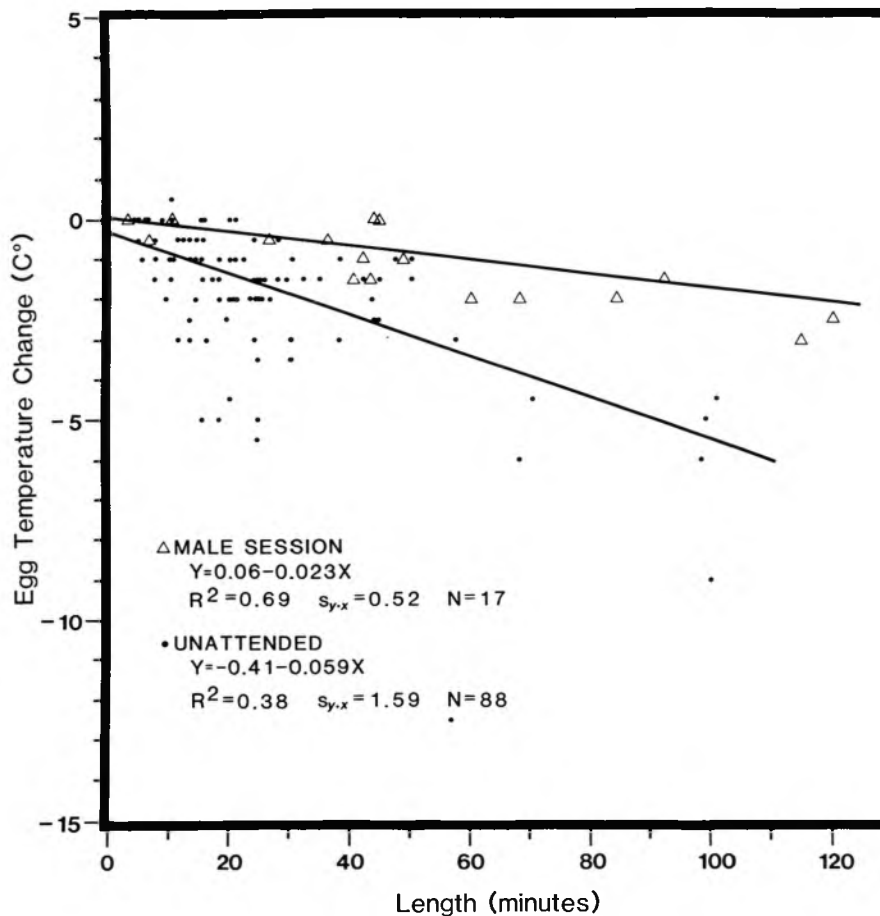


Figure 7. Relationship between the temperature change of an artificial egg placed in a captive Whistling Swan nest, and lengths of male sessions and periods when nest was unattended.

Table 10. Regression model to predict temperature change of an artificial egg during incubation recesses of a captive female Whistling Swan, Juneau, Alaska, 1983. Data from days 1-9 and 21-24 of incubation. Standard errors of regression coefficients in parentheses. Regression coefficients significant at  $p < 0.005$ .

Variable	Regression coefficient	
length (min) <sup>a</sup>	-0.059	(0.005)
difference between air and egg temperature (C°) <sup>b</sup>	-0.052	(0.019)
presence of rain <sup>c</sup>	-3.561	(0.439)
cross-product of male session indicator variable and length <sup>d</sup>	0.037	(0.006)
a-constant = 1.105 (0.460); $R^2 = 0.69$ , $s_{y,x} = 1.07$ , $n = 105$ (88 unattended periods and 17 male sessions).		

<sup>a</sup>length coefficient for absences.

<sup>b</sup>equal to difference between egg and air temperature at start of unattended period or male session.

<sup>c</sup>equal to 1 if true, 0 if false.

<sup>d</sup>equals difference between length coefficients for unattended periods and male sessions.

lowered constancy about 10% during middle and late incubation and increased the proportion of recess time feeding, by late incubation she foraged almost 30% a day, or half the prelaying level. Onset of incubation had minor effect on male 3-82's daily activities despite his relatively high constancy (Table 11). Foraging remained at a level similar to that during prelaying because he spent 60% of recess time feeding.

#### Predators

Twenty-one interactions between wild incubating swans and predators were gathered by observation and filming. Most involved arctic fox *Alopex lagopus* (n=14) or red fox *Vulpes vulpes* (n=2). During 12 observations a fox passed the swan without threatening and the swan did not interrupt its sleeping spell (n=7), became alert (n=4), or assumed *hiding posture* (Hawkins 1986) (n=1). During remaining encounters the fox walked toward the nest, the swan threatened, and the fox left. Only once did a fox bare its teeth and half-charge the nest.

#### Hatching and nest departure

Hatching brought dramatic changes in behaviour. Some of the longest female sessions occurred, in two cases exceeding 46 hr for wild females; mean constancy of wild females rose to about 95% (n=10) (Figure 3). Wild females shortened sleeping spells (incubation:  $\times = 1.87$  l/min<sup>2</sup>, se=0.04, n=926; hatching:  $\times = 0.98$  l/min<sup>2</sup>, se=0.07, n=65; F=38.45, df = 1,924, p<0.001) and percent time incubating with head on back

dropped to less than 10% (female 2-83: 7.6%, female 3-83: 8.8%). Females usually did not put their heads on their backs unless the male was nearby. *Settling* and *resetting* became less vigorous then ceased about a day before nest departure. *Egg-moving* became infrequent and stopped, as did packing materials about the breast and sides after changing position. Instead, females stood, poked in the bowl, preened, especially the breast, then gently sat with wings slightly spread.

Wild males made more frequent trips to the nest ( $\times = 7.3$  visits/day, se=0.87, n=10) and male nest visits increased in length during hatching (incubation: median=8.5 min, n=262; hatching: median=47.0, n=68). On day 32, after cygnets appeared dry, but not ready to leave, females at three wild nests took short recesses. Males then usually stood or walked about the nest. However, at two wild nests males sat on the bowl for a total of seven sessions lasting less than 3 min each, and at a third nest the male had two sessions lasting 139 and 79 min.

Close monitoring of hatching was possible in captivity. Egg-clicking (Vince 1969) was heard on the afternoon of day 36. The next morning (07.50 hrs), one egg had pipped, embryos peeped, and the female repeated soft whoops. By late afternoon (19.25 hrs) at least two cygnets had emerged. Cygnets appeared dry the following morning (07.30 hrs) and the adults escorted them from the nest about 7 hr later. In the wild, nest departures were between 14.00-18.00 hrs (n=4), or in the morning (07.29 hrs) (n=1). At two nests, the cygnets followed the male from the nest to a nearby pond (<20m) during a female recess. When

**Table 11. Activity budget of a wild Whistling Swan pair (3-82), Colville River Delta, Alaska, 1982.** Activities expressed as percent of daily activities and in parentheses as a percent of recess activities. T<0.01%.

Behaviour	Percent of activities							
	Pre-laying	Female Incubation			Pre-laying	Male Incubation		
		Early	Middle	Late		Early	Middle	Late
foraging	56.4	15.4 (48.1)	23.3 (58.2)	28.6 (68.2)	35.0	43.2 (61.8)	38.3 (61.3)	39.8 (65.6)
stationary	25.6	6.7 (21.0)	6.4 (16.2)	5.6 (13.6)	38.5	7.3 (10.4)	6.4 (10.3)	5.9 (9.8)
comfort-maintenance	3.2	4.8 (15.0)	3.8 (9.4)	3.3 (7.9)	3.1	1.6 (2.3)	0.8 (1.3)	1.9 (3.1)
alert	0.7	0.1 (0.4)	0.1 (0.2)	0.1 (0.3)	9.7	2.7 (3.8)	3.3 (5.3)	3.2 (5.3)
social behaviour	2.1	0.9 (2.9)	0.5 (1.2)	0.4 (0.9)	2.2	1.7 (2.4)	0.8 (1.3)	1.0 (1.6)
nest-construction								
or -maintenance	2.6	0.1 (0.5)	0.4 (0.9)	T (0.1)	1.3	0.3 (0.4)	0.6 (0.9)	0.2 (0.3)
locomotion	9.4	3.9 (12.0)	5.5 (13.9)	3.8 (9.0)	10.2	13.1 (18.8)	12.1 (19.5)	8.7 (14.4)
mean constancy	-	68.1	60.0	58.1	-	30.1	37.7	39.3
number of time-budget observations	5064	966	1215	2705	4838	2207	1709	2750



females returned, they poked into the bowl, *settled*, then arose and joined the male and young. At an island nest (1–81) two cygnets left with the male while the female brooded the others. They returned to the nest after 50 min, and the entire brood departed with their parents 40 min later. Pairs escorted broods from upland nests to nearby lakes by walking and swimming from pond to pond and did not return to the nest. Cygnets were brooded on the island nest, but use dropped with each day following nest departure.

#### *Effect of nest monitoring on wild birds*

Film changing disturbed incubating swans. Personnel were in view of nests an average of 31–81 min while travelling to and from cameras. During almost half (42.6%) of film changes ( $n=74$ ) the incubating swan left the nest, and a mean of 64 min ( $se=7.8$ ,  $n=29$ ) elapsed before incubation resumed. Pair constancy averaged 23 min ( $se=5.79$ , range=0–162,  $n=58$ ) lower on film change days, a significant difference ( $F=12.47$ ,  $df=1,127$ ,  $p<0.001$ ). However, film changing did not affect male and female constancy when individuals were examined ( $p>0.05$ ) or when swans were grouped by sex (males:  $F=0.17$ ; females:  $F=0.09$ ;  $df=1,127$ ,  $p>0.50$ ). Response to film changing differed by sex. Females were present during 73.5% of film changes when previous monitoring enabled identification ( $n=68$ ), and had higher probability of remaining on the nest (76.0%) than males (5.5%). Females who left were more likely than males who had left to initiate the session following the person's departure (83.3% vs. 58.8%) and returned sooner ( $\bar{x}=46.8$  min,  $se=11.52$ ,  $n=10$ ) than males ( $\bar{x}=90.6$  min,  $se=14.89$ ,  $n=10$ ).

## Discussion

### *Energetics of female incubation*

Afton (1980) proposed that body size has been fundamental in shaping waterfowl incubation behaviour because fasting endurance increases with size (Calder 1984). Large female waterfowl tend to be more attentive to their nests than smaller waterfowl, which must forage intensively during incubation recesses to meet maintenance requirements (Afton 1979). Whistling Swans did not fit the general

waterfowl pattern because, despite their large size, mean incubation constancy of wild and captive females was between 60–85%, similar to many ducks, and wild females foraged heavily during incubation recesses (this study; Scott 1977).

Female ducks and geese typically lose weight during incubation because nest attendance restricts foraging. Body weights of incubating female Whistling Swans are unavailable but the rapid drop in female constancy during early incubation suggests they lost weight. Aldrich and Raveling (1983) found incubation constancy of captive female Canada Geese *B.c. moffitti* declined gradually as incubation proceeded. Loss of body weight paralleled declining nest attendance until a critical lower weight was reached, and thereafter weight loss slowed because females increased recess and foraging time. Bromley (1984) found a similar pattern for wild female Dusky Canada Geese except foraging during late incubation prevented further significant weight loss. Both felt the rapid increase in recess time during late incubation coincided with lipid reserve depletion. The sharp drop in nest attendance of wild female Whistling Swans during early incubation suggests that females depleted lipid reserves before mid-incubation more quickly than female geese. Stabilisation in female constancy between days 10–15 of incubation, which lasted until a few days before hatch, suggests that recess foraging then approximated female energy needs and weight loss slowed or ceased.

Mean incubation constancy of wild female Whistling Swans varied as much as 18.8% or 4.5 hr day of recess time. Less attentive females may have initiated incubation with smaller lipid reserves than more attentive females. Captive female Canada Geese who are heavier at the beginning of incubation (believed due to greater lipid reserves), are more attentive to their nests than lighter females (Aldrich & Raveling 1983). Lipid levels of female waterfowl have been related to habitat use on spring staging areas (Gauthier *et al.* 1984) and to whether the female has bred before, i.e. first-time breeders are lighter than females with prior breeding experience (Aldrich and Raveling 1983). Whistling Swan use of spring staging areas has not been studied, but birds leave wintering grounds in North Carolina at low weight with small lipid reserves and, like northern-breeding geese, must acquire materials important for reproduction from

the spring staging areas (Bortner 1985). Breeding experience could influence lipid levels of female Whistling Swans. However, it seems probable the wild females with low incubation constancy (3-82 and 3-83) were the same bird because they used the same nest mound, in which case a female maintained relatively low incubation constancy in consecutive years. Perhaps swan breeding territories differ in the amount of food and/or its nutritional quality to such a degree that female foraging efficiency is affected. Hohman (in press) believes food availability in wetlands used during incubation recesses influenced the constancy of female Ring-necked Ducks *Aythya collaris*. In addition, individual differences in foraging ability of female Whistling Swans, and male willingness to incubate, perhaps related to male reserve levels, could influence female nest attendance. Whatever the reason, biparental incubation appears to allow females more flexibility in allocating time and energy to incubation than when females alone incubate.

Mean incubation constancy of the captive female was similar to that of two wild females, but the relationship between day of incubation and female nest attendance differed markedly from that in the wild. Wild and captive constancy were similar at the onset of incubation, but thereafter instead of falling to a stable level, the captive female increased her attentiveness (Figure 2). Interpretation is difficult because the captive female was not weighed nor her food consumption measured. Food was probably more readily available than in the Colville River Delta, and maintenance requirements were probably lower because movement was restricted and Juneau was warmer. However, the captive female foraged about 13% per day during early incubation (Hawkins 1986), similar to the wild female under close observation (Table 11). Assuming incubation constancy is related to body weight, foraging during early incubation may have enabled the captive female to gain weight and be more attentive to her nest during later incubation. This reaffirms the idea that females have relative flexibility when allocating energy to incubation.

*Factors influencing male incubation, and its benefits and costs*

Links between territorial defence, ag-

gression, and male incubation suggest the primary stimulus of male nest attendance was defence and the function was protection of the eggs. Prelaying nest visits by solitary captive and wild males included aggressive display and calling. Males of wild pairs (3-82, 3-83) with the highest frequencies of defence-initiated recesses exhibited aggression toward females upon being relieved of incubation duty, and incubated significantly more than other males. Territorial defence by either or both members of wild pairs preceded 15% of nest exchanges. A relationship between aggression and male incubation was substantiated by an unusual observation following nest departure. Male 3-83 left his family to chase a swan 5.5 hr after he and his mate escorted the cygnets from the nest. He flew to the nest after successfully evicting the intruder and sat on the empty bowl 21 min before rejoining his family.

Minimal incubation by the captive male was the most striking difference between captive and wild nesting behaviour. Other studies of captive Whistling and Bewick's Swans found no male involvement (Johnstone 1957; Evans 1975) or high involvement similar to that of wild males (Evans 1975, 1977). Captive behaviour indicates that male incubation is not essential for successful embryo development, and suggests that risk of egg predation, and time and energetic constraints favour male incubation.

Tundra-breeding geese and swans cannot re-nest because of the short arctic summer so protection of the clutch is vital to breeding success. High nest attentiveness is an important defence against egg predation (Drent 1970; Harvey 1971). Though nest attendance of wild females varied considerably over the course of incubation, consistent male attendance during female recesses meant the nest was rarely left unprotected. The captive study supports a connection between male nest attendance and likelihood of egg predation because the pen provided some protection from predators, confined the pair near the nest, and the male responded to ravens and human visits by sitting on the eggs more.

Were predator protection the sole function of male nest attendance males could remain near the nest rather than sit on the eggs. As Evans (1975, 1977) suggested, a male slowed egg cooling by sitting on them. This apparently had beneficial energetic

consequences for females and young. Comparison of the incubation period in captivity with that in the wild suggests that sitting by wild males was the primary reason incubation and hatching took 6–7 days less in the wild. Therefore, the time when wild females had to restrict foraging was reduced, and additional time was provided for young to fledge (Scott 1977; Cooper 1979), for the female to complete the post-breeding moult, and for migration preparation. When males incubated, females took relatively infrequent, long recesses which were probably less demanding because the eggs had to be rewarmed less often, and females may have had to exert less energy to rewarm them due to the male effect on egg cooling rate. In addition, females usually flew to and from foraging sites and, because flight is the most energetically costly behaviour, few, long recesses probably were more efficient than many, brief ones.

Costs of nest attendance to males appear minor. Incubation may expose males to greater risk of predation. Arctic foxes were the most important predator of Whistling Swan nests in the Colville River Delta (L. L. Hawkins, unpubl. data) and probably are throughout most of the *columbianus* breeding range. The large body size of swans apparently allowed swans effectively to protect themselves and the clutch from predation because foxes rarely tested incubating swans. In addition, males were less likely than females to expose themselves to risk. Males sometimes hid beside the nest in apparent effort to avoid conflict with other swans, but females did not. Males rarely remained on the nest when personnel visited nest-monitoring cameras, resumed incubation following such a disturbance less often, and, if they returned, did so more slowly than females.

Incubating could have detrimental energetic consequences for males. Nest attendance could restrict their foraging, particularly during the laying period, if they were highly attentive. However, despite the high incubation constancy of male 3–82 ( $\times=35.8\%$ ), he foraged for a similar time per day during prelaying and incubation. Other wild males were not closely observed but it seems likely that nest attendance during incubation did not adversely limit foraging because they incubated about 10% less than male 3–82. The energetic cost of incubating eggs is under debate, but males

apparently did not actively maintain the temperature of the eggs so energy expended probably did not exceed, and was less, than that expended sitting outside the nest. Males usually incubated with head on back, a heat-conservative behaviour (Harvey 1971), and nests provide additional thermal insulation.

#### *Quality of male and female incubation behaviour*

The greater time investment and the greater influence females have on timing and length of male and female incubation sessions suggests the quality of male care differs from the female's. Indeed, a captive male slowed heat loss but could not indefinitely maintain the temperature of an artificial egg. Egg heating is enhanced by the presence of a brood patch (Bailey 1952) and behaviour promoting contact between brood patch and eggs (Beer 1961; Drent 1970). Differences in the incubation behaviour of the captive male and female suggest reasons why the male did not heat the eggs as well as the female. Differences in the incubation behaviour of wild mates corroborate direct evidence obtained in captivity.

Kear (1972) stated that swans heat eggs by fluffing the breast feathers around the eggs and directly applying the skin to their surfaces. Female breast preening prior to initiating a session, lacking in males, probably facilitated this. Like other female swans (Kear 1972; Cooper 1979), *down-pulling* by female Whistling Swans was minor compared to that of ducks (Caldwell & Cornwell 1975; Siegfried *et al.* 1976) and geese (Hanson 1959). However, its occurrence suggests females possessed a specialisation for heating eggs and hatchlings that males lacked because they did not *pull down*. *Shuffling* of the feet during *settling* positions eggs to increase intimate contact with the brood patches in gulls (Beer 1961). The captive female *shuffled* the eggs into erected breast feathers as Evans (1977) described for a captive female Whistling Swan. In contrast, the captive male weakly pushed against the sides of the bowl with his feet and his feathers remained flattened against his breast when he sat on the eggs. In other captive studies, male Whistling (Evans 1977) and Bewick's Swans (Evans 1975) did not position the eggs among the breast feathers, although in sitting they fell

forward and pushed the sides of the bowl with the feet. *Shuffling* by wild males appeared to have greater vertical than forward movement, in contrast to that of females, and probably did not move the eggs among the breast feathers.

Scraping and shoving during *settling* and *resetting* form and maintain the nest bowl (Cooper 1979), expose and arrange the eggs (Beer 1961; Drent 1970), and ultimately facilitate heat transfer to the eggs. In gulls, tactile feed-back from the eggs is important in eliciting *settling* (Beer 1961). If conditions in the nest do not release *shuffling*, or return the necessary stimulation following *shuffling*, the bird performs *settling* again (Beer 1961). Male behaviour suggested that they were less tactily sensitive to eggs and nest materials than females. The captive male did not perform *settling* or *resetting*. When initiating an incubation session, wild males did not always perform *settling*, and repeated the behaviour less often than females, who consistently performed *settling*. When wild broods followed males from nests during female recesses, females returned to the nest, *settled*, then quickly joined their families, and did not return to the nest. However, as noted earlier a male sat on an empty bowl for 21 min after his young left the nest.

Characteristics of incubation rhythms of wild swans provide further evidence females are more adept at heating eggs. Females incubated more as wind chill rose or if there was precipitation – times of thermal stress. Males seldom incubated during hatch, when heat is required to dry and brood the cygnets. Male ability to maintain egg temperature probably varied with environmental conditions. Ball (1983) concluded that male Barn Swallows *Hirundo rustica*, which lack brood patches, can incubate as well as females during the day under mild temperatures (20–25°C). The captive male swan once maintained the temperature of the artificial egg for 45 min. Although eggs cooled when the male was on the nest, embryonic development can occur to 25–27°C (Drent 1975). A brood patch may confer an advantage most apparent during times of thermal stress (Bailey 1952; Ball 1983).

#### *Evolution of male involvement in anatid incubation*

There appear two patterns of involvement

by male anatids in incubation. The more primitive is exhibited by whistling ducks where male and female have similar roles. Northern Red-billed Whistling Ducks *Dendrocygna a. autumnalis* alternate nest attendance on average every 24.9 hr (Chronister 1985). They do not *pull down* (Kear 1970), have similar abdominal vascularisation (Rylander *et al.* 1980) and regulate egg temperature equally well (Bolen & Smith 1979). The second pattern is found in Black Swans, Bewick's Swans and Whistling Swans where females make greater investment in incubation. Braithwaite (1981) reported that in a captive Black Swan colony both sexes may participate in incubation but usually the female has larger responsibility, in most cases leaving the nest to feed for brief periods. Others usually found female Black Swans on the nest at night and males incubating from mid-morning until late afternoon (c.f. Kear 1972), for 5–6 hr (Howey *et al.* 1984). Small amounts of down are present in Black Swan nests (Scott *et al.* 1972), suggesting females have specialisation for heating eggs. Female Bewick's (Evans 1975) and Whistling Swans were primarily responsible for incubation, *pulled down*, and assumed a greater role in incubation during times of thermal stress.

I suggest incubation by male anatids is favoured when: 1) high incubation constancy is essential to reproductive success, and 2) female fasting necessary to maintain high nest attendance is energetically prohibitive. Anatids with male incubation are highly attentive to their nests although in most cases the advantages have not been identified. During daylight hours, Red-billed Whistling Duck pairs averaged 96.5% incubation constancy (Chronister 1985). Black Swan nest attendance has not been quantified, but Braithwaite (1981) described how among established pairs male and female promptly assume incubation when their mate leaves the nest. Evans' (1975) descriptions of captive Bewick's Swans indicate the nest was seldom left unattended. Incubation constancy of wild Whistling Swan pairs averaged 96.6–99.3%. Sparse evidence suggests female waterfowl do not fast or suffer extreme weight loss during incubation when males are involved. Weights of female Red-billed Whistling Ducks did not change significantly during incubation (Chronister 1985). Black Swans rarely undergo hypertrophy of protein and fat

reserves prior to breeding (Braithwaite 1982) suggesting foraging during incubation recesses is necessary to meet female energy needs. Female Whistling Swans recessed on average 5.0–9.5 hr per day, and primarily foraged during that time.

Female fasting necessary to maintain incubation constancy may be energetically prohibitive in the short term, or in the long term because it seriously lowers the future reproductive value of the female. Red-billed Whistling Ducks are small (mean female weight = 839 g) and this probably limits female ability to incubate at a high level (Afton 1980; Chronister 1985). It is less apparent why a large bird like the Whistling Swan would not, especially when female geese and most other female swans are solely responsible for incubation and highly attentive to their nests. Male incubation appears one aspect of a conservative reproductive strategy. Theoretical ecologists suggest survival rates are associated with remaining reproductive value (Pianka & Parker 1975). Species with high survival rates should invest less per reproductive effort than species with a lower expectation of producing future offspring. Depending on the number of eggs laid, female Whistling Swans commit 14.7–22.0% of winter body weight to a clutch (mean winter weight = 6.3 kg (Sladen *et al.* 1981); egg weight = 280 g (Scott *et al.* 1972); range of mean clutch size = 3.30–4.95 (Lensink 1973)), less than northern-breeding geese do (c.f. Krapu *et al.* 1985). This suggests the Whistling Swan life history strategy is more conservative than that of geese.

In addition to investing less energy in each clutch, it would be advantageous for male and female Whistling Swans, which are long-lived and maintain a long-term pair bond (Evans 1979), to share nesting tasks to further reduce individual demands associated with breeding. Male and female parental roles of Whistling Swans during nesting are less specialised than those of geese; males were more active in defence (Hawkins 1986), and females more active in incubation, but both sexes participated in each. In conjunction with more generalised parental roles, the rapid decline in constancy of female Whistling Swans during early incubation suggests nutrient storage is not as sex specific as in geese.

There is insufficient information to identify specific mechanisms favouring male involvement in Whistling Swan incubation.

However, Whistling Swans are relatively large waterfowl and body size profoundly influences the physiology, ecology and life-history strategy of a species (Calder 1984). In addition, constraints associated with breeding in an arctic environment are probably a major influence. Avian energy requirements increase exponentially with body weight (Lasiewski and Dawson 1967), and an increase in body size prolongs the time needed to lay and incubate eggs, complete the post-breeding molt, and rear young. The arctic environment, however, is less productive, and provides less time to complete these tasks than more temperate areas.

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#### Summary

Whistling Swan *Cygnus c. columbianus* nesting behaviour was studied in the Colville River Delta, Alaska, from 1981 to 1983, and in cap-

tivity. Study objectives were to: 1. quantify male and female nesting behaviour, and identify factors influencing involvement of each sex in incubation, 2. compare male and female ability to heat eggs, and 3. determine the effect of nest attendance on the daily activity budgets of male and female.

At a wild nest monitored during laying, the male sat on the nest following laying of the first egg. This pattern continued, and during incubation, wild males consistently sat on the clutch when their mates departed. In captivity, however, the male frequently stood beside the nest but rarely sat. Mean female incubation constancy ranged from 60.4–83.0% and differed significantly among individuals. Nest attentiveness of wild females declined curvilinearly with day of incubation, then increased sharply at hatch. Females were more attentive on days with precipitation and as wind chill increased. Male incubation behaviour primarily appeared to be a protective response against egg predators and appeared linked to aggression and territorial defence.

Females provided the eggs better quality care than males. Females *pulled down*, but males did not, suggesting that females possessed a brood patch. The temperature of an artificial egg rose a mean of 2.4°C when the captive female sat on the nest. The egg cooled when the male sat on the

nest, but 2.5 times more slowly than when he did not sit. Although the male had lesser ability to heat the egg than his mate, the insulative protection males provided appeared important. Incubation in captivity required 38 days, but 31–31 days in the wild, probably because wild males sat on the eggs during female recesses. Incubating reduced the time females could forage. However, wild females increased foraging during middle and late incubation by taking more frequent and longer recesses. Despite incubating an average 35.8% a day, a wild male foraged for a similar time per day throughout the incubation period as during prelaying.

Although male incubation was not essential for successful embryo development, it appeared highly beneficial. Male nest attendance: 1. protects the eggs from predators, 2. may shorten the incubation period by at least 6–7 days, and 3. probably reduces demands placed on females during breeding. Male involvement in incubation may be favoured in anatids when high incubation constancy is essential to reproductive success, and female fasting (necessary to maintain high nest attendance) is energetically prohibitive. Fasting may be prohibitive in the short term because of constraints imposed by body size, or in the long term because it seriously lowers future female reproductive value.

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