

Breeding behaviour of captive Bewick's Swans

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Breeding in the wild

No behavioural study has been made of Bewick's Swans *Cygnus columbianus bewickii* breeding in the wild. They nest for the most part north of the Arctic Circle in a range from the Kola Peninsula (c. 35°E) to about 160°E. Those swans breeding east of the River Lena (125°E) are sometimes differentiated as *Cygnus columbianus jankowskii*. These birds fly south-east to winter in China, Japan and Korea, while those to the west come to East and West Germany, Denmark, the Netherlands, England and Ireland (Ogilvie, 1972).

According to Dementiev & Gladkov (1952) Bewick's Swans usually arrive on their breeding grounds in the second half of May, coinciding with the beginning of the thaw. They prefer an old nest site and the female looks after the restoration. The nest is usually built on a dry elevation in marshy land, is constructed of old sedges and moss, and said to be lined with down. It is 50–60 cm high and about 100 cm in diameter. There is an unrestricted view all round and the birds have a territory of some 2,000 hectares. The first eggs are laid at the end of May.

Accounts of clutch size vary. However the statement by Hilprecht (1956) that there are usually five eggs seems reasonable, as pairs with five cygnets are not infrequently seen in the wintering grounds. Incubation lasts 29–30 days and it is said that the female incubates alone. When she has to leave the nest, she may or may not cover the eggs with feathers or down (Dementiev & Gladkov, 1952).

Bewick's Swans only recently bred in captivity and the opportunity was taken to expand these limited field accounts by close observation at Slimbridge (Gloucestershire) and at Bentley (Sussex).

History of captive breeding

In November 1948 a wild male Bewick's Swan, thought to be in its second winter, was caught at Slimbridge, and in February 1950 it was paired there with a wild-caught adult female obtained from Holland.

On 2nd June 1956 a nest was begun using rushes. The next day both birds were building, and subsequently the female was sitting on

and shaping the nest. The first egg was found on 6th June, and two more completed the clutch. The male was not seen to help incubate, nor did he defend the nest strongly. Two eggs hatched on days 29 and 30, and one chick fledged (Johnstone, 1957).

The pair (which was moved to a more desirable pen in 1957) then bred regularly (Table 1). The usual avicultural technique of removing the first clutch for incubation by a foster parent (usually another swan species) was successful in inducing the production of a second clutch, although under natural, high arctic conditions, replacement clutches would not be expected. The female incubated the second clutch herself. Intervals between the first clutch being removed and the second started ranged between 13 and 26 days. In 1960, 1973 and 1974 the female was left her first clutch; in the last two years out of consideration for her age.

In September 1962 the male died. The following spring an adult male (No. 2) was taken under licence from among the wild migrants to Slimbridge and feather-cuf. However he did not settle and when fully-winged again in September 1963, flew off, to be recovered the next May in Arkhangel Province, USSR.

The female was then given one of her 1961 offspring (No. 3). She laid again in 1966 but all the eggs were infertile. Young were hatched in 1967 and 1968, but none in 1969, the male dying that June.

Another adult male (No. 4) was taken under licence from the wild at Slimbridge in December 1969, but although he settled quite well with the female, there were no signs of nesting. One of the 1962 offspring (No. 5) was therefore introduced into the pen on 28th March 1973. He had never been well-paired nor shown much aggressive behaviour.

No obvious change in the behaviour of either male was noted, and only the slightest preference by the female for male No. 5. She was throwing nesting material around on 28th April, but not near the site used since 1957. As she was aged at least 25, it was thought she was perhaps too old to lay.

Male No. 4 was then removed, and only 21 days later the first of five eggs was laid, on 4th June. It is interesting that she laid in early June, just as the very first time, whereas in the intervening years she laid in the first three weeks of May or even in April. However, after the earlier gap of three years, she laid 'on time'

Table 1. Record of breeding Bewick's Swans at Slimbridge. The same female was involved in each year.

Year	Male	Age of male in years	Date of first egg	No. of eggs 1st clutch	No. of eggs 2nd clutch	Hatched	Reared
1956	No. 1	9	6 June	3	—	2	1
1957	No. 1	10	7 May	5	3	0	—
1958	No. 1	11	30 April	5	3	3	1
1959	No. 1	12	3 May	5	4	4	2
1960	No. 1	13	1 May	6	—	4	4
1961	No. 1	14	12 May	4	3	2	2
1962	No. 1	15	1 May	6	3 or 4	2	2
1963	No. 2	Ad.	—	—	—	—	—
1964	No. 3	3	—	—	—	—	—
1965	No. 3	4	—	—	—	—	—
1966	No. 3	5	8 May	5	4	0	—
1967	No. 3	6	9 May	6	5	3	2
1968	No. 3	7	8 May	6	3	7	5
1969	No. 3	8	20 May	5	3	0	—
1970	No. 4	Ad.	—	—	—	—	—
1971	No. 4	Ad.	—	—	—	—	—
1972	No. 4	Ad.	—	—	—	—	—
1973	No. 5	11	4 June	5	—	1	1
1974	No. 5	12	8 May	6	—	4	3

in 1966. Perhaps this was because she and her third mate had much longer to get used to each other.

For many years this female and her various mates were the only Bewick's Swans breeding in captivity. Now, however, some of her offspring have also bred. The young raised in 1967 nested as a pair for the first time in 1970 at Bentley, Sussex. The three eggs were unfortunately lost to predators. However in 1971 five eggs were laid, of which one hatched and was reared. The following year there were six eggs in the first clutch and four in the second, of which three hatched and were reared. In 1973 seven eggs were produced, the largest clutch ever recorded. The second clutch was five, but only one egg of the twelve hatched and the chick died. In 1974 there were six eggs in the first clutch and four in the second, of which one hatched. In all three years the second clutch was started 14 days after removal of the first.

At Olney, Buckinghamshire, a male raised at Slimbridge in 1968 was paired with a wild-caught female sent in 1961 from the USSR. This female laid five eggs in 1973 but only one hatched and the chick died. In 1974 three eggs were laid. One chick hatched and was reared.

At Branf er , in Brittany, France, a male offspring of the original Slimbridge pair bred with a Whooper Swan *Cygnus c. cygnus* in 1970. Four young were hatched, and two reared.

Other records of Bewick's Swans breeding

in captivity are at Takamatsu, Japan, in 1962 (three hatched and reared); at Moscow in 1968 (five hatched, none reared), 1970 (two hatched, none reared), 1971 (four hatched, two reared) and 1972 (three hatched, one reared); and at Askaniya-Nova, USSR, in 1971 (two hatched and reared). Moscow also hatched Bewick's and Jankowski's Swan hybrids in 1970 (one) and 1971 (two), but none were reared (International Zoo Yearbooks).

Breeding behaviour

The Slimbridge pair was studied in 1973 and 1974, and George Lessiter kept notes on the Bentley pair in 1974.

Copulation

The best descriptions of copulation were made in 1975 (just before this paper went to press) when, although they already had a cygnet from 15th May, the Slimbridge pair were seen copulating (by D. Scott) or attempting to (by the author) nearly every day between 19th May and 4th June. Amazingly another clutch was started on 4th July.

Usually the female Head-dipped in the water, with wings lowered, and head and neck feathers extremely ruffled. The male joined in with his wings slightly raised. When the Head-dipping was synchronised (after about two

minutes), the male mounted, holding the female behind the head, so that she was quite submerged. This lasted about 20 seconds, when one bird was once heard to make a soft low sound. Both then bathed, and the female usually left the water quickly and preened. Copulation failed when the male lost interest and gave up Head-dipping without mounting.

Nest sites and egg-laying

Slimbridge 1973

As usual the birds were provided with a straw pile on the traditional site across the pond, about ten metres from a public path. This was rejected in favour of another site behind a lavatory building, erected at the side of the pen since she had last nested. This site, where they were given more material, was completely hidden from the main path but lacked natural cover. The nest was already screened on two sides by wattle fencing; a further screen was erected on the third side. The fourth side gave access to the pen and pond but was shielded by the building.

The first egg was laid on 4th June in a poorly constructed nest. The urgent requirement may have been to get out of the public gaze. However our efforts at screening were not enough, and eventually the lavatory had to be closed for the duration of incubation. The screens, however, allowed a cautious observer to be within two metres of the birds without disturbing them.

A second egg appeared next day. An interval of two days between eggs is usual among swans (Kear, 1972) and it seems that the female was surprised too, for the egg was laid on the path, several metres from the nest. Unfortunately it was cracked and had to be taped up. Further eggs were laid on 7th, 9th and 11th June.

Slimbridge 1974

By May 1974 the pair had been settled in a new, larger pen for over nine months. At the end of April the female was getting 'heavy' and so was given three nest piles. One was near a public path, the second closer to a service path, although the pen was fenced off from both. The third site was equidistant between the paths, and was preferred. It was on a ridge backing on to a wall, by which it was sheltered. The nest measurements were: overall diameter—74 cm; diameter of cup—30 cm; height from ground to base of cup—60 cm.

On 1st May the female was building, and the first egg was laid on 8th May. A new one

appeared every two days until by 18th May she had laid six.

At the time of laying the whole nest was very visible. However the surrounding vegetation grew up, so that by the time of hatching only a little of the incubating bird could be seen.

Bentley

Here the Bewick's are given nesting material in a roofed bower of branches and wattle, always in the same position. Nest size: overall diameter—80 cm; diameter of cup—38 cm; depth of cup—8 cm. The first clutch was removed on 30th May, and a new egg was found on 14th June. The nest had been built up between 13th and 14th June (i.e. after the first egg had probably been laid) and the male was seen building on the afternoon of the 14th. Further eggs appeared on 15th, 17th and 19th June.

Both at Slimbridge and at Bentley each egg was removed for safe keeping as it was laid, and replaced with a dummy. When the clutch was complete, the eggs were returned.

Recording methods during egg-laying and incubation

At Slimbridge these were:

(a) Prolonged periods of observation, mainly during incubation in 1973. As viewing facilities in 1974 were not nearly so good and descriptions of behaviour had nearly all been made, the main method then was:

(b) Spot checks on an hourly basis—to see which bird was on the nest and what the other was doing. Observations by other staff members could also be used, as the yellow and black bill patterns of the two birds were quite different, and the male alone had a large plastic leg ring. In 1974, data from a few longer sessions were incorporated by noting which bird was on the nest in each hour. Both birds were recorded if there was a changeover within the hour. If one bird remained on the nest from one hour to the next, it was allocated to both.

At Bentley the observations were purely spot checks.

The egg-laying phase

In 1973, on the day the third egg at Slimbridge was laid, the male was sitting on the nest at 14.30, very hot and panting. He was on again the next day from 11.15 to 12.40,

and at 13.30 and 17.05. On the first occasion the female was feeding up to 12.25, then preened before going to sleep. On the second she was feeding, on the third sleeping.

This impression, that the male spent much time on the nest during the laying phase, thus allowing the female extra time for feeding, was confirmed by observations and spot checks the following year.

The male's role was clearly also to guard, not simply to stay on the nest. In 1974, on the second day of laying, the male had been sitting on the nest from at least 07.30 when at 08.19 the warden approached to make an inspection. The male threatened by raising his wings, then stood up and started calling. The female dashed over to him, joining in a triumph ceremony as she ran. Typically the birds face each other and stretch up as much as possible (often with one foot half off the ground), call loudly with their heads pointing up at up to a 45° angle and wave their partially or almost fully opened wings. The head may be pumped up and down, particularly before an attack. When the threat is over, head pumping usually occurs only as the triumph ceremony subsides, the neck otherwise being fully stretched (see Figure 9). As the warden checked the nest, the male struck him twice with his carpal joint. He then 'flew' after him, head down and wings raised, three times: as the warden left the pen, when he stood at the side, and as he disappeared from sight. Two more dashes followed after two minutes, as if this were the residue of aggression, for there was nothing to drive off. After the first dash the pair had a triumph ceremony. After the second, the male returned quickly to the nest, called and wing-flapped by himself.

Four minutes later he dashed off again when he saw the warden in another pen. Another triumph ceremony followed, then another dash by both birds, the male leading. After that the female went and stood by the nest, and at 08.47 the male resumed sitting. Just before then the morning food barrow had arrived. The male spread his wings in threat, and did not feed before going on the nest. This had had no bird sitting on it for periods of 9 and 13 minutes.

If undisturbed, however, the male remained on the nest. On the seventh day he was sitting when the observation began at 11.42. During the session he changed his position four times, the first only after 72 minutes. A change-over began at 15.07 and was completed in five minutes. He went instantly to the pond to drink, having obviously been very hot and panting as early as 13.48.

While the female was off the nest her dominant activity in each minute was noted. Sleeping and sitting doing nothing were combined as resting. Walking and drinking were combined, as the latter was nearly always preceded by the former. In 205 minutes her activities were—preening 87 (on land, 72; on water, 15); feeding 74 (54 and 20); resting, 23; walking, 18; and 'playing' with a dead fish in the water, 3.

Spot checks in 1974 during laying at Slimbridge, which lasted ten days, showed the male on the nest 20 times, the female 13, and twice neither bird was on the nest. On the first day the male was off, building, from 18.27 to 18.33, then the female sat. The next day the male walked off at 18.27 (he had been standing on the nest, building from at least 18.23) to discourage a Ne-Ne *Branta sandvicensis* pair on the public path. When the observer left at 18.35, neither bird was near the nest and it was raining and blowing hard.

During laying at Bentley, which lasted six days, the male was seen on the nest 15, the female 12, neither bird six times. The behaviour of the Slimbridge and Bentley pairs was thus very similar.

Incubation

The observation periods in 1973 were on the 3rd day of incubation 07.22–16.13 (I); 12th day 09.06–17.24 (II); 19th day 09.22–15.52 (III); and 26th day 14.50–19.13 (IV).

Johnsgard (1965) states that males of the 'northern swans' "do not typically take part in incubation although a male Bewick's swan at the Wildfowl Trust has been observed to do so". This referred to the original male, although Johnstone (1957) had not seen this behaviour.

Other instances of the males of northern swans occasionally sitting on the nest during incubation are the Trumpeter *Cygnus cygnus buccinator* (Griswold, 1965) and the Whooper *Cygnus c. cygnus* (Kear, 1972). The male of a pair of Whistling Swans *Cygnus columbianus columbianus* which breed at Guelph, Canada, showed no interest in the eggs in the nest (R. Wenting, pers. comm.). The situation was, however, complicated by a two year old female, one of their former offspring, being in the same pen, and showing considerable interest in the nest. She 'guarded' it when the parent female was off, which was seldom.

The Bewick's male at Slimbridge, however, spent a lot of time on the nest (Table 2). As already indicated, the data for the two years

Table 2. % of total time male was on the nest during the incubation period

I—1st to 7th days of incubation; II—8th to 14th; III—15th to 21st; IV—22nd day to the end.

	I	II	III	IV
Slimbridge 1973	2	22	32	16
Slimbridge 1974	19	36	42	36
Bentley 1974	36	33	23	33

were not strictly comparable, 1973 being based on periods of observation, 1974 on spot checks. Nevertheless, it is quite obvious that the male was on the nest much more than 'occasionally'. In 1974 the male was seen on the nest on 32% of the checks at Slimbridge and 31% at Bentley.

In 1973, at Slimbridge, the male was on the nest only 2% of the time during the observation period on the third day of incubation. He was then still very new to the whole business, while the female had many years of experience and so might have been attempting to do as much of the incubation as possible. This initial enthusiasm is perhaps reflected in the following year, when the male's attendance at the nest for the first week was noticeably lower than later in incubation. It is also much lower than the comparative Bentley figure, where the two birds had had equal nesting experience.

There was also a low figure in the fourth week in 1973. However, the observation period was very much later in the day than in the preceding weeks and an explanation was suggested by the Bentley observations the following year. There the spot checks were spread throughout the day, including early morning and late evening ones. Between 05.30 and 07.30 the female was on the nest 17 times, the male only twice, while between 20.00 and 22.00 she was on 26 times, the male twice. During the rest of the day, the female was on 56, the male 42 times. This may indicate the role of the male. It was not certain that he actually incubated the eggs. He would settle on them with a rocking sideways movement, but he did not obviously shuffle the eggs up amongst his feathers to brood them. The large eggs would lose heat slowly, and no doubt the male by simply sitting on the nest would retard this process during the day. The female's more frequent presence on the nest in the early morning and late evening, when temperatures are lower, suggests full incubation was then necessary.

The periods the male was seen on the nest ranged from 3 to 94 minutes, with an average of 26. In the four 1973 observation sessions he was on the nest once, twice, four times and three times respectively. At Olney the male was also reported to sit on the nest during incubation (C. Marler, pers. comm.).

Nest relief ceremony

The male could not walk right round the nest at Slimbridge in 1973, as one side was too close to a screen, but he would restlessly approach the other three sides. Sometimes he preened briefly. Then he began to pass loose material towards the nest. This sometimes occurred without any reaction from the sitting female, and the male was then extremely aggressive towards any intruder. On other occasions, however, the female joined in the general titivation of the nest and rose to get material out of her reach. Sometimes she simply stood without nest-building, and, as soon as she was clear of the eggs, the male sat on them, occasionally poking downwards into the nest first.

The eggs were usually only uncovered from a half to one minute. No attempt was ever made by the departing bird to pull material over the eggs, and there was no nest down. If the female was nest-tending as she rose, she might continue to build for a couple of minutes once the male had sat. Otherwise she walked away quickly. If the break was a short one, she would only drink. If longer, she drank, fed (on grain in the water), bathed and preened. When she returned to the nest the male usually greeted her (Figure 1), or sometimes a triumph ceremony developed as the female approached. The change-over was then quick and efficient. At the edge of the nest the female sometimes made some nest-building movements, but usually she stood on the rim and the male got up at once. He then slipped off, while the female poked in the nest (Figure 2), and generally tidied the rim for perhaps a few minutes. During this time she would sit and rise several times (often turning the eggs in between), until she was comfortable. The male meantime nest-built intensively and the female often joined in for a time (Figure 3). The male's nest-building could last up to 20 minutes, and vegetation was sometimes uprooted. He then dozed or went to sleep. He was noticeably less alert and aggressive to an intruder at this stage.

The main difference between the sexes was in their behaviour preceding the actual take-over. The male usually walked round restless-



Figure 1. Male on nest greeting female on her return.

ly, preening and passing loose material, and uttered a repeated, very soft call at least when newly on the nest. This sometimes began as the female stood to leave, and indeed, if the relief period was short, he might keep it up all the time. The sound was very similar to that made later by the female when leading the young to the water. The female's take-over was much more positive. She did not make the soft call but might give a couple of loud calls as she walked quickly towards the nest. Although the male might sometimes rise and sit again, the second time perhaps greeting her, he always left the nest quickly. The impression was that the male would willingly have continued sitting, but that the female was determined to take over again. At times it could almost be said she 'pushed' him off.

The bird on the nest stayed there until the

other was close and available for relief. Only once during incubation was the female seen to walk off the nest while the male was still ten metres away. He instantly hurried to the nest, passing her (without greeting) and sat down. The eggs were not uncovered for more than a minute. The female meanwhile had gone rapidly to the water for a drink, and stayed off for another hour. This was in 1974 when the male had already had a year's nesting experience. Similarly, in 1973 the female was never seen idling off the nest, but in 1974 she was several times observed a few metres away, just sitting.

The male, when not on the nest, acted as guard and rarely went out of sight. This was particularly striking in 1973 when, because of the nest's situation, he could not feed, bathe, or even do much patrolling within sight of it. He simply sat about a metre away.

Figure 2. Nest relief.



Figure 3. Post-relief nest building.



Movement on the nest

The female would sit for between 7 and 42 minutes, average 18, without changing her position. (The intervals between rising and sitting as she initially made herself comfortable are not included.) Very often sequences of moving and settling were in the same direction, for example eight resettlings all proceeded clockwise. Turning the eggs was a separate activity, occurring, on average, every 36 minutes. It seemed the male poked downwards into the nest much less often than the female, and this only occasionally when he first took over sitting.

Nest maintenance

The sitting bird might casually move a few bits of loose material on the rim of the nest, but generally both birds co-operated in nest-building. However, when just one bird was tittivating or building on the nest, it was nearly always the female; off the nest, nearly always the male. Of course, they were not seen equal times on and off the nest (on the nest: female—1331 minutes; male—258 minutes). Nevertheless, this is further indication that the nest is principally the female's domain, the male merely taking over when necessary and doing his ritualized building off the nest as a prelude to sitting.

The length of building sessions varied, but by far the most was seen on the 19th day of incubation, when the pair built practically the whole day. It became so vigorous that on seven occasions the female walked off the nest to get material. This was not part of a change-over; once, when she was off for 9 minutes, the male did not get on the nest at all but helped to build, twice he did get on but each time after waiting 3 minutes, and twice it seemed he would have got on but was prevented by the female.

On this day the taped up egg had broken and was laying two metres away. It was addled and the stench was quite overpowering. Although egg-carrying is rare in waterfowl, Perrins (1962) reports a case of a female Mute Swan *Cygnus olor* taking the shell of a damaged egg four or five metres from the nest. It seems likely therefore in the present case that the egg was damaged in the nest and, giving offence either because it was wet or tasted or smelt bad, it was removed. Birds' sense of smell is known to be not very acute but, if the swans could smell *anything*, they could not have missed this! Whatever the reason, it may have led the birds to refurbish

the nest substantially in order to remove the traces of the accident.

Hatching

Slimbridge 1973

One of the two remaining eggs started to hatch on 14th July (the 30th day of incubation). The female appeared to become excited by what was happening underneath her and, standing up, trampled the emerging chick. The chick and remaining egg were quickly removed to an incubator. The egg never hatched however (the embryo was deformed with too large a head), but the chick was returned to its parents (who had meanwhile been given wooden eggs) the next day.

Slimbridge 1974

Hatching started on 16th June (the 29th day of incubation) and once again the female trampled one egg, this time killing the chick, which, however, already had an infected yolk. The other eggs were removed and three hatched in an incubator. The chicks were returned to their parents the next day.

Bentley 1974

One of the four eggs hatched on 23rd July (the 31st day of incubation).

Observations were not continued at Bentley after hatching. In 1973, at Slimbridge, the whole family was moved after one day to a larger pen, with better water. Therefore the whole situation must have been somewhat abnormal without the nest.

Nest-exodus

In 1974 the three young were returned to the nest at 08.00. The weather was sunny, following torrential downpours the previous day. Their early behaviour is described in some detail as the opportunity for such observation is rare.

At 08.22 they were still on the nest, by the female's breast. The moment the observer came into view the male tore across the pen, head lowered and wings flapping. His behaviour was the most aggressive ever seen, apart from when a warden was actually in the pen.

As the family was obviously being upset, the observer retired until 08.57. The female was then halfway down the side of the nest, the male beside it. When the female and chicks reached its base, he climbed up and



Figure 4. First chick falls in.



Figure 5. Female tramples (to attract chicks).

Figure 6. Second chick 'flies' in.



stood on the top. A warden appeared at 09.05, but the male chose to stay on top of the nest until the warden started to leave, when he chased aggressively across the pen. He then returned at once to the top of the nest. Another warden was passing at 09.12 and the male came out several metres from the nest but he quickly returned to its top. One of the chicks followed him. The rest of the family were still within a few metres of the nest, for the chicks only took a few unsteady steps before flopping on the ground. Once off the nest, the female, unlike the male, made a continuous gentle monotonous 'kuk-kuk' sound. This occurred about every five seconds, with almost every step, until the water's edge (12 metres from the nest) was reached at 09.25. Thereafter it was made at varying intervals, increasing in frequency, apparently when the female wanted the chicks to follow her. She only stopped making this sound when she settled with the chicks two hours later.

At the water's edge the female occasionally preened and plucked at the grass. Then she 'trampled' the ground with the same movement as that made in the water to stir up the pond bottom when feeding. There was no obvious reaction from the chicks.

At 09.30 the female and chicks set off back towards the nest but stopped halfway there in a splashy part of the sward. There the chicks were first noticed to pluck at the vegetation and the female trampled again, this time very slowly (5 steps).

After seven minutes they turned again towards the pond and, at 09.40, the female entered the water. The photographs show just what an awkward spot she had chosen by taking the most direct route to the main pond. Three smaller ponds were closer. The launching point had an almost perpendicular drop of 15 cm to a concrete ridge, after which there was a similar drop to the water. Her 'kuk-kuk' increased at times to three syllables, and was almost non-stop. One chick fell on to the concrete ridge and joined its mother within one minute, falling haphazardly into the water (Figure 4). At this point the female trampled very hard, twice in succession. In the water this did have an immediate effect: the chick came within 5 cm of her tail, and one of the other chicks sitting on the bank, uttering regular, high-pitched distress squeaks, stood up (Figure 5). It, too, got on to the ridge, but spread its wings to launch itself into the water (Figure 6). This had taken another minute. The female trampled again but the third chick seemed very reluctant and squeaked incessantly. It eventually fell in at 09.46.

At this point the male left the nest, but returned one minute later. The female trampled hard for the chicks and they pecked at floating matter.

At 09.50 the female left the water at the same place as she had entered it. Two of the chicks managed with much difficulty to struggle out within a minute but the third could not make it and squeaked continuously. The female was calling too, and when it swam two metres away, apparently to find another exit, her calling became louder and higher pitched. She trampled in five separate bouts and eventually, at 09.54, the chick got out, seemingly very exhausted. During the third chick's efforts to land, the male came to within two metres of the party but by 09.56 had returned to his stance on the nest. From then until 10.05 the female trampled on land ten times, producing no reaction from the chicks, who were resting and preening intermittently. The female also preened and by 10.08 was only calling occasionally.

The male left the nest at 10.14 for two minutes, and at 10.17 he came towards the female and chicks who had started slowly towards the nest. He was flicking his wings a lot, perhaps indicating nervousness. The female only flicked hers very occasionally. The male led the way to the nest and, after a couple of alarms, the party reached it at 10.25. Two minutes later the female was back on the nest and, after poking eight times in it, she was sitting with the chicks on the rim by 10.31. One chick was knocked off during the female's settling process but climbed back up. The male stood guard five metres from the base.

At 10.34 the female and chicks left the nest, while the male briefly resumed his stance on the top, then followed the others. They reached the edge of the pond but the male turned back to look at the nest and was followed by one chick, despite the female's calls and his silence. They rejoined the party and the female got into the water, again at a fairly difficult spot although she was within two metres of a sloping area. The chicks, however, did not get into the water, although one ran to the edge when the female trampled. Possibly the male beside them on the bank was a distraction. The female only stayed in the water one minute and emerged at 10.44. The chicks sat, preened and fairly often bobbed their heads for the next fifteen minutes. The male was alert and wing-flicking and at 10.57 started off towards the nest. He was followed by one chick, but the female and the others, although they started after him, veered to the small pools. The whole family

followed, although only the female got briefly into the water.

Between 11.05 and 11.09 the female trampled. The male also trampled once, slowly and awkwardly. Then he returned to stand on the nest but left it after two minutes to chase a party of visitors.

At 11.15 the whole family went into one of the small side ponds, which have easy slopes. Both adults trampled in the water but one chick climbed out alone after 5 minutes. The female repeatedly called it and, after following the family along the bank for four minutes, it finally joined them. The female then got out and the male and chicks followed. Trampling was noted 10 times from 11.25 to 11.36 (but only five times in the next 15 minutes). By 11.56 she appeared quite settled on the ground with the chicks by her. The male had gone to stand on the nest twice: for two minutes at 11.30 and four minutes at 11.44. He returned for a third time at 11.59 and only left at 12.26 when the female displayed because of disturbance from visitors. She and the chicks were ten metres from the nest but only five metres from the public. The male returned to the nest at 12.33 and shortly afterwards, the female and chicks having started towards the nest, he came off and led them. However, the whole family reappeared coming away from the nest two minutes later. The male appeared to become discouraged, thereafter spending only very short periods on the nest. At 13.05 he returned to it, but came off again immediately. At 13.30 he went to the nest but left as soon as the female called.

At 13.32 the female took the chicks into the water, the male following. She and two chicks re-emerged at 13.45, the third remained in the water with the male. The female trampled frequently, and the third cygnet landed and rejoined her at 13.52. Two minutes later the male also left the water. The family then appeared to be settling down in the same spot they had used before and the observations were ended.

The only comparative observations on nest-exodus behaviour were at Bentley in 1971 (Secrett, 1972). There it had been very wet with heavy deluges for the first two days of the chick's life. During this time the female kept the chick on the nest, presumably the driest spot in the pen. On the third day, which was bright and sunny, the chick was led to the water for the first time by its mother.

The Slimbridge male's behaviour, standing on the top of the nest, observed only that first day, might indicate that he was guarding it for use by the female and the chicks, but it must have been damp after the torrential rain. It

was remarkable how the female walked the chicks round for such a long time when they were obviously very young and weak. On subsequent days the female brooded the chicks in the area where she first settled.

Trampling

This was discussed briefly in the last section and should perhaps be described in a little more detail. While it looked like the movement made in the water to stir up the bottom of a pond, it could equally be likened to a speeding up of the motion made when a bird settled on the nest. It happened several times in each bout, usually on the same spot and facing the same direction. On one occasion this was so for all eight bouts.

In the detailed observations during the first five weeks of life, 14 bouts by the female were recorded. These lasted from one to seven minutes, an average of 2.9. The number of trampling movements in each bout ranged from one to eight times. The proportion of time spent in trampling bouts decreased during the five weeks, as follows: 2.4%; 2.1%; 1.8%; 1.4%; 0.3%.

Not infrequently, the chick might watch but make no movement. However, that it was intended to be an attracting movement is supported by the circumstances in which it occurred, often beside the chick, indeed almost over it, or as the chick approached; and by its being the prerogative of the female, decreasing in use as the chick became older. In 1974 it was last noticed on the chick's 47th day, when the bout consisted of just one trampling action.

Trampling in the water for food was performed by both male and female, and both did it for the chick without feeding themselves.

Interaction within the family during rearing

Observation sessions were undertaken in 1973 during each of the first five weeks of the chick's life for 82, 415, 111, 73 and 365 minutes. Two categories of behaviour were examined; parent/chick interaction, and the defensive behaviour of the parents.

Interaction of each parent with the chick

The movement of the chick towards the parents, whether they were moving or still, is examined in Table 3. It was very striking that the chick followed or went to the female 23 times, to the male only 5 times. Even when it went to them both, 9 times out of 16, it went primarily after or to the female. In 39 of 44 cases (89%) the female was thus directly involved. In three of the other cases, the male and the chick were at once joined by the female (in one case she was in the middle of drinking when the male moved off); in another, the female moved as soon as the chick went to the male and the chick then instantly switched to her; in the fifth, the family were settled and the cygnet moved towards the male, and sat and grazed.

Table 4 examines what happened when the chick initiated the movement. Again in 62 of 72 cases (86%) the female was directly involved and, in another seven, in a secondary role. In one of the three exceptions the female joined the male and chick within the next minute; in another, the female's action was not recorded, and in the third, the male moved after the cygnet, probably in a defensive role.

On 15 occasions it was not clear whether adult(s) or chick had initiated the movement. Six times the chick moved with the female, and in three of these cases the male joined

Table 3. Movement of chick to parents

Chick follows or goes to:	Week					Total	
	I	II	III	IV	V		
♀ only	3	10	3	0	7	23	
BOTH	♀ first	4	1	1	0	3	9
	Both together	4	2	0	0	1	7
	♂ first	0	0	0	0	0	0
♂ only	1	2	1	1	0	5	
TOTAL	12	15	5	1	11	44	

them. Once the chick moved with the male and the female joined them. Eight times they all moved together. The chick was seen to move 'independently' (i.e. did not follow, and was not followed) only 14 times in the five weeks. Five of these were in leaving the water, and on four other occasions it only moved a few paces. Completely independent movement was therefore rare, even as the chick got older. The chick's interaction, recorded over the five weeks, are totalled in Table 5. The importance of the female to the chick is very clear throughout (Figure 7).

In Table 6 the proportion of times the chick took 'independent' action in each week is shown. A general trend towards more independence of action by the chick is clear until, curiously enough, the fifth week.

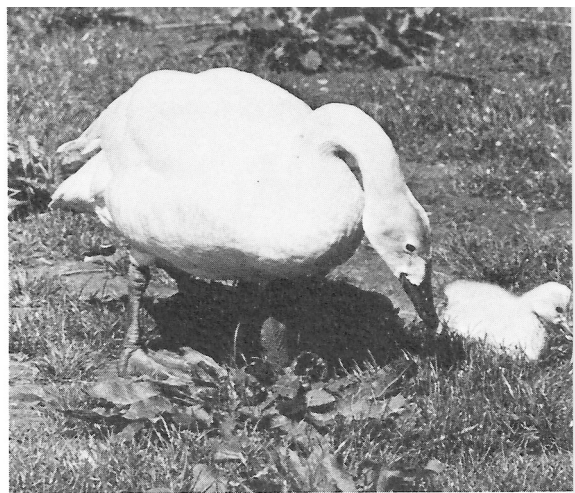


Figure 7. Chick's close association with female.

Defensive behaviour of the parents

This occurred usually on the approach of people or waterfowl along the path outside the pen. The reaction depended on time of day (people were usually ignored within the more populous hours) and the noise created.

The behaviour can be divided into three approximate categories. Least intense was Category A, when the bird was *alert* or *watching*, standing still with its neck stretched up and looking in one or more directions. Category B involved the adoption of an *aggressive posture* but, as in Category A, there was no change in position. Aggressive

Table 4. Movement of parents to chick

Chick followed by	Week					Total	
	I	II	III	IV	V		
♀ only	4	7	2	0	5	18	
BOTH	♀ first	7	6	1	2	2	18
	Both together	0	7	9	2	8	26
	♂ first	1	1	2	1	2	7
♂ only	0	0	1	1	1	3	
TOTAL	12	21	15	6	18	72	

Table 5. Chick's movements during first five weeks

Interaction with	♀	♀	BOTH	♂	♂	Neither	Total
	only	first	Both together	first	only		
Occasions	44	30	41	8	8	14	145
%	30	21	28	6	5	10	

Table 6. Comparison of following and independent movement of chick during first five weeks.

Week	I	II	III	IV	V
Chick follows	48	34	23	13	35
Chick initiates action	52	66	77	87	65

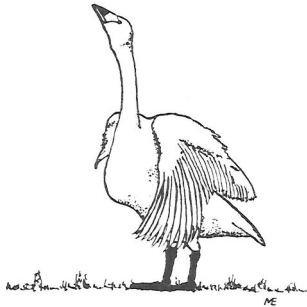


Figure 8. Triumph ceremony by female.

posture in the female involved only joining in a triumph ceremony (Figure 8) with the male. It occurred when danger threatened or receded, for example when a warden went by. Other aggressive postures shown by the male, were standing still with wings spread, bill pointing slightly upwards; also *ground staring* (Figure 9). In this, the bird stands with its head at anything from 40° to 90° to the ground, with the neck either bent or straight. The feathers on the back of the neck or back are ruffled, the wings may be open or closed. It usually happened when a human

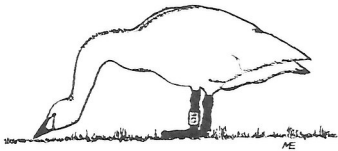


Figure 9. Male ground-staring.

was very close. It may be displacement behaviour, for an attack was never seen to follow. The female was once seen doing it during incubation. In the water the male submerges his head, leaving all of his ruffled neck visible, and blows bubbles. The wings are slightly raised.

Category C involved *aggressive movement* towards the intruder, usually running towards it with head a few centimetres from and parallel to the ground. Also in this category came patrolling the fence, either ground staring, or with wings half open, or simply pressing the breast against it at intervals. Each incidence of defensive behaviour ended with the bird starting some other definite action. Table 7 shows that the female gave no Category C aggression and only showed half as many instances as the male in categories A and B. Obviously she could not rush around defensively with the chick attempting to follow. That was the male's task.

Unusual circumstances, however, provided an exception. During the fourth week in 1974 the three chicks were, as a matter of routine, caught up and treated in their pen against the nematode worm *Acuaria*. During this process the male rushed and threatened, but did not strike a blow. It was the female who became extremely aggressive, striking the chicks' captors repeatedly, apparently extremely angry and quite unafraid for herself.

In more peaceful movements, when neither parent had to play an active role, they often manoeuvred themselves so that the chick was in between them. Often the parents faced each other (and the chick). When in the water, which brought the family nearer to the public, the female was usually nearest the chick and the male fairly alert. Both in water and on land the male would put himself between the rest of the family and people.

Table 7. Aggression of parents during first five weeks. Categories of increasing aggression A, B, C.

Week	Male Category			Female Category		
	A	B	C	A	B	C
I	7	0	1	2	0	0
II	21	10	12	13	6	0
III	4	1	4	3	0	0
IV	10	2	8	5	0	0
V	10	3	5	4	2	0
Total	52	16	30	27	8	0

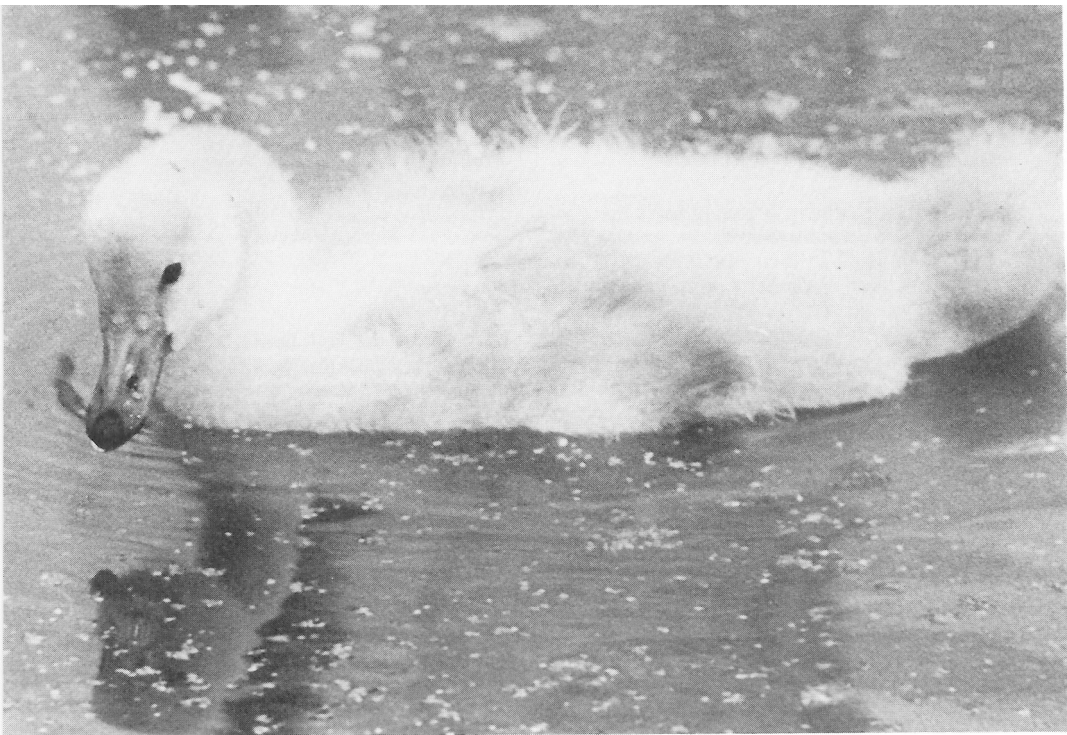


Figure 10. Chick at five weeks old.

Aggression by chick

This was first seen in the fourth week when the chick (already on the water) chased a duck that had just landed in the pond. The parents followed.

Growth of chicks

Two of the three hatched at Slimbridge in 1974 grew apace. The third was slower and died before fully feathering. Growth in the wild to a fully fledged stage is reported as 40–45 days (Dementiev & Gladkov, 1952). Secrett (1972) reported that a Bentley chick began to feather at seven weeks and Johnstone (1957) that a Slimbridge one showed signs of feathering at eight weeks. At five weeks old two of the three 1974 cygnets had no visible feathers (Figure 10), while by nine weeks they had only small traces of down by the tail and faint wisps left on the neck (Figure 11). By thirteen weeks they were fully feathered, the legs were dark grey and the bills pink, apart from black nail and a centimetre of grey white fuzz at the sides there the bill joined the feathering proper. It was just possible to tell them apart by the very faint beginnings of pattern on the bill.

Figure 11. Chick at nine weeks old.



Discussion

The rarity of captive breeding indicates that the Bewick's Swans at Slimbridge and Bentley may be unusual in their reactions to the environment, and their behaviour may not be wholly typical. The conditions of captivity itself may also modify behaviour from what would occur in the wild.

Thus juxtaposition in a fairly small pen (less than 500 square metres) may have helped the re-pairing process whereby one female took a succession of five mates. Nevertheless, re-pairing after the loss of the mate has been observed in the wild wintering flock at Slimbridge. In many cases a bird has left in March with one mate and returned the following winter with another (the original mate never being seen again, true divorce being unknown). Similarly the smallness of the territory may have emphasized the aggressive tendencies of the male and, for that matter, his readiness to sit on the nest during both the egg-laying period and incubation proper. Yet the aggressive behaviour itself and the methods whereby a smooth change-over at the nest is managed must all be part of the normal repertoire.

The nest-exodus behaviour is obviously modified by the circumstances of captivity and the necessary avicultural interference. Yet the constant calling of the female and her trampling are clearly the normal behaviour whereby the young become 'imprinted' on her and learn to follow and keep close. The marked preference of the growing chicks for the female during subsequent weeks certainly stems from this early activity.

One day it may be possible to check the data gathered in this study against what oc-

curs under the natural conditions of the Siberian tundra.

Summary

A history of the first Bewick's Swans *Cygnus columbianus bewickii* to breed in captivity, and a survey of captive breeding since, are given.

Two breeding pairs were studied. Nest sites and breeding times are described. Both male and female helped shape the nest. During laying the male spent more time on the nest than the female, and during incubation, contrary to what was believed of northern swans, the male was on the nest a third of the time.

The nest exodus is described in detail, emphasizing the female's constant calling, and the male's preoccupation with the nest. During the first five weeks of life there is strong interaction between female and young, with some growth of independent action, while the male's role is that of protector.

There is a brief account of chick development after five weeks.

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