A case of bigamy in the Canada Goose

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Records of polygamy in free-flying Canada Geese *Branta canadensis* are scarce. Brakhage (1965) found 17 cases in a full-winged but sedentary flock in Missouri that increased from 265 birds to 550 between 1961 and 1964: 16 involving a male with two females and one a male with three females. We here report another case involving a male and two females, in Sweden, of interest because all three individuals had long histories of successful breeding with other partners. We compare it with a somewhat similar case history of Whooper Swans *Cygnus cygnus* in northern Sweden, reported by Blomgren (1974) and discuss their wider implications.

Study area and birds

Our observations were made at Kronängen, an enclosure belonging to the Tovetorp Zoological Research Station, University of Stockholm, and situated about 90 km south of Stockholm (58.58 N, 17.09 E). In this enclosure of about 20 ha, 4–7 pairs of Canada Geese are nesting in ponds and small lakes where they can be watched from observation huts. Like most of the Canada Goose population of Sweden, these birds are free-flying, migratory, and subjected to hunting (Fabricius 1983). Colour banding is used to identify individuals, and records on the life histories of the birds have been kept since 1966 by E. F.

Observations

Arrival and behaviour of a widowed female in 1984

A female Canada Goose, colour code number 176, which was hatched in 1974 and had nested successfully with male 877 since 1976, returned alone in the spring of 1984. When first seen on 9 April, she followed a pair of Canada Geese, male 122 and female 042, also newly arrived. The male of this pair was hatched in 1969 and was thus 15 years old, while the female was hatched in 1976. Both of them had previously nested with other partners. After female 042 was widowed in 1980 and male 122 lost his mate in 1981, they formed a pair and had nested successfully together since 1981. With both his first and second mate, male 122 had held the top position in the social rank order among the geese that nested at Kronängen. Female 176 with her now lost mate had held a position next to male 122 and his mates.

On 9 April, the widowed goose 176 was tolerated by the pair and even allowed to feed with them. Next day, a complete triumph ceremony between male 122 and female 176 was seen, indicating that some bonding had developed between them (Lorenz 1965; Fischer 1965), but immediately after the ceremony female 042 attacked 176 and chased her away. Keeping about 10 m from the pair, she then tried persistently to approach the male whenever the female 042 happened to be at some distance from him, only to be attacked and driven away as soon as the latter returned. The male began to show territorial behaviour and the trio moved to one of the ponds which had been 176's nesting pond from 1977 to 1983. Female 042 had nested elsewhere with 122 and her earlier mates. This pond was about 75 m long and 30 m wide. There were 10 small artificial islets with grass and some juniper bushes.

Nesting

On 18 April, female 176 was seen sitting in a nest on one of the islets (about 2.5 m in diameter) while the pair 122 and 042 walked on the ice nearby. On 21 April, she was incubating there, and 042 was also incubating, on another islet 30 m away. The male patrolled in the pond, which was now free of ice, vigorously attacking all other geese that tried to intrude. This situation continued throughout the incubating period.

There were complications on occasions. At incubation pauses, when the female temporarily leaves the nest to feed and bathe, the gander normally rushes to his mate, joins her in a triumph ceremony and escorts her until she returns to the nest, whereupon he withdraws (Cooper 1978). Male 122 attended both his females in this way during their incubation pauses, but when both of them were out on the water simultaneously, he first escorted 042 until

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she had returned to her nest, whereupon he turned to 176. As incubation went on, 042 became increasingly aggressive towards 176 during the incubation pauses, even temporarily preventing her from returning to her nest. At first, she only threatened 176 when swimming past her nest islet, escorted by 122, but from 10 May overt aggression was observed. Female 042 sometimes flew from her own nest to attack 176 when the latter tried to return to her nest islet after an incubation pause.

From 16 May, the triumph ceremonies between the male and 176 began to appear somewhat incomplete, the male not approaching the female as closely as normal and the terminal cackling phase (Lorenz 1965; Radesäter 1974) was sometimes lacking. The ceremonies between the male and 042 remained complete and intense.

Hatching and nest exodus

On 20 May, the eggs in the nest of 176 hatched while 042 was brooding them, having temporarily left her own nest well covered with down. Female 176, which had presumably been driven off her nest, attempted to return in the early evening. She attacked 042 but eventually withdrew, whereupon she was also repeatedly attacked on the water by male 122. Now and then some young came out on the nest rim and on these occasions the male approached the islet, but no exodus took place and in the late evening all goslings were invisible under the brooding 042, while her own nest was left unbrooded.

Early next morning, 042 was still brooding in the nest of 176 but the latter was also on the islet in a sleeping or submissive posture less than 1 m from the nest. The two birds were partly screened from each other by a small juniper bush. The male swam close to them, but after a while he gave the rolling call (Lorenz 1965; Radesäter 1974) and flew towards the nest islet of 042. The latter then flew with him, leaving the nest of 176 and returning to her own eggs. Female 176 now returned to her nest and brooded her goslings. The young of 176 were now very mobile and four of them swam out on the water where the male tended them, while one was still brooded by the mother. On several occasions the male brought the young to the nest islet of 042 where they tried to get under her, but she did not lift her wings to let them in. In the afternoon the remaining gosling of 176 left the nest and swam out to the male. The mother followed hesitantly at some distance. Eventually she joined the group, so that a family of the male with 176 and her five young was formed. Although they otherwise behaved as a normal family, the female did not let the young in under her when sitting down. This situation lasted for some hours, but in the evening all the young had assembled close to the still incubating 042, while 176 swam alone or stood in her empty nest. The male now showed ambivalent behaviour, attacking her vigorously but interspersing his attacks with triumph ceremonies, which appeared complete. They were performed after attacks by the male on some nonnesting Canada Geese which intruded on the pond. Female 176 sometimes joined in the attacks. As it grew dark 042 let all the young of 176 under her wings and into her nest, where at least some of her own young had now hatched, while 176 sat in her empty nest.

Next morning, 22 May, the young of 176 were again tended by the male in the pond, while 042 remained in her nest. Female 176 occasionally approached her young but the male made neck movements combining threat with those of the cackling ceremony, whereupon she withdrew. In the course of the morning, 042 several times left her nest, where four young could now be seen, and swam to join her mate with the young of 176. On such occasions she repeatedly flew to attack 176. In the afternoon the male was swimming with the five young of 176, joined by 042 and three of her young, one of her goslings remaining in the nest. The eight young had joined very closely and followed the pair 122/042 which attacked 176. A combined family of the male with one female but the young of both females was thus formed, while the second female was attacked by both members of the pair and kept at a distance of 15 m or more from the family.

Association of the widowed female with an additional male and integration of more young into the combined brood

After having been expelled from the combined family, 176 was not seen to make any further serious attempts to approach her young. She soon joined a group of nonnesting Canada Geese which had assembled at a small lake to moult. On 1 June, she was

seen attended by a young Canada Goose male. This male remained with her until both birds left Kronängen shortly after moulting.

The young of the combined brood soon became very mobile. While moving between the different waters within the enclosure, the family incorporated additional goslings. On 25 May the pair 122/042 was seen with 16 young. A maximum of 20 was reached on 22 June, after which the number of young stabilised at 18. This integration of young from other families followed a pattern that has been observed fairly frequently in the Canada Goose (Geis 1956; Collias & Jahn 1952; Sherwood 1967; Hanson & Eberhardt 1971; Fabricius 1979). The pair had obvious difficulties in keeping this large group together. Some young often lagged behind. The male and the female could sometimes be seen each tending part of the brood, even in different ponds. A varying number of young would temporarily be attended by another adult female, 432, which, since 25 May, had persistently followed the family at a distance, three of her own young having been incorporated in the combined family.

There were three other Canada Goose families and five Greylag Goose *Anser anser* families in the study area (Fabricius 1983). The Canada Goose family of 122/042 clearly dominated all of them, but only when male 122 was present. On occasions when the two mates were each tending separate parts of the brood, the male still dominated all the other families, while the female was dominated by some of them. This was the case irrespective of the number of young which followed the respective parent bird at any particular encounter.

Return of the birds in 1985 and formation of a stable trio

In 1985, male 122 returned on 13 April together with both females 042 and 176. The young male with whom the latter female had associated herself the previous June was not seen. The three birds moved closely together and no aggression was seen within the group. The male made complete triumph ceremonies with both females and on occasions stood between them, performing the neck movements of cackling and rolling in turn with each of them. From 13 to 21 April the male tended to keep more closely to female 176 while 042 followed at a distance, and during this period three copulations between the male and 176 were observed. Once 042 approached the couple and all three birds joined in the pre-copulatory neck dipping, but the male only copulated with 176. After 21 April, the roles were reversed, the male now paying more attention to 042 and a copulation with the latter female was observed.

The two females nested in the same pond as in 1984 but not on the same islets, the distance between their nests being now much less, only about 14 m. Female 176 began her egg-laying on 17 April, and 042 two days later. Incubation proceeded peacefully until 24 April when 042 flew from her nest to attack 176 who, during an incubation pause, had performed a triumph ceremony with the male. Female 042 then for a while prevented 176 from returning to her nest. Such aggression occurred on several occasions during the rest of the incubation period, culminating on about 8 May. It was always during incubation pauses and a provoking factor appeared to be triumph ceremonies between female 176 and the male. However 042 during her own incubation pause also swam up to the nest of 176 to threaten her or even to drive her off her eggs. But unlike the previous year, the male never took part in the attacks on 176, nor did he threaten her.

The eggs of 176 hatched on 23 May and at nest exodus next day the male joined her and, followed by the four goslings, swam to the nesting islet of 042 which had meanwhile also hatched, likewise four young. There the two broods combined but when female 176 tried to follow her young she was driven away by 042 and returned to her empty nest. Female 042 then swam over, followed by the combined brood. Apparently still broody, she sat down in the nest of 176. This bird was still on the same islet, where she had withdrawn into clumps of tall junipers, and all young except one soon joined her in grazing there. Female 042 still made one attack at 176, but from then on the three adult birds moved together and the young ran freely between them, so that some of them would follow one and some the other female or even the male. Both females brooded the young in cold weather although the whole brood spent the night under 042 during the first two weeks. Later on some young also stayed by 176. A stable trio had been formed and both females attacked alien geese, thus contributing to the success of the

group, while the male after attacking other geese performed triumph ceremonies with whichever female happened to be closer. At a later stage some young from other pairs were again incorporated into the group, as in 1984.

Discussion

While Brakhage (1965) reported 16 cases of a male with two females in a flock of Canada Geese where there was a pronounced shortage of males, the events described here comprise the only occurrence of bigamy noted during 17 years (1969–85) of observations at Kronängen, where the sex ratio has also tended to favour females. A factor contributing to this uneven ratio could be that females tend to return to their place of birth and try to establish themselves there, while young males are less philopatric.

In the particular case observed by us the occurrence of bigamy might have been facilitated by earlier relations between the individuals involved. In 1979, both the females 176 and 042, had been included with their broods in a combined family dominated and led by 176 and her late mate 877. During the eight years when 176 had nested before losing her mate, she had, after the hatching of her young, regularly lost encounters with the family of male 122 and thus experienced his high social status. The bigamous behaviour of male 122 might also have been favoured by the circumstances that female 176 was in both years slightly ahead of 042 in her reproductive cycle and thus probably more receptive at the onset of breeding. Possibly this could also have influenced the choice of nesting at a site which had earlier been used by this female but never by 042.

The consequences that the behaviour of the three birds had for their individual fitness, in terms of the potential number of surviving offspring (Hamilton 1964), were most clear cut in the case of 176. Judging from all the years of observation at Kronängen, a young male with no or little earlier nesting experience would have been less able to protect her in the combats over territories and nest sites. Mating with the male of an old established pair was her best chance of producing fertilized eggs and incubating them successfully. Now she could nest under the protection of a dominant male and hatch her young, which then became integrated into a family which held the top position in the dominance hierarchy, with all the advantages this gave in terms of reduced competition for food and high probability of preserving family identity. The male 122 also gained increased individual fitness by mating with more than one female.

The situation was more complicated in the case of the female 042. The events at the incubation pauses demonstrated some of the disadvantages of sharing the protection of her mate with another female, though her aggressiveness towards 176 would, when successful, have counteracted this. Dominance of one female over the other was also observed in the cases of bigamy reported in Canada Geese by Brakhage (1965) and in Whooper Swans *Cygnus cygnus* by Blomgren (1974).

By adoption the pair increased their family size, thereby probably improving their success in later encounters with other families in winter flocks (Boyd 1953; Raveling 1970). The presence of adoptees could also lower the risk for the individual offspring of capture by predators (Lazarus & Inglis 1978). On the other hand, by temporarily abandoning her own nest, female 042 jeopardized her eggs. Ravens *Corvus corax* were seen close to the pond, and other frequently occurring egg predators were Hooded Crows *C. cornix* and Herring Gulls *Larus argentatus*.

The events described here closely parallel a case of bigamy in the Whooper Swan described by Blomgren (1974) on a remote forest tarn in northern Sweden. In five successive years, a male nested with two females, showing no aggressiveness whatsoever towards either. He copulated with both and all three joined in triumph ceremonies in connection with territorial defence. One of his mates was slightly aggressive towards her rival, generally keeping her at some distance. The females had their nests close to each other and no serious hostility between them was seen at their incubation pauses, even when these were simultaneous. When hatching began in one nest, the other female might approach it, sometimes leading both females to brood side by side. The female whose nest it was then nipped at the other female and sometimes temporarily drove her off. When some young had hatched in a nest where their mother still incubated remaining eggs, the active young were seen to follow either of the two other

adults. As in the Canada Geese, the integration of the two broods thus began at an early stage.

In the first nesting season of the Canada Geese, there was a striking difference between the geese and the swans in the high level of aggressiveness in the first female and finally also in the male. In the second season, the parallel with the swans became almost perfect. The persistent tolerance of the male and lower aggressive level of his mate enabled the second female to stay with the brood. In the Canada Geese this probably was a result of a strengthened bonding between the male and the second female and of habituation to her presence in the first female. In the case of the Whooper Swans the life history of the birds involved prior to the first observation of the established trio was not known. The increased tolerance towards the second female that the first female showed shortly after hatching in 1985 could further have been facilitated by the common tendency in this species to form combined broods.

When seen against the background of current theory on evolutionary strategies connected with individual fitness (Hamilton 1964) and parental investment (Trivers 1972), these two cases of bigamy in Anserini raise some more general questions. Although Orians (1969) concluded that polygamy will always be advantageous to males, some counteracting factors are obvious in the geese and swans where the male helps protect the offspring. Too many females would reduce the efficiency of this behaviour. For the same reason females of established pairs should aim at counteracting bigamy by their mates. On the other hand, single females would gain from mating with already mated males because of the early pair formation but late sexual maturity in the Anserini. According to observations in the Kronängen colony, pair formation in Canada Geese begins at an age of 1–2 years while full sexual maturity is not reached until 2–3 years (see also Brakhage 1965; Craighead & Stockstad 1964). Consequently most unpaired males available in the breeding area in spring are not sexually mature.

Another question concerns the development of the tendency, seen not uncommonly in several species of Anserini, to adopt young from other pairs into their families. Some possible advantages have already been mentioned, but there are disadvantages. It is evident that there is a number of young above which it becomes difficult for the parent birds to keep such a créche together, and possibly a large number of young could also in itself increase the risk of predation (Glasgow 1977; Lazarus & Inglis 1978).

Generally, evolutionary strategies have developed as a result of selection pressures favouring behaviour which tends to increase individual fitness under given circumstances. But it should never be forgotten that when the behaviour of an individual animal in a particular situation leads to an advantageous result, this does not necessarily prove that it is part of an evolutionary strategy developed to deal with that category of situations. For example, while adoption of young may result in increased individual fitness, it could still occur simply as a consequence of unselective mechanisms eliciting parental behaviour towards their own very young goslings. When such unselectiveness leads to abandoning of the female's own eggs it could be disastrous. Similarly, a widowed goose could choose an already mated male, not because of a strategy evolved to meet with a situation like hers, but because he displayed the dominant and sexually active behaviour typical of an old and experienced gander, for which the female geese show a strong preference (Lorenz 1979). As this behaviour is typical of old and experienced ganders, a widowed goose could well choose a widowed male if available, as was actually observed with female 042 and male 122 in 1981 (see above).

Behaviour is dependent on complicated interactions between strategies, in the evolution of which advantages and disadvantages have been balanced, as well as on all the diverse stimuli connected with ever changing situations. Observations of the behaviour of a few individual birds can give no more than glimpses into these intricate systems of interacting ultimate and proximate causalities, but they show that a wide field of research is still open.

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Summary

In a case of bigamy in the Canada Goose *Branta canadensis* a ten-year-old female, which had

nested successfully with the same male since 1976 returned alone in the spring of 1984. She approached the 15-year-old male of an established pair which had nested together for three years. Although persistently attacked by the female, the widowed female was tolerated by the male and both females then nested with him. The male initially tolerated the second female while the first female attacked her with increased frequency as incubation proceeded. Even the male then became aggressive towards the second female. When the young of this female hatched, the first female drove her off her nest and brooded the young there, leaving her own eggs unbrooded but covered by down for about one day. She then returned to her nest where the young eventually hatched. Meanwhile the young of the second female were tended by the male who finally brought them to the nest of the first female where the two broods joined. The pair then drove the second female away and thereafter alone tended a combined brood of young hatched by the two females, later incorporating young hatched by at least two other pairs.

The three birds returned in the spring of 1985 keeping closely together as a group without any aggression. The male first copulated with the second female and later with his first female. Both females again nested in the same pond. This time the male remained tolerant throughout the whole nesting season while his first mate again attacked the second female towards the end of the incubation period. The young of the second female again hatched first, but this time the first female remained on her own eggs until they hatched. As previously, the male brought the young of the second female to the nest of the first. Soon after her nest exodus the young began following all three parent birds which then formed a stable trio within which no further aggression was observed.

The occurrence of bigamy in this particular case might have been facilitated by previous relations between the birds involved, and the second female being slightly ahead in her reproductive cycle and thus probably more receptive.

These events are compared with a strikingly similar case in Whooper Swans *Cygnus cygnus* and the wider implication discussed in terms of current theory on individual fitness, parental investment and evolutionary strategies.

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