

SOCIAL BEHAVIOR AND BREEDING SUCCESS IN CANADA  
GEESE (*BRANTA CANADENSIS*) CONFINED UNDER  
SEMI-NATURAL CONDITIONS

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An attempt is being made to reestablish the Canada Goose as a breeding bird in Wisconsin. This is being done by use of large, outdoor enclosures adjacent to appropriate habitat, in which wing-pinioned adults are maintained. The resulting young birds are not wing-pinioned but are allowed to fly over the surrounding fence, in the expectation that they will settle and breed in the adjoining marshlands. The present study was carried out in an eleven-acre enclosure at the Horicon Marsh Wildlife Refuge, Wisconsin. The main objective was to ascertain to what extent and in what ways loss of productivity in the Canada Goose population at the various stages of the breeding cycle was related to social behavior. With this objective, a detailed study of the social behavior of marked individuals was made.

The set-up and the general plan of the study were established by Jahn, while most of the observations were made by Collias, who also prepared and organized the report. This study was financed by the Wisconsin Conservation Department with federal aid in Wildlife Restoration funds under Pittman-Robertson Project W-6-R. We wish to express great appreciation to Cyril Kabat, Research Coordinator, and James Hale, Chief Game Biologist, of the Wisconsin Conservation Department, for permission to publish the data. Kabat also provided much help and useful advice at the outset of the project. We are grateful also to the other personnel of the Wisconsin Conservation Department who aided this study. We wish to thank Mrs. Elsie Collias for preparation of the illustrations.

Observations on the behavior of Canada Geese in the Mississippi Valley have been reported by Johnson (1947), Elder and Elder (1949), Hanson and Smith (1950), and by Kossack (1950), while Balham (1954) has made a study of the behavior of Canada Geese at the Delta Waterfowl Research Station in Central Canada. In the Western States, Canada Geese often concentrate on islands to nest; losses from intraspecific strife have been reported (*cf.* Hammond and Mann, 1956). Considerable information on the migratory behavior of Canada Geese, a topic not covered here, is available in Hochbaum's recent book (1955).

#### METHODS

In the spring of 1952, when this study was effected, the enclosure at Horicon contained 38 adult males and 34 adult females, including three pairs known to have bred the preceding spring. There were also a good many wing-pinioned Mallards present, while various kinds of ducks often visited the enclosure from the adjoining marshlands.

In general, adult male geese were distinguished by a red plastic collar fastened by means of snaps around the neck, and also by an



of crushed oyster shell, of an abundant supply of greens, as well as various natural forms of aquatic and terrestrial growing vegetation. The pellets and oyster shell were fed to the birds from hoppers. A wheat field was planted in the enclosure at such a time that the young wheat plants became available for grazing by goslings as well as adults.

Observations were commenced on March 14, 1952 and were terminated on May 29, 1952. The actual observations were made from two to four days a week, and ranged from 4 to 13 hours a day, as a rule covering about 8 hours a day. In March there was a total of 70½ hours of observation, in April, 101½, and in May, 104½. The total number of hours of observation forming the basis of this report was 276½.

#### PHENOLOGY

Some signs of breeding behavior had already begun when observations were commenced on March 14, since some males were seen defending the vicinity of their female from other males. At least half of the pairs were already formed by this time, and probably many of the birds had remained paired during the winter.

The first territorial defense was seen on March 14, but may have

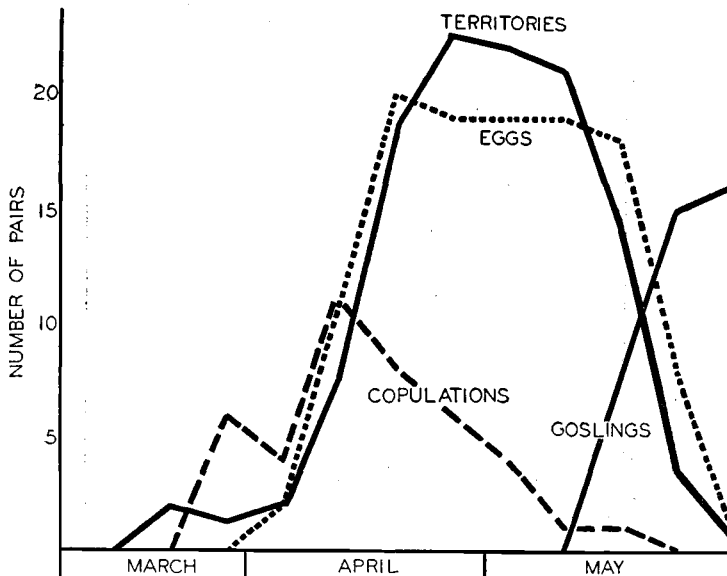


FIGURE 2. Phenology of breeding behavior in the Canada Goose breeding colony at Horicon Marsh, 1952. The ordinate shows the number of pairs of geese seen on territory, copulating, with eggs, or with goslings. This graph refers to all geese in the colony that showed any signs of breeding activity.

occurred earlier. The first copulation was seen on March 26 (by Frank Burrows); the first egg was laid on April 4th; and the first gosling hatched on May 13th. Figure 2 shows in graphical form the seasonal progression in terms of frequency of various breeding activities, including territorial occupancies, copulations, numbers of pairs with eggs, and numbers of pairs with goslings.

The peak of copulations preceded that of territorial occupancies; the latter coincided closely with the peak of egg-laying. Since copulation by a given pair ceases once the full complement of eggs has been laid, the lag in the curve of egg-laying behind that of copulations is as expected.

Since the normal incubation period runs about 28 days, and 5 or 6 days are required for laying all the eggs of a normal clutch, the peak of pairs with goslings should generally come about 33 or 34 days later than the peak of pairs with eggs, assuming a fair degree of nesting success in the population. This time distribution was found to be the case. Of 19 pairs with eggs, 18 laid their first egg in the two-week period, April 6-19, whereas of 16 pairs which hatched goslings, 15 hatched their goslings in the two-week period, May 11-24.

Breeding phenology is of course affected by weather, especially dur-

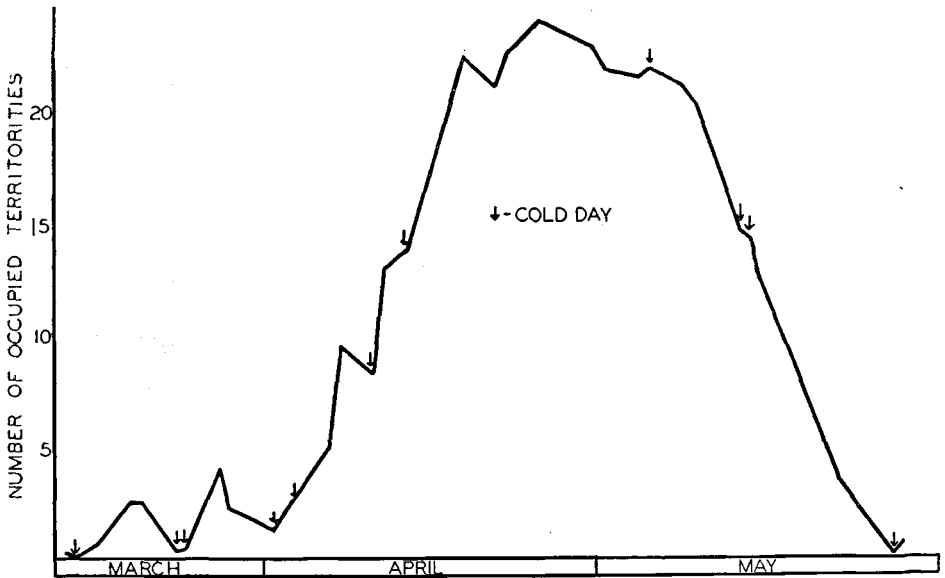


FIGURE 3. Influence of abnormally cold days (arrows) on territorial activity in Canada Geese at Horicon Marsh, 1952. The ordinate shows the average number of pairs on their territories at the start of each observation hour during the day. The graph begins with March 14th.

ing the early part of the breeding season. Adverse weather may delay the onset of breeding activities. Of the various factors of weather, one of the most important is probably temperature. To measure its influence on territorial occupancies, at the start of each hour the observer noted down the numbers of nesting sites that were occupied by geese, and he also took notes on the weather conditions prevailing during each observation day.

Figure 3 shows that abnormally cold days inhibited territorial activity early in the breeding season prior to egg-laying and before all the ice was melted in the pond, but such cold days had little if any influence once the breeding season got well under way, i. e., after egg-laying in the population was well started.

After territorial activity had virtually ceased, the birds flocked together to a greater extent. On the morning of May 29th, the observer counted 56 geese in the wheat field, not including goslings. This was the largest aggregation seen since before the start of the breeding season.

#### BREEDING BEHAVIOR

*Pair formation.* Many of the adult geese were apparently paired at the time when observations began on March 14. However, only three pairs were marked and known from the preceding spring; these were R x W, R/Y x W/Y, and R/G x W/G. Of these, Male R x Female W had been checked also during the fall and early winter and it was noted that they remained together as a consistent pair throughout, together with their young of the 1951 hatch. However, many of the adult geese were seen gradually to form pairs with the advent of the 1952 breeding season.

The sexes have similar plumage in Canada Geese, but the female is smaller and differs characteristically from the male in behavior. She is less aggressive, has a very different voice (see p. 486 *infra*), and often tends to hold her head lower. No doubt these characteristics aid sex recognition.

Successful pair formation in the competition for mates depended both on *specific preferences* and on aggressive *dominance relations* between individuals. One or the other factor might be more important in particular instances. *Preferences* were indicated by persistent tendency of a bird to follow a specific individual. *Dominance* was expressed by defense of the vicinity of the female with special reference to potential or actual sex rivals. Some examples will be mentioned.

Male RO took Female W/G, apparently the mate of Male R/G, by repeatedly driving the latter away from her, eventually killing Male R/G. This was the only pair known from the preceding year which was broken up by other birds. Although Male RO was noted to drive Male R/G over 50 times from Female W/G, Male RO generally tolerated a young bird of the previous year next to female W/G and presumably the offspring of this female and Male R/G. Male Canada Geese almost never attack their mates, but on two occasions Male R/G was actually seen to bite at Female W/G in an apparent attempt to drive her from the vicinity of Male RO.

Female AR, who was persistently attended by two males, tended to follow the subordinate male (-O) rather than the dominant male (AO), who limped along behind her, with an old foot injury. Eventually the latter male was defeated and driven from the female by the formerly subordinate male, -O, who thereupon paired with the female.

On the other hand Male AO had for a while the preference of Female -B, who frequently sought his company, in preference to that of subordinate Male YB, who persistently followed Female -B, and eventually won her after revolting against and defeating Male AO in a vigorous and relatively long battle.

For a time these five geese could be seen together day after day, Female AR either leading the assemblage or following Male -O, with Male AO tailing her and with Female -B in turn following Male AO. Male AO spent most of his time keeping the two subordinate males away from the immediate vicinity of Female AR.

Male RB was followed by two females, RB and -A. Female -A dominated Female RB and occasionally drove her from the vicinity of Male RB. She was seen to copulate three times with Male RB, but this male paired with the other female, which he evidently preferred since he persistently followed Female RB about, whereas he often ignored the perambulations of Female -A.

Sexual activity was sometimes an evident factor aiding pair formation. After losing Male RB, Female -A one day engaged in precopulatory display near the unpaired males, AB and BA, each of whom attempted to copulate with her. Male AB defeated Male BA in the fight that ensued, and subsequently soon copulated and paired with the female.

A paired male after aggressive altercations with other males habitually returns to his female and repeatedly honks and emits a snoring vocalization. The honking tends to be directed away from the female and toward the opponent, but the prolonged snoring vocalization is directed toward her, as the male holds his head low and neck outstretched toward her. Once a male began to snore to a female this could be taken as a positive sign that the two were paired, especially if the female joined the male in honking at other birds, often alternating her yipping with his deeper honking so as to give the impression of a duet. Possibly these vocalizations all serve to strengthen and to help maintain the pairing bond. The birds seem very sensitive to vocalizations, and mates know each other's voice, as was suggested one day by an incident near the duck house. The observer came near a group of geese, and only one of these honked, and at once its mate,

which happened to be on the other side of the duck house with some other geese and not visible, honked in reply. Whenever members of a pair that had been separated came together again they almost invariably vocalized together.

Members of established pairs may develop considerable attachment for each other. One male lost his mate during the period of incubation, her death being due to unknown causes. Her body, half-sunken in the water, was discovered one morning, with the male keeping vigil nearby, and well out of his customary territory. Her body was removed, but for two days the male continued to visit and rest near this spot, and he made no effort to pair with any other female during the remainder of the nesting season.

There was some evidence that mates may at times be soon replaced, when lost. Thus, after Male R/Y died of unknown causes, his mate, Female W/Y continued to sit on her eggs for about ten days in the face of frequent persecution by other birds. She then paired with Male YA, one of the males which had been driving her from her eggs, and about this time she also deserted her eggs.

Birds that did not pair normally were likely to seek the company of others of their own sex, resulting in some definite unisexual pairs. This was true of both males and females. There was an excess of unpaired males present in the enclosure. One male attached himself to the caretaker whom he apparently regarded as his mate, for he would drive other geese from the caretaker's vicinity, and give the snoring call (see p. 483 *supra*) only to the caretaker, whereas he would hiss at other humans. He often waited at the gate for the caretaker to appear each morning, and would honk a greeting while the man was still some distance away.

Pair formation was influenced by weather if the pairing was relatively weak and of very recent duration; cold weather tended temporarily to separate such pairs.

*Breakup of families.* At least six of the pairs were associated with young birds of the preceding year at the start of the 1952 breeding season. In general these families broke up at about the time that the parents started to establish a territory for the new breeding season. However, intolerance toward the young was likely to be manifested shortly before this time, particularly when the birds were hungry during competition for food, since the young birds were then closely associated with the parents. Thus, Male R was observed to drive his own fully-grown young (of the preceding year) from the vicinity of the food over 30 times. These young had been banded the preceding

year and were definitely known to have been raised by Male R and his mate.

The break-up of families depended a little on the weather. On the day that Female R- laid her first egg, there was a snowstorm, and she and her mate left their territory for a while, and were seen swimming toward the food site with their yearling between them. This was the only family reunion noted once territory was well established, and it was of very brief duration, since the yearling did not feed with its parents.

After leaving their families, the yearlings tended to flock together, as well as with non-breeding two-year-olds and adults. The free-flying young geese generally would form small flocks that would leave the enclosure for part of the day, to fly out over the adjoining marshland to varying distances, sometimes out of sight of the observer.

*Selection of nest sites.* The female usually selects the nest site, leading the male about on exploratory jaunts, getting up on nest islets, and poking about inspecting these heaps of branches, twigs and hay with her beak. But when a desirable nest heap was already occupied by other birds, the male would forge ahead to take the lead in driving the other birds away, and if he was successful the female might then mount the potential nest site and inspect it.

The search for a suitable nest site might take one to many days, depending in part on the availability of good nest sites and in part on the dominance status relative to competitors for specific sites. Male AR and his mate got a late start and were rather low in dominance. They found most of the desirable nest sites already occupied. One morning they were seen to visit nine different nest sites in the space of an hour, being evicted from most of these sites by birds that had already laid claim to the sites in question.

Some birds preferred to build their own nests along the shore, constructing them of dried and dead weed stalks, and largely ignored artificial nests still unoccupied. Two of the artificial nest heaps overturned when the ice melted and the birds showed no interest in them until marsh hay was placed on them.

Nest sites were selected both before and after the ice melted from the pond.

Both of the two pairs whose nesting sites of the preceding year were known nested at about the same location in 1951 and 1952.

*Establishment of territories.* Once a nesting site was selected both members of the pair generally stayed close by. Their claim was announced to all other geese by loud honking and other threatening



actions, particularly by the male, whenever intruders came near. Typically, the male would sally forth at an intruder in the vicinity, with neck outstretched and head held low. If the intruder stood his ground or came closer, a fight would probably ensue, in which the territorial owner was usually, but not always, the winner. Should he lose, the intruding pair, if searching for a nest site, evicted the resident pair, or if not in need of a nest site, but having asserted their domination, merely continued on their way, perhaps pausing a few minutes to inspect the nest of the vanquished pair. As a rule the owner of a territory successfully drove off intruders without the necessity of a fight; often merely a honking defense sufficed. The intruder would move away, sometimes with the neck fluffed out, whereas the more aggressive bird always kept his neck feathers smooth and appressed. On returning to the female, the male would both honk and utter his snoring vocalization, and the female would chime in with her distinctive voice, her short staccato honks or yips alternating with the louder, longer and more resonant honks of the male. The honking duet was also given as intruders approached, but the snoring sound was more likely to be given after the encounter. The retreating birds were far less likely to vocalize than was the winner, and frequently fell silent.

A special display was often engaged in by the male with respect to intruders. With neck stretched up he would abruptly flip his beak upwards, simultaneously rolling the head, showing off to advantage the white cheek patches. This head-flipping, which possibly serves a threat function, seems to indicate indecision, since it was generally seen at the moment when a bird was likely to change from one behavior pattern to another, for example, from standing in one spot to charging an intruder, or to flight from an enemy. Head-flipping was characteristic of the males, but was only occasionally seen in females. This action was strongly associated with display of the white cheeks, which are a brighter, clearer white in the spring than in the fall. Perhaps this peculiar display, which has a warning connotation as well as threat and mild alarm, evolved from shaking mud from the beak preparatory to flight.

Sometimes when the observer or a goose approached a territorial bird, its body plumage was abruptly raised, and if the intruder passed at too great a distance to provoke an active attack, the plumage was again appressed after a vigorous shake, as if the bird had "shaken off" a state of tension.

A human intruder was treated in much the same way as were intruding geese by a territorial male. A female on her nest frequently

would not honk, but rather hiss repeatedly at a man coming close to her. The male would not only honk and flip his head, displaying his white cheeks, but he would also pump his head up and down just as the female might do. This pumping display (also done against geese) indicates incipient attack, and consists of a vacillation between lowering the head with the base of the neck drawn back slightly to facilitate striking out and a return to a resting position, perhaps not unmixed with fear of the intruder. On a closer approach of the intruder the head pumping would begin to include another component in which the lowered head was thrust out in the direction of the intruder, and finally, should the man persist in his approach to the nest, some ganders would actively attack. The black and blue bruises inflicted by the strong jaws and blows of the powerful wings demonstrated the potency of the male in defending his home and mate.

The role of dominance in the establishment of nesting territories was most clearly demonstrated by instances of circular dominance relations. Thus, in a contest over Nest Site 33 that went on for several days, Male BR would drive off Male AO and his mate; Male BR would then be driven off by Male AA, and in turn Male AA and his mate would be driven off by Male AO (Fig. 1). This cycle would be repeated indefinitely, until some male dominant to all three, such as Male O-, would come along and take over the nest site.

Repeated evictions and repeated attempts at reestablishment on a given nest site, covering a period of time anywhere from a few minutes to several weeks before such attempts were given up, were the rule for birds of relatively low dominance status. The resulting picture was a complex network of movements and shifting ownerships of the more heavily contested nest sites. Figure 1 shows the number of successive owners of different nest sites laying more than momentary claim to these nest sites.

Size of territories varied greatly with the individual bird. Some of the males defended more than one of the artificial nest sites, especially where the nest sites were close together (Fig. 4). In every case the great majority of the territorial defenses of a male centered about the nest site of the female.

The size and shape of territories changed with time and circumstances. At first Male YO defended not only the future nest site of his mate (Nest Site 26), but occasionally he defended the four neighboring nest islets as well. Later, as these islands came to be occupied by other pairs he restricted his defenses to his own nest islet. In

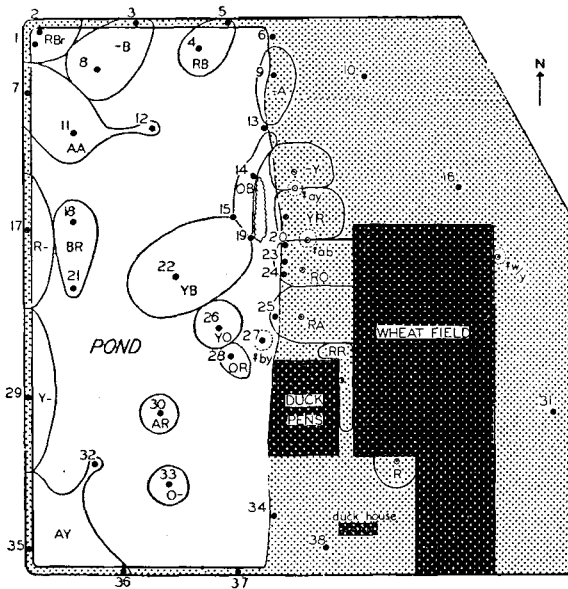


FIGURE 4. Diagram of the eleven-acre enclosure, showing established goose territories on May 1, 1952. Artificial nest sites (black dots) are numbered, ganders are named by letters. Territories of unpaired females are shown by dotted lines about the nest site. The stippled area is land.

contrast, Male RO, which wedged in between two powerful and established males, for a time did not even “dare” to honk, and his female was often driven from her nest during the egg-laying period. But in a few weeks his territory had enlarged considerably, and he soon honked at and later fought with his neighbors, defeating one of them. In general, after a bird defeated its neighbor in a fight the territorial boundary moved in the direction of the loser’s ground.

The sound of honking served to excite the aggression of the territorial males. One peculiar case gave a clear example of this. Whenever any geese would honk just outside the bounds of his territory, a certain male would thereupon often attack and drive from her eggs an unpaired female which had her nest at the edge of his territory. The disturbed honking of his own female frequently excited the aggressiveness of a male, and might lead to fights between otherwise relatively peaceful neighbors.

In the pre-egg stage territorial activity was greatest in the early part of the morning (Fig. 5). But this extra activity in the early part of the morning was only slightly, although consistently, greater than at

other times of day. As the season progressed, this slight early morning peak advanced to still earlier hours, as did the sunrise.

Defense of territories about the nest sites by both male and female, but particularly by the male, continued until the eggs hatched, and the young left the nest, after which time the parents seemed to lose all interest in territorial defense.

The importance of the male in territorial defense was made evident by cases in which there was no male to defend the nest site. Female W/Y lost her mate by death late in her incubation period, and although she had been sitting very steadily up to the time the male was lost, her eggs failed to hatch. The reason was that with loss of her guardian she became subject to the domination and disturbance of other pairs as well as of unpaired males, who drove her repeatedly from her eggs, resulting in death of the embryos, presumably from chilling.

*Sexual behavior.* Copulations were often seen to occur between members of a pair before, as well as after, selection of a permanent nesting site by the pair. When they occurred before establishment of a territory, copulations took place in any convenient stretch of open water with a depth of six inches or more. After territorial establishment the location of copulations was invariably in a portion of the pond nearest the nest site. No copulations were observed taking place on land.

Pre-coital behavior consists of dipping the head deep under the water and then lifting it and at the same time throwing water over the back with the back portions of the head and neck, in a manner similar to the movements of bathing. But, unlike ordinary bathing, the wings are not used; they are kept folded in their normal resting position. This pre-copulatory display, which may be initiated by either the male or female, gradually increases in frequency and intensity over a period of 30 seconds to two minutes or more. The male works closer to the female, and typically grasps the feathers of the back of her neck as he mounts. The female may keep her normal floating position, or she may stretch her neck down at a low angle with the surface of the water partially or completely submerging during the copulation, which lasts only a moment or two.

Post-copulatory behavior is very characteristic. Both birds stretch the neck up high and inclined slightly backward, with the beak tipped upward, and often rotate so that they face one another, breast to breast. Typically the male half raises his wings without unfolding them, in a swan-like pose, and he then gives a snoring vocalization,

relatively brief and weak, compared with his ordinary greeting snore to his mate. Meanwhile, the female begins to dip her head vigorously into the water and to lift it again, throwing water over her back in exactly the same fashion as in the pre-coital display. The male then joins her in this. One or both birds may rear up in the water and flap their wings either before or in between sessions of the head-dipping display. After a few seconds to several minutes of this activity, the birds retire together to a nearby spot along the shore and preen themselves.

A two-year-old pair was seen to copulate in the breeding pen, and the details of their behavior were essentially similar to the situation in adults. Yearlings sometimes engaged in the head-dipping movements in quite typical pre-coital fashion, and once one yearling was seen to mount another, but immediately after dismounting neither bird assumed the typical "swan-like" pose, as adults would do right after a successful copulation. The sex of neither of these yearlings was known.

One male (-Y) was habitually attended by two females (OA and AY), and he was seen to engage in the pre-coital display with both females simultaneously, but when the display worked to its climax, surprisingly enough one of the females, OA, mounted and apparently copulated with the other female, AY, but there was no post-coital display.

As this case suggests, copulatory behavior, in the excitement engendered by the pre-coital display may sometimes be remarkably indiscriminating. In another case where one pair of adults engaged in pre-coital display, a two-year-old nearby joined in the display and then mounted and copulated with the adult female. Immediately following the copulation the two-year-old bird "swanned" his wings and gave the characteristic post-coital vocalization.

Sexual behavior was contagious, and the pre-coital display was likely to set off similar behavior in both paired and unpaired birds in the vicinity. Similarly, copulations by one pair sometimes appeared to stimulate copulation by other pairs.

Unisexual pairs of males or females not infrequently engaged in pre-coital display, but none of these displays was ever seen to lead to copulation.

It was our impression that copulation was likely to be least disturbed when it took place on the home territory. Pairs not yet established on their own territory were sometimes interfered with during the phase of pre-coital display, and driven away by some more dominant bird.

Like territorial occupancy in the pre-egg stage, the frequency of copulations tended to be well distributed throughout the day, although there was a slight early morning peak (Fig. 5). Early in the

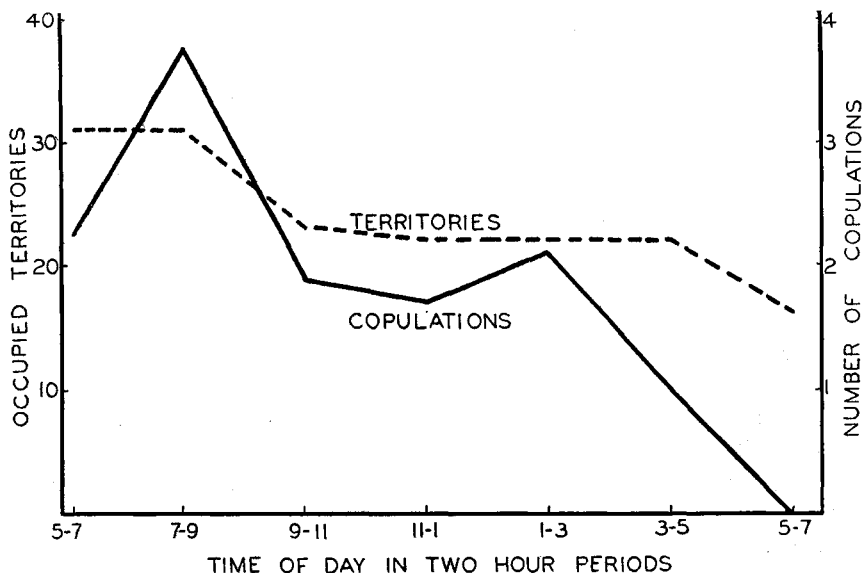


FIGURE 5. Time distribution during the day of 52 copulations and of territorial activity in the pre-egg stage in Canada Geese. The number of nest sites occupied by geese was recorded at the start of each hour of observation. The number of copulations seen and the number of territories occupied are given per 10 hours of observation (ordinate) and the data are summarized by two hour periods for time of day (abscissa).

breeding season copulations were seen most frequently during the warmest parts of the day, whereas later in the breeding season most copulations were seen in the cooler part of the morning. Thus, 8 of 12 copulations observed before the ice in the pond was all melted (before April 2), took place between 11 a.m. and 3 p.m. But only 10 of the remaining 40 copulations seen (in April and May), took place between these hours, and 21, or more than half, took place before 10 a.m.

*Nest-building and egg-laying.* One female was watched building a nest in a site entirely of her own selection and with nesting materials not provided for her. After rounding out an initial depression in the earth, she gathered nesting material as far as her long neck could reach, stretching out and breaking off small pieces of dead weed stalks, 3 to 6 inches long, with her beak. She then passed each piece

of weed stalk from one side to the other across her breast, continuing the movement backwards along one side of her body and dropping the material onto the rim of the nest. After exhausting the supply of nest material within convenient reach she rose and worked her way slowly from the nest to a distance of six feet, breaking off pieces of weeds and dead grass and tossing them to one side and behind herself as she worked along. She would then return to the nest, work in some of the added material, get up and again work over her previous route, picking up and throwing back nesting material. By this means, material for the nest was moved in toward the nest from the surroundings in successive relays. This nest material was pulled in and then worked into the rim of the nest with the beak while she sat on the nest, until the rim of the nest had reached a height of 5 inches. At intervals she rounded out the nest hollow, turning and shaping it with her breast, and sometimes scraping back with her feet. It took her about four hours to complete the nest (6-10 a.m.), and she then covered over the completed and empty nest with her beak. Within 45 minutes she was found to have laid her first egg in the nest.

Very rarely a male was seen to help the female gather nest material and build the nest, but even in these rare cases his efforts seemed crude and lacking in intensity.

In the days just preceding egg-laying, the female may show a strong urge to graze, spending an increased portion of her time during the day grazing. The male on the other hand continues his normal strong attachment to the territory, and in some cases where the nest site was separated by some distance from the grazing area, the male was seen repeatedly calling and trying to lead the female back to their nest site.

Female W was checked daily for egg-laying by the caretaker, George Amelong. She laid one egg a day except for the fifth day, on which she did not lay. Females do little sitting on the eggs until the clutch is completed, but the eggs are carefully covered after each one is laid.

The average clutch size for 17 pairs of geese in which the female was an adult (3 or more years old) and was probably not interfered with during egg-laying (as was Female W/G by Male YR and Male RA) was 5.2 eggs.

As a rule, down is not added until after 3 or 4 eggs have been laid, although different females vary in this respect. Female AA added down after laying only 3 eggs, and on the same day Female W with 4 eggs, and destined to lay a larger clutch than did Female AA, had as yet added no down. The down is plucked from the breast with the beak, and not only down feathers, but some breast contour feathers may be added as well.

Nest building continues to some extent throughout the period of incubation. A female, while sitting on her nest, may reach down to the outer and lower border of the nest, pick up nest material in her beak and then deposit it on the rim of the nest close to her body. This procedure, combined with occasional scraping back with the feet used alternately, results in a typical low cone-shape to the outside of the nest, and prevents the nest from becoming flattened down.

*Incubation.* During the egg-laying period the female comes to sit on the eggs more and more of the time, until finally when the clutch is completed she sits on the eggs almost continuously, except for brief rest periods. At the same time pre-coital display and copulatory activities cease (Fig. 6). The female does all of the incubating, while

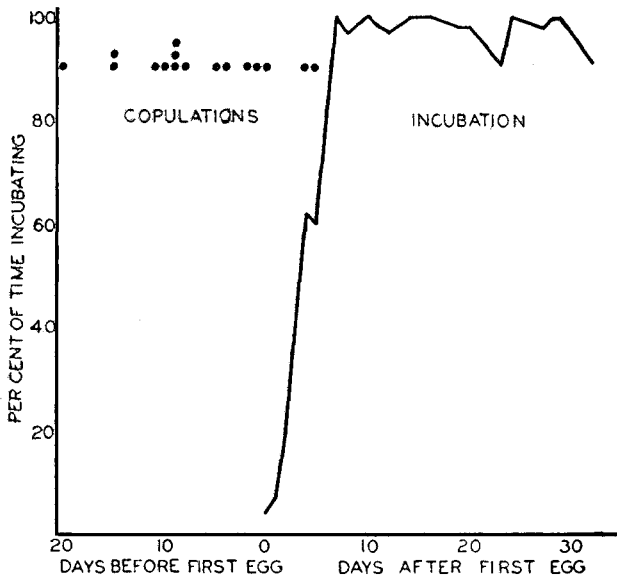


FIGURE 6. Inverse relationship between sexual (copulations) and parental (incubation) behavior in Canada Geese. Each dot refers to one copulation seen on that day. At the start of each observation hour it was noted for each female whether or not she was on her eggs. Only 11 pairs that were seen to copulate and also to incubate eggs are included.

the male stands guard nearby. She was not usually seen to leave her nest more than two or three times a day. She leaves in order to rest, feed, drink, bathe and preen. Her absence from the nest varied in length from four minutes to over two hours, usually being less than one hour.

When a female left her nest and eggs, the event was made quite



conspicuous by the male who would honk loudly while accompanying her. The male gave the impression of being disturbed by the absence of the female from her nest, and he frequently tried to lead her back to the nest before she was ready to return, and when she did return, he served as a honking escort.

On reaching her nest the female almost invariably would stand over the eggs preening her belly and lower breast and apparently working loose some feathers, since a bare area soon appeared from the midline of these areas and increased in lateral extent day by day, during the first part of incubation. The habit of the female of standing over the eggs soon after leaving the water may also help dampen the eggs and improve their hatchability.

Should the eggs fail to hatch after the normal 28 days incubation period, the female may continue to sit for some time. One unpaired female with infertile eggs continued to sit on these eggs for a total of at least 35 days before deserting her nest. Female W/Y, whose mate died before the end of her incubation, failed to hatch out her eggs, because of repeated disturbances by other birds. She continued to incubate despite these disturbances for a total of 37 days.

The average length of incubation from the date of the last egg until completion of the hatch was 28.6 days for eight broods of Canada Geese, for which the dates were accurately known.

*Parent-young interactions.* (a) *Hatching and initial acquaintance-ship.* The goslings hatch over a range of about a day, much less than the range involved in the laying of the eggs. This difference is undoubtedly due to the fact that the female does not begin very steady incubation until all of the eggs have been laid (Fig. 6).

After hatching, the goslings are usually brooded in the nest for the first day. The down soon dries in the nest, but even when dry a very young gosling needs to be kept warm, and quickly becomes cold to the hand when removed from the parents. Reasoning by analogy from work with various ducks (Collias and Collias, 1956), we suppose that this initial day in the nest permits the young ones and their parents to become acquainted and conditioned to each other, and serves later to help maintain family unity, after the goslings leave the nest.

(b) *Leaving the nest.* After the first day, the goslings leave the nest, in part due to their own exploratory tendencies and in part due to parental encouragement and example. When the female steps off the nest and moves a little to one side, the goslings tend to follow, as they would any large object moving slowly away from their imme-

diate vicinity. Thus, a one-day-old gosling removed from its family to be weighed, when placed on the ground right after being weighed, did not at once return to its parents and siblings, plainly visible at or near the nest site some 40 feet away, but instead followed the human observer as he walked off in nearly the opposite direction from its natural parents.

Parental vocalizations may also serve to lure the goslings from the nest when necessary. Excursions from the nest at first amount to only a few inches or a few feet, and the goslings repeatedly return. These excursions are gradually extended to greater and greater lengths, and within a day or two expeditions might be undertaken to any part of the 11-acre enclosure. In the family progressions, the young goslings move along in a compact group between both parents. Usually the female leads, while the male takes over the lead when the situation calls for aggressive attack or defense. During the first few days after leaving the nest, the parents would usually lead their brood back to the original nest to be brooded for the night.

(c) *Initial self-maintenance activities.* The goslings must feed and drink for themselves and be able to seek safety on the water with the parents, after they have left the nest. Goslings that had not yet left the nest were often seen to bite at green grass blades and other green vegetation overhanging the nest, but usually they did not seem able to tear off and eat anything as a result of such mouthings until after they had left the nest. On first leaving the nest two broods of goslings were seen to go to the edge of the water, drink, enter the water and swim about, all for the first time in their lives, without the inducement of parental example or leading, although the initiation of such activities might often be facilitated by parental example.

The goslings fed largely on wheat sprouts in a wheat field that had been planted for their benefit, leaving alone thistles and most other weeds in the field. They also fed on fresh green sprouts of various plants along the muddy shoreline, and on submerged aquatics. Where the water was too deep for the goslings to reach the submerged aquatic plants the female was seen in one case to reach down and pull up the plants, while her downy young ones fed on bits of the plants which they pulled from her beak. A few days later these same goslings were observed to tip up, pull up and eat water weeds in the shallow water near shore, on their own initiative.

At the food hoppers where pellets containing a prepared diet for the geese were fed, the parents seemed to be powdering up the pellets, making it easier for goslings less than a week old to feed on the material.

(d) *Maintenance of family unity.* When lost or otherwise separated from other geese, a gosling would give loud and repeated distress calls, sounding quite like the peeps of lost baby chicks of the domestic fowl. These distress notes attracted the parents. When reunited with its family a gosling would promptly switch to contentment notes, somewhat reminiscent of the contentment or pleasure notes of chicks of the domestic fowl (Collias, 1952).

During the first week the goslings were brooded quite often during the day; after the first week it was evident from general observation that they were brooded less frequently, although no data were assembled on this point. All of the females brooded their downy goslings when it rained, and at night.

In defense of their goslings the parent geese, especially the male, often attacked other geese that came too near the family; the male sometimes even attacked human beings. Interestingly enough, in defending their goslings, parent geese, unless at a very high pitch of excitement, ordinarily did not honk. This relative lack of honking was in marked contrast to their raucous behavior while maintaining territory. Honking by another goose on or near its territory seems particularly to stimulate aggressiveness of a goose, and evidently absence of honking in parent birds serves often to give them and their young ones safe passage across the territories of geese that had not yet hatched out their goslings.

Parent birds, as well as goslings a week or more old, would attack strange goslings that ventured near, especially if there was a wide discrepancy in size from goslings in the family, permitting ready recognition of strangers as such. Adoptions of strange goslings were most likely to occur when both own and strange goslings were less than one week old, and of about the same size. These younger goslings have apparently not yet become thoroughly acquainted and attached to a specific parent bird, nor their parents to them. Adoption is also facilitated by dominance of the foster parents. When a gosling accidentally gets into another brood and is allowed to remain with that brood, its parents may be thwarted in their endeavors to get it back, by the aggressive attacks of the other parents defending the vicinity of their own brood. Usually, however, the original parents succeed in calling their own goslings out of another brood with which they might have intermixed, and goslings possibly recognize the voices of their own parents. Whether or not the gosling stays with and is permanently adopted into the other brood depends in part on the degree of attachment of the gosling to its own parents, and in part on the

degree of attachment or indifference of the parents to their goslings, as well as on other circumstances, such as the degree of tolerance or intolerance of the foster family towards the newcomer. Adoptions were rare in the case of goslings more than one week of age.

Relatively permanent adoptions were common in the somewhat crowded conditions prevailing within the breeding pen, and three pairs of birds lost their entire broods through adoption by other parents. The family of Male Y- and Female Y-, a particularly dominant pair (Table 1), grew larger each week, and by the time their own goslings were a little more than two weeks of age, their total brood had increased by adoption to some 20 goslings, about three times the original size of the brood.

As the goslings grew older their aggressiveness greatly increased. When less than a week old they would hiss at a human captor, and when over a week of age, battles between goslings were not infrequent. Strange goslings from other families were particularly prone to be attacked, but fights sometimes involved members of the same brood. It was not long before the goslings seemed to share to some extent in the dominance status of their parents, and it was remarkable to observe a downy gosling only about two weeks old forge well ahead of its father to drive an adult gander away from the food hopper.

*Interrelationship of different behavior patterns.* Reproductive behavior in the Canada Goose, as in many other birds can be divided into the sexual phase and the parental phase, perhaps also dominated by sex hormones and prolactin, respectively (*cf.* Collias, 1950). Figure 4 illustrates the inverse relationship between the sexual and the parental phases of reproductive behavior in Canada Geese. Once the complete clutch has been laid, copulations soon cease and pre-copulatory displays become rare. Relative predominance of sexual activity or of parental activity does not however imply mutual exclusiveness, in an all or none sense. Some behavior patterns, like that of territorial aggressiveness, seem to belong to both the sexual and the parental phases. It is not unlikely that a certain amount of gonadal endocrine activity continues in males while the female is incubating, and that this may be responsible for much of the aggressiveness of the male.

Excitation of one drive may sometimes lead to some secondary excitation of another drive. Thus, after the termination of a territorial fight between males, the female of the territorial owner (generally the winner) may go into a frenzy of pre-copulatory display, but such display was not seen to lead to copulation. An unpaired female,

which was often driven and kept for a while from her nest and eggs by an adjacent dominant male, meanwhile often stood five or six feet to one side and picked up and moved back dead weed stalks in typical nesting movements. This apparently irrelevant or displacement behavior would seem to point to a close relationship of some sort between the nest-building and the incubation drives in these geese. Tinbergen (1940) has reviewed quite similar instances in other birds.

#### VOCALIZATIONS

Some ten or more different vocalizations were observed in Canada Geese. These sounds are listed below, together with the situation that seemed to provoke each. This list is not intended to be exhaustive.

1. *Hiss*. Directed against other geese, ducks, and especially against humans near the nest. Apparently signifies threat and alarm at *short distances*. For example, one female on her eggs repeatedly hissed at the observer when he approached within a few feet, and then switched to honking when he moved off, reverting to hissing each time the observer returned close to her.

2. *Honking*. The honking of the male is loud and resonant, and each honk seems to be relatively prolonged, as compared to the short, staccato honking or yipping of the female. It is probable that spectrographic analysis would reveal characteristic differences in the frequency components in the voices of the two sexes. Geese characteristically honk in at least five different situations: (1) in territorial advertisement and warning to intruders, (2) as a *long-distance* call or answer to the mate when separated by more than just a few feet or yards, (3) as part of the greeting ceremony when mates come together after having been separated, (4) as an alarm call when a man or dog, for example, approaches a wild flock, or when a gosling is threatened or seized by a man and gives its distress calls, and (5) in flight or when about to take flight. The honking seems to be of the same essential character in all of these situations, although it is possible that significant nuances of this vocalization under different circumstances have escaped the observer. There seem to be two common elements in the various stimulating situations, first, some element of *alarm*, and secondly, functioning of the call over some *distance*. In the case where geese honk in flight one may reasonably assume that fear of separation from companions provides the occasion for honking, just as a flightless male may honk down his free-flying mate when she takes wing. The alarm and the distance functions of honking may

help to explain the loudness of this call compared to others, and its strident and high-pitched character.

3. *Short-distance call of the mate.* This call is a low, short, rather soft grunt, given repeatedly, about once a second: *kum! kum! kum!*, etc. Sometimes it is double-noted, sounding like *wah kum!*, the first note being low and brief and the second, higher and abrupt. A free-flying male was observed to give the short-distance low call on trying to get his wing-pinioned mate to fly off with him, but when he actually began to run into the wind and took off, he switched to the usual loud honking. Another example may be cited. A female left her nest and eggs to drink, and then she swam toward the food site, while the male trailed up to 50 feet behind her repeatedly calling *kum! kum!* in an apparent effort to induce her to return to her nest. He continued to lag, and soon the mates were separated by a considerable distance, whereupon he suddenly began to honk loudly, and swam rapidly to join the female as she came near the feeding area. Both sexes give the short distance call.

4. *Short distance call to the goslings.* This is a rapid series of short, low, soft grunts, quite similar to the preceding call, but often faster and not so loud. Possibly it is the same call. Either sex may give it, but it is most often heard from the female.

5. *Special greeting call for the female.* This rather loud, prolonged, snoring vocalization is peculiar to the male who directs it only to his mate. It is heard when a pair has just formed, and whenever the male and female come together after a period of separation, whether or not any aggression against other geese was involved. Possibly it functions to reinforce the pairing bond.

6. *Post-copulation call.* Immediately following copulation the male gives a brief, light snore, while assuming the characteristic posture that has been described in preceding pages.

7. *Scream of pain.* An abrupt, high, rather short scream, heard when one gander was taken by surprise and received an unexpected bite from another.

8. *Distress call of adult.* A loud *oh!-oo, oh!-oo*, etc., heard when one bird was seized, held and bitten by a dominant bird. It was sometimes heard when a bird was separated from its mate by a fence.

9. *Distress call of gosling.* A loud peeping, typically given when a gosling was lost, or was removed from its family by the observer.

10. *Contentment notes of gosling.* A light, rapid series of soft notes: *wheoo, wheoo*, etc., given, for example, when the gosling was returned to its family.

## DOMINANCE ORDER

These birds show a dominance order which centers in good part over competition for food. In competing for food one bird would advance at another, often honking at the same time, and as it came near, the aggressor would lower its head nearly to the ground, and with the long neck outstretched, except for its basal portion curved back ready to strike, the bird would charge with open threatening jaws at the goose it intended to displace or keep away from the food. Should the bird which was attacked retreat it was adjudged to be subordinate. No interaction was tabulated unless one bird was definitely the aggressor, and the other definitely retreated. Rarely, a bird threatened failed to retreat, and ordinarily a fight for dominance then ensued in which the contestants attempted to seize and hold each other by the base of the neck with the beak, meanwhile repeatedly administering powerful blows at each other with the wings. A fight

TABLE 1  
DOMINANCE ORDER OF 38 MALE CANADA GEESSE AT HORICON MARSH  
IN THE BREEDING SEASON OF 1952

Domination-subordination ratios (d:s) are shown for various degrees of breeding success. The d:s ratio for any given male refers to the number of birds dominated (d) and the number of birds to which that male was subordinate (s).

*Males which held territory:*

Mate hatched out goslings (aver. d:s ratio of males, 15:7)

Male	d:s ratio	Male	d:s ratio
R	19:1	YR	16:7
AY	31:1	-Y	12:9
-B	18:2	RR	8:7
Y-	21:3	RB	10:10
YO	21:7	-A	8:9
RA	12:4	RO	9:11
OB	15:5	OR	7:9
R-	19:7	BR	7:20

Eggs of mate lost (aver. d:s ratio of males, 7:11)

BY	5:2	-R	5:17
R/Y	12:9	Red-breast	2:12
YB	11:15		

Mate did not lay eggs (aver. d:s ratio of males, 8:10)

O-	14:8	AA	6:8
-O	18:14	A-R	3:5
AR	11:12	AB	3:7
AO	8:10	A-	1:19

*Males which failed to hold territory and to pair effectively (aver. d:s ratio, 3:13):*

OO	6:12	YA	2:11
YY	3:12	BB	2:13
BA	3:13	OA	1:10
B-	4:14	OY	0:9
R/G	4:19		

attracted the attention of and excited other geese, some of which would honk, while those nearby were likely to orient themselves towards and watch the contestants.

The dominance hierarchy that resulted was reinforced by aggressive-submissive interactions at food, and was habitual and consistent as a rule, although some 18 reversals were observed during the breeding season, probably often due to competition for mates. It was not always possible to separate aggressive competition for food from defense of the vicinity of the mate, since early in the breeding season at least, mates ordinarily accompanied each other to the food area.

Both male and female adults as well as younger birds had their place in the dominance order. However, males almost never attacked their mates. Since the dominance of the male over other males seemed crucial for nesting success, emphasis was placed on ascertaining the dominance order of the males as shown in Table 1. The number of paired relationships possible among the 38 males of this table was 703, as calculated by the formula,  $n(n - 1) / 2$ , and of these relationships there were observed 345, or about half.

Circular dominance relations were not uncommon. Thus, Male R dominated Male AY, which dominated Male R/Y, which in turn dominated Male R.

The female and young birds of a family to a considerable extent shared in the male's dominance, although when they were not in his immediate vicinity their status was likely to be altered, especially when they attempted to attack ganders.

#### ROLE OF BEHAVIOR IN REDUCING BREEDING SUCCESS

The factors reducing productivity in the breeding colony at Hori-con were almost entirely factors connected with social behavior. Predation and mortality from parasitism were apparently nil, although the pen was surrounded merely by a fence enclosing one corner of the marsh. (However, two adults died from unknown causes.) Flooding was not a factor in loss of any nests, nor was weather the cause, directly or indirectly, of any losses, although the birds were just as exposed to the elements as they would have been had there been no fence about them.

One pair of two-year-old birds successfully hatched out six goslings on top of a muskrat house in the marsh some 150 yards south of the enclosure. This pair is not included in this account which refers entirely to conditions within the breeding pen.

*Factors reducing productivity at each stage of the breeding cycle.*



With respect to success in breeding, the geese may be grouped into five categories: (1) pairs that hatched out goslings, (2) pairs that laid and incubated eggs, but failed to hatch young, (3) pairs that held territory but failed to lay and incubate eggs, (4) pairs that failed to establish territory, and (5) geese that failed to pair normally.

Table 2 summarizes the gains and losses within the breeding pen during the breeding season of 1952. There were 73 adult birds on hand at the start of the breeding season; also included in the tabulation are one pair of two-year-olds that laid and incubated eggs, and a couple of two-year-olds, each of which paired with an adult bird, making a total of 77 breeders to be considered. Within the pen, 16 pairs hatched 71 goslings.

TABLE 2  
GAINS AND LOSSES OF CANADA GEESE IN THE BREEDING PEN AT HORICON MARSH,  
DURING THE BREEDING SEASON OF 1952 (TO MAY 29TH)

	Gains	Losses	Per cent loss
Adults present at start	77		
Adult mortality		3	4
Eggs laid (23 clutches)	133		
Eggs lost:		62	44
Dropped eggs		6	
Clutches lost (seven)		35	
Infertile eggs of successful pairs		10	
Inviab. embryos of successful pairs		11	
Goslings hatched (by 16 pairs)	71		
Gosling mortality		5	7

It may be seen from Table 2 that egg loss was the greatest source of loss, considering gross age categories, since only 4% of the adults and only 7% of the goslings were lost (to May 29, 1952), whereas 44% of all eggs laid were lost.

It is useful to consider the relative losses in *theoretical* breeding potential that occurred at different stages of the breeding cycle, since this type of consideration helps us to decide just where and when most of productivity is lost. Table 3 shows the different percentage losses at each stage of the breeding cycle, assuming a clutch size of 5 eggs. This table brings out the importance of factors concerned with failure to lay eggs, at least in nests. Over half the birds assumed to be capable of breeding failed to make nests in which they laid and incubated eggs; one-fifth of the birds failed even to pair up effectively. The nine pairs that failed to lay eggs in nests were involved in unusually frequent territorial clashes, and most of them were unable to maintain stable territories for any length of time. Four of the 5 pairs

(and perhaps all 5) that lost their clutches did so because of disturbance to the female from other geese, related to a lack of effective male defense. It would seem that over half the loss in breeding potential could be ascribed to factors having to do with territory, *i. e.*, to lack of effective territorial establishment or defense (Table 3). The possible alternative is that many of the females that were sufficiently motivated to defend territories and to copulate, for some reason were not sufficiently in breeding condition to lay eggs. These two explanations are not completely antithetical.

If we take 5 eggs as a general figure for average clutch size, the 41 males and 36 females present should have raised 180 goslings, instead of only 66 (to May 29), as their theoretical breeding potential. Tak-

TABLE 3  
RELATIVE LOSSES IN THEORETICAL BREEDING POTENTIAL AT VARIOUS STAGES IN THE BREEDING CYCLE, ASSUMING THAT EACH PAIR OF ADULTS COULD HAVE RAISED FIVE GOSLINGS

	Numbers lost	Per cent of total
Failure to pair effectively (11 males and 5 females, equivalent to five pairs)	25	20
Failure to lay and incubate (9 pairs)	45	37
Loss of entire clutch during period of incubation (5 pairs)	24	20
Inviability and infertile eggs in nests otherwise successful	21	17
Gosling mortality	5	4
Adult mortality	3	2
Totals	123	100

ing into account a slight adult mortality, it may be calculated ( $123/180 \times 100$ ) that about 70% of the theoretical increase in population was lost (Table 3).

Although failure to lay eggs, as well as loss of eggs once laid, was the most important source of loss in productivity, the breeding potential was frittered away to a greater or lesser extent at all stages of the reproductive cycle. It is pertinent to consider in more detail the various mechanisms involved at each step in the cycle, insofar as these mechanisms could be observed or deduced.

Geese (including Males R, R-, AY, Y-, YR, and R/Y) with a previous history of rearing families successfully, were among those likely to succeed again. But we did not know the breeding history of many pairs. Part of the reason for the success of experienced birds was their relatively high dominance status (Table 1).

The evidence that high rank of the male in the dominance hierarchy during late winter and early spring increases the chances of an

individual male and his mate to breed successfully is shown in Table 1.

Twenty per cent of the loss in breeding potential came from failure of some birds to pair effectively (Table 3). As Table 1 indicates, part of this reason was probably due to low dominance status. Factors of individual preference and fixation were also important, being true of both males and females.

For some weeks, Female -Y trailed after Male -Y, which was already closely attended by Females AY and OA; he preferred (often followed) and paired with Female OA. Both Females AY and OA dominated Female -Y, and occasionally would drive her back away from the vicinity of the male. Female -Y eventually stopped following this or any other male, but Female AY laid, and for 35 days incubated, a clutch of infertile eggs at the edge of the territory of Male -Y x Female OA. But the male never defended Female AY directly from other males; he occasionally drive her off her eggs himself.

The same type of situation but in the opposite sex, was manifested by Male -O, which persistently maintained his interest and fixation with respect to the apparent mate of Male AO. Eventually he defeated Male AO in this competition, but so late in the season that none of these three birds managed to breed.

Unisexual attachments among seven males, as well as in two of the females may also have acted to delay normal pairing with the opposite sex, until advance of the season made successful breeding impossible.

Male RY and Female AB showed very little interest in specific individual geese, for unknown reasons.

Male OO became attached to the keeper, and thereafter made no attempt to pair with any goose.

Only one of the unpaired geese, Female -A, was seen to copulate.

Thirty-seven per cent of the loss in breeding potential was due to failure of nine pairs to lay and incubate eggs (Table 3).

One of these pairs included a non-territorial adult male which was wing-pinioned, but paired with a free-flying two-year-old female. The latter bird often flew off with a two-year-old male, leaving her adult male alone much of the day. The other 8 pairs (including Males O-, AR, AO, -O, AA, AB, A-R, A-, and U), although they defended territory, seemed unable to hold a stable territory for any length of time, and shifted about a good deal from place to place (Fig. 1). In these pairs one female, AR, was first mated to Male AO, and then to Male -O. Male O- was the most dominant male of these pairs that defended territory but did not lay, and was probably capable of holding territory long enough to breed, but his mate, Female O-, refused to accept the nest site (33) that he defended most often. This nest site, although it appeared to be suitable in terms of construction and materials, and seemed to be popular with many pairs (Fig. 1), was located in the main line of traffic of the geese going to and from the feeding area from various parts of the pond.

Part of the reason for failure to lay eggs might have been due to fixation on specific nest sites, involving considerable and often unsuccessful competition, until with advance of the season the physiological state of the birds changed in a direction unfavorable to egg-

laying. Furthermore, pairs that were most often displaced from nest sites were also the ones that generally did not lay eggs. These evictions were related to low dominance. The domination-subordination ratio per male was 7:11 for 13 males evicted from at least one nest site at which they had spent most of one day or more trying to establish themselves, whereas the d:s ratio was 15:7 for 16 males which were never so evicted, and which for the most part bred successfully.

Failure of normally paired geese to lay eggs was not due to lack of copulation. There were observed 21 copulations by 11 pairs that failed to lay and incubate eggs, for an average of 1.9 observed copulations per pair, and 10 of these 11 pairs were seen to copulate. In contrast, for 21 pairs that laid eggs which were incubated, there were observed 24 copulations, an average of only 1.1 observed copulations per bird, and only 14 of the 21 pairs were seen to copulate.

Inadequate diet or lack of food does not seem a likely explanation for failure of some birds to lay eggs. At least the food was provided in some abundance, and was adequate for egg-laying by many of the females, as well as for a high egg production by the many Mallard ducks maintained for this purpose within the same large enclosure. All of the Canada Geese dominated the Mallards, and had precedence to food over all ducks.

Perhaps the six dropped eggs found belonged to birds not able to maintain a stable territory, but attempting to lay in some other bird's territory, since all of the six dropped eggs were found within occupied territories in which the resident female laid a full clutch of her own. Furthermore, females were seen on two occasions to be repeatedly attacked by males, just before the female laid an egg in her own nest at the edge of the territory of the attacking male.

Twenty per cent of the loss in breeding potential was due to loss of the entire clutch by five pairs of birds (Table 3).

Four of these five clutches were lost as a result of evictions of the pair from its territory or of the female (of Male R/Y, who died) from her nest by more dominant birds. The fifth clutch, that of Male YB x Female B-, was lost with the death from unknown causes of the female, after three weeks of incubation. Although not observed, possibly dominance by other geese was involved here also, since the male coincident with the death of the female, lost all of his tail feathers. This phenomenon was noted in the breeding season, only when a male had lost a severe fight and was pursued by the victor, which would often seize the tail feathers of the retreating loser, sometimes pulling out some of these feathers. One of the evictions involved a two-year-old pair. A few days after the male had been beaten and the female evicted temporarily from her nest by a neighboring male, the nest was observed to be deranged and the eggs were out of the nest. The two-year-old female rolled one of these eggs toward herself, but since she was

standing to one side of the nest, the egg rolled into the water instead of into the nest cavity. Soon afterwards the dominant pair came and displaced them from the nest, and shortly after this the remaining egg was seen sinking in the water.

Seventeen per cent of the loss in breeding potential was due to infertile and inviable eggs in nests from which goslings were hatched. Ten such eggs were infertile, while eleven contained embryos that had died in the egg.

There is a suggestion in the data that relatively infrequent coition contributed to the occurrence of the infertile eggs. Eight females laid infertile eggs (not including unpaired females), and only two of these eight females were seen to copulate, for a total of only three copulations. On the other hand, eleven of the females that hatched out goslings, laid only fertile eggs, and all of these eleven females were seen to copulate, for a total of 17 copulations.

The occurrence of inviable embryos showed no connection with inattentiveness of the female during incubation, as measured by the number of times a female was seen to be absent from her nest and eggs, once she had begun steady incubation, as checked at the beginning of each hour of observation. Nine females that had at least one dead embryo in the clutch, were seen to have only 9 such absences from the nest during the incubation period, whereas 7 females with no dead embryos had 12 absences. There may however be some relationship between the clutch size and inviable eggs, and the data suggest further investigation of this idea to be worthwhile. Thus, 8 of the 9 females with one or more inviable eggs each had 6 or more eggs in her full clutch, the average clutch size for these females being 6.4 eggs. In contrast, 6 of 7 females with no dead embryos each laid 5 or fewer eggs, the average clutch size being only 4.9 eggs.

Only four per cent of the loss in breeding potential (to May 29) was due to gosling mortality, including 5 dead goslings. Three of these were from one nest, of which two were found dead on the nest on the date of hatching; the other one made it to shore, but was very weak and was finally abandoned by its parents, which went away with their remaining three goslings. Then another family came along and one of the adults and one of the goslings of this family bit the helpless and abandoned gosling. The latter was then put in a brooder where it later died. Another gosling was found with its head caught in a wire fence and when extricated proved unable to walk and later died in the brooder. The fifth dead gosling was found dead in the weeds along the shore; the cause of death was unknown.

Only two per cent of the loss in breeding potential was in terms of adult mortality, although 2 of the 3 deaths of adults resulted indirectly in loss of an entire clutch. Both of these two deaths, one of a male and one of a female, were due to unknown causes. The remaining death was of an adult male gander, killed by a rival male competing for the same female.

*Factors having a regulatory effect on population density.* Some fac-

tors take an increasing percentage of a population as density increases (Nicholson, 1935), while certain other factors take a decreasing percentage as density increases. This latter type was probably not operating in the present case, since the geese were already too crowded. It refers to such things as Darling's (1952) idea of a threshold of numbers that must be reached to provide sufficient social stimulation to facilitate breeding in some species of birds. It was indeed observed that sexual display and coition, like most of the activities of the geese, were contagious, tending to spread from one pair to another, but, as previously pointed out, those pairs that failed to lay eggs were seen to copulate more often than those that did lay eggs. This observation of course does not exclude the possible importance of social stimulation to facilitate breeding at lower population densities than that with which we were concerned.

A limited number of nest sites for which the birds compete would be expected to exert density-dependent effect with increase in numbers of birds. Amount of shoreline may be an important factor in providing suitable nest sites for effective breeding. A number of pairs chose to build nests on the shore, before some of the artificial islet nests were occupied. This included most of the more dominant pairs. Ten of 16 nests on or near the shore produced goslings, but only 5 of 12 islet nests produced goslings. It seems likely that in the event of disturbance eggs on islet nests are more likely to be lost by rolling out of the nest into the water. Suitability of the available nest materials is of course important, and islet nests with branches and twigs, but temporarily without marsh hay, generally found little favor.

Increase in the number of nest sites has a limited influence, since, beyond a certain degree of crowding, the territorial space requirements of the birds begin to act as a limiting factor. Aggressive behavior of this type was probably the most important cause of population limitation in the breeding colony under the crowded conditions that existed. Many of the territorial males defended more than one of the artificial nest sites (Fig. 4), effectively preventing other geese from becoming established thereon.

Dominance operated as a density-dependent factor in conjunction with fixation on or preference for a given nest site. The more crowded the population, the more chances there are for two pairs to compete for the same nest site. As Figure 1 shows, some of the nest sites changed occupants and owners repeatedly during the breeding season.

All of these factors operate jointly with seasonal factors that regulate the time of the breeding season, probably including such things

as gradual change in the relative lengths of day and night, as well as temperature and other factors. Subordination to dominating geese, inability to establish a foothold against the resistance of territorial incumbents, unsuccessful fixations on certain nest sites or on certain individuals as potential mates, all serve to delay, and by delay may finally prevent entirely, effective breeding by many individuals.

#### SUMMARY

The breeding behavior, vocalizations and dominance order of Canada Geese (*Branta canadensis*) confined under semi-natural conditions at Horicon Marsh, Wisconsin, are described in some detail, with special reference to social interactions between individually marked birds.

Pair formation depends both on specific preferences and on dominance relations between individuals. The nest site is selected by the female of a pair; she is escorted in the search by the more aggressive male. Repeated attempts at establishment on suitable nest sites and repeated eviction by more dominant birds is the rule for birds of relatively low dominance status.

When regular incubation begins, copulation ceases. After hatching, the goslings usually spend a day in the nest before leaving. During their first week goslings are apt to become lost, and are readily adopted into some other family. However, the early development of aggressiveness against strangers by the goslings, as well as by their parents, tends to preserve the integrity of each family.

Loss in productivity of the breeding colony was very largely due to the territorial behavior of the birds themselves resisting the crowded conditions. In the breeding season of 1952 at the Horicon Marsh colony, about 70 per cent of the theoretical or potential increase was lost. In turn, this loss was traced mainly to (1) failure of birds to pair effectively, (2) failure to lay and incubate eggs, and (3) to loss of the clutch once laid, all generally as a result of domination by other birds.

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**Aves de Caza de Venezuela.** Hno. Ginés and Ramón Avelado H. 1958. Sociedad de Ciencias Naturales La Salle, Mon. no. 4. 236 pp., 18 col. pls., numerous figs. and maps. Price, Bol. 20 or U.S. \$6. Editorial Sucre, Caracas, Venezuela. (Available: Sociedad Venezolana de Ciencias Naturales, Apartado 1521, Caracas, Venezuela.) This attractive and well-designed book treats the game birds of Venezuela. All regularly occurring species of Tinamidae (13), Anatidae (18), Cracidae (14), Phasianidae (4) and Columbidae (19), as well as the Common Snipe (*Capella gallinago*), are described, their scientific and vernacular names given, and their ranges outlined. Valuable information is provided on habitat, and, when available, on nesting and behavior—sometimes based on previously unpublished data. The distribution of each Venezuelan subspecies is illustrated by a map. Most species (many of them little-known) are depicted in color plates, those by A. Almeida of Galliformes being vigorous and attractive. Unfortunately the color reproduction of pigeons is in some cases misleading. The species account for each family is introduced by a discussion of family characters, classification, and a key to specimen identification. In the preface the authors point out the need for biological data, make a plea for conservation, and recommend the sport of "hunting" with binoculars and camera. This work reflects credit on Venezuela as well as on the authors. (In Spanish.)—E. EISENMANN.