PREFLIGHT AND FLIGHT BEHAVIOR OF CANADA GEESE

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CANADA Geese (*Branta canadensis*) are highly traditional in their use of circumscribed nesting, migration, and winter localities (Hanson and Smith, 1950; Martin, 1964; Sherwood, 1966), patterns of movement and roosting in local areas (Raveling, 1969a), and timing of daily activities (Raveling, 1967: 135–157). This regularity is accompanied by facilitation behaviors (Crawford, 1939) serving mood transference and induction of reaction by contagion. Particularly prominent in Anserini are movements of the head and often the neck, which have been previously described as social signals communicating the intention to fly (Heinroth, 1911; and many subsequent papers). Purposes of this paper are to document the variation of preflight intention movements of Canada Geese as related to social status (i.e. family, single, age, sex) and thereby to discuss more fully the probable functions of behavioral and morphological patterns associated with coordination of flight. Results are based on observations of a large winter flock and from quantification of the activities of radio- and color-marked individuals and families of known social status.

METHODS

This study was conducted at Crab Orchard National Wildlife Refuge, Williamson County, Illinois. Approximately 40,000 Canada Geese (*B. c. interior* cf. Hanson and Smith, 1950: 77) spend a large part of the winter on and near the refuge. The inviolate portion of Crab Orchard refuge encompasses 22,000 acres, including 2,600 acres of Crab Orchard Lake the geese use for roosting and 5,000 acres of intertilled cropland and 2,800 acres of pasture they use for feeding.

Observations of the flock's activities and specific behavior of radio-marked geese were recorded daily from late September to mid-March in 1963–64 and 1964–65. Radio- and color-marked geese included all or parts of 10 families, 2 pairs, and 35 yearlings (77 geese). Further description of Crab Orchard, details of capture, recognition of and permanency of families and other social classes of geese, their roost and movement patterns, and techniques of color-marking and radio-tracking are provided elsewhere (Raveling, 1969a, 1969b).

RESULTS

PREFLIGHT BEHAVIOR

As a general rule the geese at Crab Orchard roosted on the lake during the night and at midday and fed in nearby fields in the early morning and late afternoon. They exhibited increasing levels of activity during the hour or more preceding flight from the roost lake by moving about and alternating periods of alertness with swimming, walking, preening, bathing, and some aggressive conflicts. The most obvious behavior sequences di-

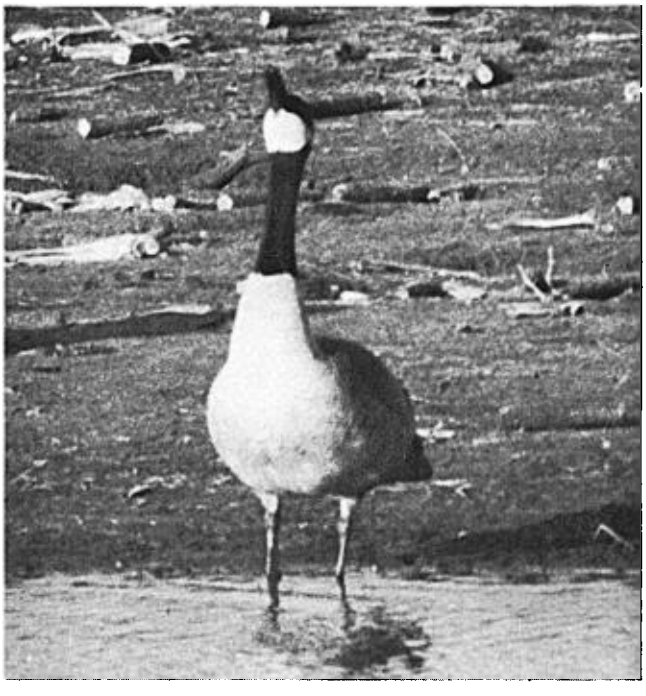

Figure 1. Preflight head-tossing by a Canada Goose.

rectly connected with the increase in activity prior to flight were distinct head-tosses and low gutteral vocalizations. These patterns also occurred before geese flew from fields during the day. In a large flock the vocalizations associated with head-tossing produced a background humming sound.

At low intensity, head-tossing consisted of slow vertical movements of the bill and head. At higher intensity the bill was held at an angle pointing up and the head was shaken from side to side. At the highest intensity some neck movements occurred while the head was shaken rapidly from side to side. The white cheek patch was displayed conspicuously and the birds stood with neck almost fully extended (Figure 1). Head-tossing usually reached its most intense stage just before the geese took flight. Geese often unfolded their wings and walked or ran a few feet in this manner before actually flying.

Head-tossing by different individuals varied greatly in amount, frequency, and intensity. Single geese of any age-sex class did much less head-tossing than pairs or families. When singles were ready to fly, they took off about 5 minutes after they began head-tossing or preflight alertness and vocalizing (Table 1). Pairs did more head-tossing than singles but also took off within a short time period. Families of 3, 4, or 5 ex-

TABLE 1

COMPARISON OF THE AMOUNT OF HEAD-TOSSING AND ELAPSED TIME FROM START OF HEAD-TOSSING TO FLIGHT BY CANADA GEESE OF DIFFERENT SOCIAL STATUS

Individual or group	Total number of head-tosses before flight $\bar{X}$ (range)	Time (min) from start of head-tossing to flight $\bar{X}$ (range)
Singles	4.5[1] (0 – 26) (N = 42)	5.2 (1 – 17) (N = 24)
Pairs	33.7 (8 – 79) (N = 6)	7.2 (4 – 12) (N = 4)
Families of 3	81 (9 – 354) (N = 19)	18 (1 – 57) (N = 19)
Families of 4	171 (2 – 389) (N = 8)	24 (2 – 64) (N = 8)
Families of 5	79 (9 – 235) (N = 22)	15 (1 – 39) (N = 22)

[1] Excludes one exception, see text.

hibited much more head-tossing and flew 15 to 24 minutes after initiating this behavior. Occasionally head-tossing by one or more members of a family occurred for an hour or longer before flight.

The most important factor influencing the number of head-tosses and length of time before flight of a family was the participation, or lack of it, in head-tossing by the gander. When an individual other than the gander initiated head-tossing, the total number of head-tosses by the family exceeded 100 and flight did not occur until an average of 22 minutes later (Table 2). In contrast, when the gander of a family initiated the preflight ceremony, the total number of head-tosses was much reduced and flight occurred 9 minutes later, on the average.

The amount of head-tossing was never equally divided among family members, and usually one individual initiated the ceremony more often than any other family member and did the most head-tossing (Tables 3 and 4). There was no consistency from one family to the next; in one group the gander usually initiated head-tossing whereas in another family it was the adult female and in another it was one of the immatures.

When the adult male initiated head-tossing, flight occurred in a short time because the other family members responded almost immediately and joined the gander in alertness and preparation for flight. The most numerous and most intense performances of preflight behavior occurred when one or more members of a family exhibited a high intensity of the

TABLE 2

COMPARISON OF THE AMOUNT OF HEAD-TOSSING AND ELAPSED TIME BEFORE FLIGHT IN RELATION TO INDIVIDUAL THAT INITIATED THE CEREMONY

Group	Head-tossing initiated by goose other than adult male		Head-tossing initiated by adult male	
	Total head-tosses by group	Time (min) from start of head-tossing to flight	Total head-tosses by group	Time (min) from start of head-tossing to flight
Pairs[1]				
Families of 3	106[2] (19 – 354) (N = 12)	21 (7 – 57) (N = 12)	39 (9 – 92) (N = 7)	12 (1 – 33) (N = 7)
Families of 4	195 (35 – 389) (N = 7)	27 (9 – 64) (N = 7)	2 (N = 1)	2 (N = 1)
Families of 5	104 (37 – 235) (N = 14)	20 (7 – 39) (N = 14)	34 (9 – 74) (N = 8)	7 (1 – 15) (N = 8)
Average All families	124 (19 – 389) (N = 33)	22 (7 – 64) (N = 33)	34 (2 – 92) (N = 16)	9 (1 – 33) (N = 16)

[1] Same as in Table 1, adult male not observed to initiate any ceremonies.
[2] Average and (range).

tendency to fly but the gander did not join the head-tossing activity. In such cases the other family member(s) repeatedly head-tossed, paced about, and often spread its wings as if to fly.

On two occasions an immature male, which almost always initiated head-tossing in his family of four, did take flight and was not joined by the rest of the family. Both times this immature returned immediately to the vicinity of his family after flying a short distance (about 50 feet one time and in an approximate ¼-mile circle the other).

BEHAVIOR AT TAKEOFF AND IN FLIGHT

When a gander initially or finally participated in preflight head-tossing and vocalizing the family members came close together. Often one bird started to extend its wings or actually jumped into the air, and then the rest of the family usually took flight immediately and stayed close together. Often the first goose of a family to take off was the individual that initiated head-tossing and had been ready for flight for the longest time.

At the moment of takeoff the low grunting vocalizations change to a loud honking. When the wings are unfolded, the band of white formed by the upper tail coverts is strikingly displayed and contrasts strongly with the black tail feathers.

TABLE 3

NUMBER OF TIMES A SPECIFIC INDIVIDUAL WITHIN A FAMILY INITIATED PREFLIGHT HEAD-TOSSING CEREMONY

Group	Number of observations	Individual initiating the ceremony: Adult male	Adult female	Immature male "A"	Immature male "B"	Immature female
Family of 3	9	5	0	▲[1]	▲	4
Family of 4	8	1	▲	7	0	0
Family of 5	10	0	7	3	0	0
Family of 5	10	7	0	3	0	0

[1] Not present in group.

Geese as a rule did not initiate flight from any position with a subflock (Raveling, 1969a), but usually swam or walked to what I termed a "starting line." Most birds took flight when they approached the point from which the geese immediately in front of them had flown after having walked or swum there.

In the large flock, singles and unrelated groups often took flight at the same time and merged into larger groups (Raveling, 1968). Unrelated geese did not necessarily remain together throughout their flight. Singles

TABLE 4

COMPARISON OF THE AMOUNT OF HEAD-TOSSING WITHIN FAMILIES IN RELATION TO INDIVIDUAL THAT INITIATED THE CEREMONY

Group	Number of head-tosses by: Immature or adult female initiator of ceremony	Group except gander and initiator of ceremony	Gander when ceremony initiated by other goose	Gander initiating ceremony	Group except gander when gander initiated ceremony
Pairs	31[1] (92%) (8–79)[1] (N = 6)	–	2.7 (8%) (0–10) (N = 6)	–	–
Families of 3	91 (89%) (16–336) (N = 7)	4 (4%) (0–15) (N = 7)	7 (7%) (2–18) (N = 7)	31 (80%) (6–81) (N = 7)	8 (20%) (0–22) (N = 7)
Families of 4	181 (93%) (33–389) (N = 7)	7 (3.5%) (0–33) (N = 7)	7 (3.5%) (0–16) (N = 7)	2 (100%) (N = 1)	0 (N = 1)
Families of 5	67 (64%) (27–221) (N = 14)	34 (33%) (10–82) (N = 14)	3 (3%) (0–21) (N = 14)	14 (41%) (4–32) (N = 8)	20 (59%) (6–44) (N = 8)
Average all families	102 (80%) (16–389) (N = 28)	20 (16%) (0–82) (N = 28)	5 (4%) (0–21) (N = 28)	21 (60%) (2–81) (N = 16)	14 (40%) (0–44) (N = 16)

[1] Average and (range).

and other families often coalesced in flight so that true family size could not be identified (Raveling, 1968). Marked families of 3, 4, and 5 geese were observed in flight on 53 occasions. As in walking or swimming movements during winter, any particular family member might be in the lead position at any one time. Occasionally other geese were in position between related family geese, but the lead position did not necessarily impart leadership (Hanson, 1965: 143). As in swimming or walking, when the gander turned and maintained a new heading, the rest of the family followed, but if an immature or even the adult female initiated a new direction of movement, the gander did not necessarily follow. If he did not the family again returned to the gander's direction of movement.

Close physical proximity of a family during flight was the general rule but family members were often widely separated if geese were flushed, apparently because adults, particularly ganders, are much more powerful fliers than are immatures. The family's habitual use of one particular roost site (Raveling, 1969a) quickly reunited them.

DISCUSSION

PREFLIGHT BEHAVIOR

Heinroth (1911: 630) described the preflight behavior of several species of geese and termed these actions intention movements. Lorenz (1935) traced preflight movements phylogenetically in the family Anatidae and concluded that in ducks preflight behavior originated from postures preparatory to taking flight. The behavior is ritualized in geese and probably represents a displacement of a motion meant originally to shake mud or water from the beak, and which has become incorporated into preflight behavior as a social signal communicating the intention to fly (Lorenz, 1952). Daanje (1950) also pointed out that the present function of intention movements in birds is often secondary to or superimposed upon the original or primary function. Other authors have also described preflight movements of geese in the context of communicating the intention to fly and of coordinating movements (cf. Armstrong, 1947: 20; Balham, 1954: 185; Davies, 1963; Johnsgard, 1965: 55; Hanson, 1965: 143).

The radio- and color-marked birds of this study enabled the variation in preflight movements of Canada Geese to be quantified and revealed the probable basis for this variation as well as more clearly defining its importance in communication. Balham (1954: 185) and Hanson (1965: 143) noted that usually the adult male initiated preflight head-tossing. In this study ganders initiated the ceremony 16 of 50 times (Table 4). Without continuous observation of entire marked families before flight one might easily conclude that the gander usually initiates head-tossing because when he does so the family unifies and flight is imminent. Yet

ganders did much less head-tossing than other family members, even when they initiated the ceremony (Table 4).

Data presented here illustrate the dependence of other family members on the gander and the importance of his role in coordinating family activities. The signal value of preflight head-tossing and associated behavior appears to be largely unidirectional; i.e. they are of great importance in the gander's coordinating a family's activity, but not vice versa. As single geese did little head-tossing, and as intense prolonged head-tossing in a family occurred when lack of family unity prevented one individual from flying, I conclude that preflight behavior in a family individual stems from a conflict of the simultaneous tendencies to fly off or to remain with the family (triumph ceremony partner(s)). An example that further supports this conclusion was provided by an immature male that had averaged 181 head-tosses before flight with his family during an average 27 minutes from the time he started head-tossing until the gander joined and they flew as a unit (7 observations). This bird was seen taking off once (not an escape situation) when he was separated from the rest of his family; he became alert, did some preening for 5 minutes, and then took flight without a single head-toss. Thus when not inhibited by the near presence of his family, his behavior was markedly different.

According to the conflict hypothesis of motivation analysis as detailed by Tinbergen (1952a), stereotyped intention or displacement movements serving as social signals often result from the simultaneous activation of two or more incompatible tendencies to behave in mutually exclusive manners, e.g. attack or flee, fly off or remain (cf. Tinbergen, 1952a, 1954, 1959, 1964; Hinde, 1953; Bastock et al., 1954; Andrew, 1956; Iersal and Bol, 1958). Preflight head-tossing is a signal resulting from a displacement behavior (Lorenz, 1952). This agrees with Tinbergen's (1952b) general statement that signals originating from displacement movements predominate in strong conflict situations. Surely, separation from a triumph ceremony partner presents a strong motivating factor in geese (cf. Fischer, 1965; Raveling, 1967: 18–33).

I interpret the few head-tosses performed by single geese as a mild conflict between the tendency to fly and the tendency to stay in the area and continue its activities (sleeping, preening, etc.). Geese frequently interrupted head-tossing to preen, bathe, swim about, or even put the head in a sleeping position. With singles the tendency to fly soon predominated because the individual was not held back by triumph ceremony partners that were not ready to fly.

Only one exception to the usual pattern of single geese was observed. A single yearling female gave 217 head-tosses over a 25-minute period when the evening flight from the lake had just ended. This goose had

become alert and ready to fly after the geese in her vicinity had already flown. She did not fly but resumed slow swimming, walking, and feeding at the edge of the lake after her prolonged bout of head-tossing. Single geese usually took flight and joined nearby geese as they took off (Raveling, 1968). The fact that the evening flight was over and no geese took off around this yearling apparently stopped her from flying.

How much signal value head-tossing behavior has among the flock as a whole is unknown. Geese are stimulated by many factors that lead to coordinated flight. The sight and sound of other geese taking off appears more important than head-tossing in stimulating and coordinating the flock as a whole, whereas head-tossing functions most importantly as a signal preparing a family for flight and ensuring family unity of action.

Distinctness of morphological patterns of the head region of geese are correlated with preflight head-tossing. Movement of the white cheek patches appears to enhance the conspicuousness of head-tossing in Canada Geese via the vertical lifting of the chin. White-fronted Geese (*Anser albifrons*) do not lift the chin, but have an exaggerated side-to-side head movement with the bill pointing forward that magnifies the conspicuousness of the white patch at the base of the bill. Adult Blue and Lesser Snow Geese (*Anser c. caerulescens*) have all-white heads and they also exhibit lateral head-tossing, but the movement is much more rapid, almost vibrating, as compared to Canadas or White-fronts. Thus as Lorenz (1935) pointed out for many behavioral patterns, head-tossing is older phylogenetically than the morphological pattern accompanying it. Selection has operated on behavior and morphology to create efficient, distinct signals in closely related species.

BEHAVIOR AT TAKEOFF AND IN FLIGHT

Associated with regular flight formations of Canada Geese are distinctive plumage patterns. The sudden appearance of the white upper tail coverts and extended wings along with the characteristic change in vocalizations at the moment of taking flight serve as strongly stimulating signals to the family and other nearby geese. This partially accounts for the "starting line" behavior of a large flock taking off, which serves to coordinate flock movements and to prevent the chaos that could result were geese to take off in all directions and from all positions in the flock simultaneously.

Other species of geese also have striking, distinctive markings of the tail (White-fronted Goose), back (Blue Goose), or wings (Snow Goose) that are displayed upon the opening of the wings and while in flight. Lorenz (1937) noted how the pattern of the Greylag Goose (*Anser anser*) is probably essential to following and flock unity. It seems likely that

the while tail band of Canada Geese is important in releasing flight and in maintaining alignment and direction while in flight.

Correlated with the immatures' following position within the family and, at times, relative inability to influence the adults, especially their gander, is their relative or complete lack of morphological distinctness in the plumage areas noted above, for example the back or wing pattern on Lesser Snow and Blue Geese and the white patch at the base of the bill of Whitefronts. Immature Canada Geese have much narrower, less distinctive upper tail coverts that are often flecked with black as compared to the broad snow-white adult pattern. Similarly immatures' cheek patches are usually more flecked with black than are the adults' cheek patches. This suggests that selection has operated to reduce the effectiveness of the inexperienced immatures' social signals communicated via plumage patterns.

ACKNOWLEDGMENTS

This investigation was financed mainly by the National Science Foundation (GB-623). Additional support was provided by the Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, W. D. Klimstra, Director. Many persons and agencies contributed to the study. I particularly wish to acknowledge again the help of Wendell E. Crews, William W. Cochran, L. Arch Mehrhoff, Robert G. Personius, Dwain W. Warner, Harold C. Hanson, and W. D. Klimstra. A. Dzubin provided helpful criticism of the manuscript. Results formed a portion of a Ph.D. dissertation presented to the Department of Zoology, Southern Illinois University.

SUMMARY

Behaviors associated with the coordination of flight in Canada Geese were observed in a large winter flock and especially recorded for radio- and color-marked individuals and families. Preflight head-tossing represents a displacement resulting from the conflict over the desire of an individual to fly and at the same time remain with its family (triumph ceremony partner(s)). The amount, frequency, and intensity of head-tossing within a family depends upon the gander. The gander may or may not respond to head-tossing by other members of his family but, conversely, they respond almost immediately to his head-tossing. Thus the function of head-tossing is in coordination of family activities as led by the adult male, whereas synchrony of the flock as a whole is conditioned by factors other than head-tossing. The white cheek patches appear to function in enhancing the conspicuousness of head-tossing, as do facial patterns in other species of geese.

Change in vocalizations and the sudden appearance of the white upper tail coverts at the moment of taking flight act as final releasers of flight. Other morphological patterns act in a similar manner in other species of geese. These releasers partly account for the behavior of geese moving to

a "starting line" and taking off in sequence. This in turn promotes an orderly flight pattern as compared to what would result if geese flew in all directions from different positions within a flock at the same time.

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