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Aggressive Displays in Nonbreeding Canvasbacks

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The classical works of Heinroth (1911), Hochbaum (1944), Lorenz (1951, 1952, 1953), and Johnsgard (1965) have documented the reproductive displays of most members of the family Anatidae. Although the reproductive displays of ducks have been described thoroughly, much less is known about their aggressive displays during the nonbreeding period. Here I describe three aggressive displays that occur in nonbreeding Canvasbacks (*Aythya valisineria*), describe an aggressive pushing sequence that usually is preceded by the three displays, and comment on the function, evolution, and ecological significance of this behavior.

The study was conducted near Georgetown, Georgetown County, in coastal South Carolina during the winters of 1975 through 1977. The major research area contained four man-made impoundments where 200–500 Canvasbacks could be observed daily from early November to March. These impoundments ranged from 7.75 to 12.85 ha in size and from 0.50 to 1.50 m in depth. Three of the impoundments were freshwater, with banana water-lily (*Nymphaea mexicana*) as the major food. One impoundment had brackish water, with muskgrass (*Chara* spp.) and widgeon grass (*Ruppia maritima*) as major foods. At each impoundment, behavioral observations were made from permanent blinds or from a vehicle, with minimal disturbance to the birds. Aggressive interactions were recorded with 35-mm slides and with 16-mm movie film. Threatening and pushing sequences were timed with a stopwatch.

Smith (1977) has recognized the significance of displays as effective modes of communication. He also indicated that displays involved in aggression usually do not involve physical contact between individuals. In this paper, a display is defined as a behavioral act performed by one individual that causes a change in the behavior of a second individual. A chase occurs when one bird swims rapidly after a retreating bird with the head thrust forward and the bill slightly opened. A fight involves exchanges of biting and wing hitting between individuals.

Canvasbacks that overwinter in large open-water regions such as the Chesapeake Bay typically feed in dense flocks (pers. obser.). In my study area Canvasbacks did not feed in groups but dove at individual foraging sites (Alexander and Hair 1979). These foraging sites were separated by approximately 3–6 m and were vigorously defended against conspecifics.

I observed three distinctive aggressive displays among these birds:

1) *Bill-in-water.*—An individual (male or female) performed this display (Fig. 1a) as it surfaced from a dive, when an intruding conspecific had approached the foraging site closer than 3 m. The body profile was very low in the water, and the tip of the bill remained in the water. No bill-cleaning or feeding at the surface was associated with this display. The bird sat motionless in this posture until the intruder withdrew or intensified the encounter (e.g. chase, fight). At 3–5 m from the surfacing individual, I could detect a subdued wheezing "*rrrrr-rrrrr-rrrrr*" vocalization as the bird displayed to an intruder. When a diving bird surfaced in the absence of an intruder, neither the visual display nor the vocalization was performed. In 65% of the observed encounters, the Bill-in-water display supplanted intruding Canvasbacks.

2) *Head-pump.*—An individual used this display (Fig. 1b) as it swam toward the foraging site of a conspecific. The body profile was high on the water, and the bird performed a vigorous upward thrusting of the head 2–3 times in succession. In this display, the bill was approximately 45° above the horizontal. During the pumping motion, the emphasis was on the upward thrusting of the head rather than the downward movement, as in precopulatory pumping (Lorenz 1951). In 70% of the observed encounters, Head-pumping was adequate to supplant a diving bird.

3) *Bill-on-chest.*—Individuals that were separated by a few cm up to 6 m performed this display (Fig.

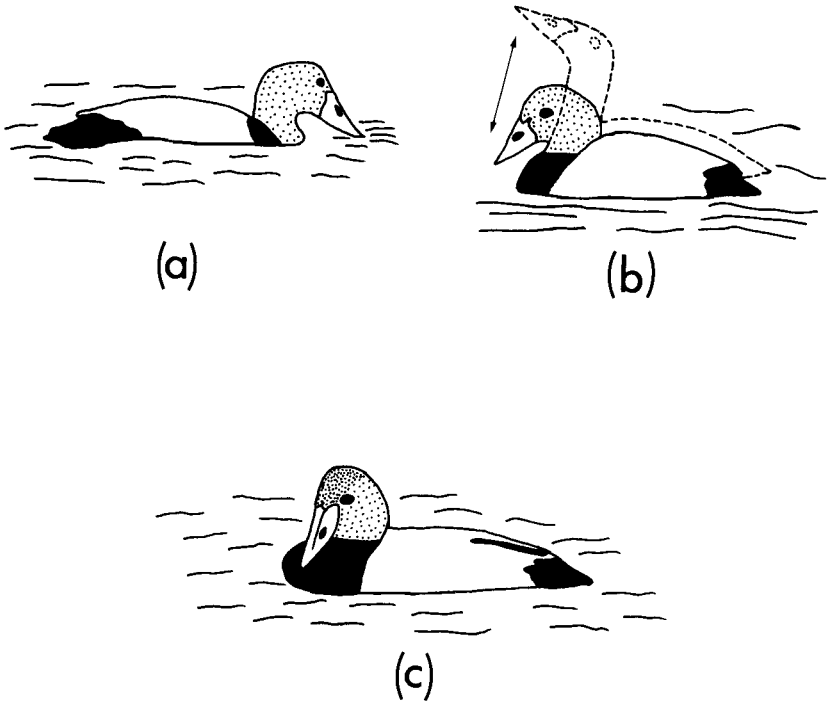

Fig. 1. Threat displays performed by Canvasbacks during aggressive encounters. (a) Bill-in-water, (b) Head-pump, (c) Bill-on-chest. Descriptions in text.

1c) from 2 s to 12.5 min. The body profile on the water was intermediate between those described above. The bill was lowered on the chest, usually to one side, and the head was pulled tightly down on the body.

The display bout of longest duration, which involved the Bill-on-chest, was between two males and occurred in two segments. In the first segment, the males mutually displayed in the Bill-on-chest posture for 12.5 min. At that point, one of the males turned away, swam directly to a nearby diving male, chased him away, and began diving. After 2.0 min this male stopped diving and swam slowly back to the foraging site of the original male. The intruding male initiated another bout of display that persisted for 9.0 min before he was chased away. The two males that participated in this display bout did not make physical contact, but swam slowly back and forth while continuously displaying from distances of a few cm to 3 m.

The displays described above often preceded a sequence of aggressive pushing that involved both sexes. The most complete sequence of displays and pushing consisted of two individuals interacting as follows: A bird diving on a foraging site was approached by a conspecific. The intruder swam toward the diving bird and, at a distance of 3 to 5 m, performed two or three Head-pumps (Fig. 2a). The diving bird began the Bill-in-water display (Fig. 2a). The intruder swam closer to the diving bird (Fig. 2b), and when they were separated by approximately 2 m, the diving bird assumed the Bill-on-chest display (Fig. 2b). The intruding bird stopped swimming, assumed the Bill-on-chest, and a period of mutual display ensued (Fig. 2c). Both birds maintained this posture as they slowly moved closer together, eventually making chest to chest contact (Fig. 2d). The birds then began to push against each other. Eventually one of the individuals began to push the other away, and intense mutual biting and wing hitting occurred. In almost every case, the initial biting was directed to the rear of the neck and upper back of each bird (Fig. 2e). The loser was either forced underwater or dove to escape the aggressor and, after surfacing, was chased away (Fig. 2f).

Seventy-four aggressive pushing sequences were timed (Table 1) with male-female encounters having the longest duration, and female-female encounters having the shortest duration. These differences however, were not significantly different (anova, $F = 2.10$, $P > 0.05$).

A total of 115 aggressive pushing sequences was observed (Table 2), with 66% terminating in fighting.

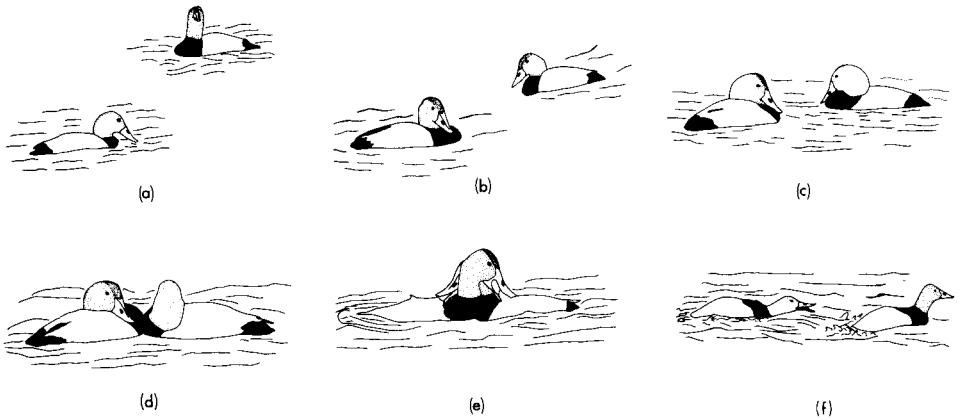

Fig. 2. Aggressive pushing sequence between Canvasbacks. See text for description.

In 39 male-female pushing encounters, males won 21 and females won 18 of the encounters, a difference that was not statistically significant ($\chi^2 = 0.10$, df = 1, $P = 0.75$).

Intraspecific aggression is common in many nonbreeding birds (Marler 1971) and often is manifested in fighting (e.g. Craig 1928; Lorenz 1963, 1964). Although fighting can be important in hierarchy establishment and partitioning of resources, it can also affect organisms by reducing foraging efficiency (MacArthur 1972), and by subjecting them to higher predation rates (Brown 1975).

Moynihan (1955) proposed that aggressive displays enable individuals to accrue certain advantages (e.g. feeding territory) without having to invest time and energy in fighting. Because of the habitat and food distribution in the areas utilized by Canvasbacks in this study, the birds could establish feeding territories and maintain them with aggressive displays and a minimim of fighting. The Bill-in-water, Head-pump, and Bill-on-chest are aggressive displays that function as threatening signals when one Canvasback intrudes into a conspecific's feeding territory. Each of these signals can act alone as a deterrent to intruders or it can function as a part of mutual display, depending upon the aggressiveness of the individuals involved.

The Head-pump display described in this paper appears to be identical in form to the "neck-stretch" that Hochbaum (1944) reported in courting Canvasbacks. Johnsgard (1965) briefly mentioned that this display was performed in a sexual context between males and females. In addition, he indicated that this display occurred in hostile encounters between courting males that were competing for a female. By late February in South Carolina, Canvasbacks had initiated courtship behavior, and mutual neck-stretching was observed between pairing birds. The Head-pump display that I have described appeared throughout the winter in nonsexual contexts between individuals that were competing for feeding territories. The Head-pump also differed from neck-stretching in frequency and intensity. It is likely that the Head-pump has a similar form during courtship and in aggressive encounters but varies in frequency and intensity depending upon the context in which it occurs.

McKinney (1970) described an aggressive "hostile pumping" display in breeding blue-winged ducks (e.g. *Anas discors* and *A. clypeata*), which I believe is analogous to the Head-pumping display described for nonbreeding Canvasbacks. McKinney reported that blue-winged ducks performed this display while defending small territories and suggested that the hostile pumping display evolved in this system in

TABLE 1. Duration of aggressive pushing sequences involving male and female Canvasbacks. n = number of observed sequences; $\bar{x}$ = mean length of sequences in seconds; SE = standard error.

	n	$\bar{x}$[a]	SE
Male-Male	33	45.26	15.10
Male-Female	27	90.51	28.87
Female-Female	14	24.69	7.88

[a] One-way anova indicates mean values not significantly different ($F = 2.10$, $P > 0.05$).

TABLE 2. Summary of Canvasback aggressive encounters involving display and mutual pushing.

		Results of encounters			
	n	No overt aggression	Vigorous chase	Fighting	% fighting
Male-Male	60	4	21	35	58
Male-Female	39	0	10	29	74
Female-Female	16	0	4	12	75
Total	115	4	35	76	66

defense of territories at a distance. It is probable that the threat displays described for Canvasbacks have evolved under similar circumstances, where small feeding territories are defended in winter. A form of head-pumping has also been reported by Raveling (1970) in agonistic encounters between Canada Geese (*Branta canadensis*) during the winter.

I believe the aggressive pushing sequence that I have described for Canvasbacks is a ritualized form of aggression that appears in the presence of limited defendable food resources. In relation to breeding birds, McKinney (1970) stated that "we expect a ritualization of fighting methods in strongly territorial species when boundary disputes are frequent." Aggressive pushing in Canvasbacks is presumably the result of an agonistic situation that occurs when two equally competitive individuals meet. When the preliminary Bill-in-water, Head-pump, and Bill-on-chest displays fail to supplant a conspecific, the more intense encounter involving pushing and fighting ensues.

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