UNDERWATER FORAGING BEHAVIOR OF CANVASBACKS, LESSER SCAUPS, AND RUDDY DUCKS¹

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Abstract. We observed the underwater behavior of captive Canvasbacks (Aythya valisineria), Lesser Scaups (A. affinis), and Ruddy Ducks (Oxyura jamaicensis) while they foraged on a variety of food items in a large aquarium. Canvasbacks probed into the substrate with the bill and body oriented perpendicular to the bottom. Lesser Scaups and Ruddy Ducks strained food items from the substrate surface by moving their bills in short, lateral arcs while rapidly opening and closing their mandibles; their bills and bodies were oriented at a 35 to 45° angle to the substrate. Scaup also fed by grasping prey in the water column, where they appeared to locate prey visually. Ruddy Ducks did not appear to select prey visually. The species also differed in their underwater locomotory behavior and postures; these differences probably are related to the prey and conditions typically encountered by each.

Key words: Canvasback; Aythya valisineria; Lesser Scaup; Aythya affinis; Ruddy Duck; Oxyura jamaicensis; foraging behavior; diving behavior.

INTRODUCTION

Although the behavior of many species of diving ducks has been described, very little is known of their underwater foraging and locomotory behavior. Diving behavior of some species has been observed in the wild from above the water surface (e.g., Brooks 1945; Humphrey 1957, 1958; Snell 1985), but turbid water hampered visibility and the foraging actions of the birds were not recorded. Only a few investigators have observed the underwater actions of captive waterfowl in aquaria. Livezey and Humphrey (1984) observed the underwater locomotory behavior of steamer-ducks (Tachyeres spp.) and Suter (1982) briefly described some of the foraging behaviors of Common Goldeneyes (Bucephala clangula), Common Pochards (Aythya ferina), Tufted Ducks (A. fuligula), and Eurasian Coots (Fulica atra).

This paper describes the underwater locomotory and foraging behavior of three species of diving ducks: the Canvasback (*A. valisineria*), Lesser Scaup (*A. affinis*), and Ruddy Duck (*Oxyura jamaicensis*). The breeding and wintering habitats and distributions of the three species overlap (Palmer 1976), but their diets differ markedly. During most of the year, Canvasbacks feed primarily on plant tubers or molluscs distributed in wetland substrates, although prelaying and laying females, and juveniles consume large numbers of aquatic invertebrates (Bartonek and Hickey 1969). Lesser Scaups consume aquatic invertebrates (primarily amphipods), both in the water column and on vegetation and substrate surfaces (Bartonek and Hickey 1969, Hoppe et al. 1986). Ruddy Ducks feed almost exclusively on benthic chironomid larvae during the breeding season (Siegfried 1973, Tome 1981) and on oligochaetes (Stark 1978) or chironomid larvae (Hoppe et al. 1986) during the winter. Each of these kinds of prey differs in mobility, antipredator response, and the environmental conditions in which they are found; thus, we predicted that the foraging behaviors of these waterfowl species would vary accordingly.

METHODS

During the summers of 1983 to 1985, we observed the foraging behavior of seven Ruddy Ducks (four males, three females), four Canvasbacks (two males, two females) and two male Lesser Scaup in a $5 \times 2 \times 2$ -m indoor concrete aquarium through four, 1×1 -m plate-glass windows. We photographed underwater behavior using a 35-mm camera and both super-8 and 16-mm movie cameras.

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The bottom of the aquarium consisted of a 4×4 array of $1.0 \times 0.5 \times 0.1$ -m wooden trays filled with 6 cm of sand that provided a substrate for the benthic prey. In 1985, we anchored into the substrate one end of several 50-cm long, 0.6-cm diameter polypropylene ropes which had been separated into fine strands. The free end of the rope floated in the water column; this simulated submerged vegetation and provided a refuge for benthic and pelagic invertebrates.

We attempted to observe each species forage on prey that they normally consumed in the wild; however, in some instances we could not obtain numbers of natural prey necessary to conduct our observations and, thus, we provided substitute prey. In some of the Ruddy Duck observations, we used wheat grains to simulate patches of benthic prey. The grains were placed approximately 1 cm below the surface of the sand in densities of 500 to 1,000 grains/m². For all Canvasback trials, we placed corn kernels in the sand in densities of 100 to 500 kernels/m² to simulate plant tubers distributed beneath the substrate surface. For all Lesser Scaup and some Ruddy Duck trials, we released several thousand amphipods into the aquarium at least 4 hr before feeding trials began. This provided time for the invertebrates to acclimatize to the experimental habitat. The majority of the amphipods attached to the substrate or to the walls near the bottom of the aguarium.

At least 5 hr before each observation session, we placed the birds in pens beside the aquarium and deprived them of food. We observed each species separately, but also observed the Lesser Scaup and Ruddy Ducks together. During all observation sessions at least two individuals of a species were in the aquarium.

RESULTS

GENERAL UNDERWATER LOCOMOTORY BEHAVIOR

All species initiated dives similarly. Immediately before diving, the birds exhaled and brought both feet forward, close to the body on each side of the mid-sternum region. Each dive began when the bird swept both feet simultaneously in a ventral-posterior direction ("power stroke") while arching the neck forward into the water. The head and neck entered the water when the feet were approximately half-way through the power stroke. During the descent, the legs were rotated laterally from the normal swimming posture to a position near or above the horizontal plane of the bird. The birds used simultaneous strokes of the legs to propel themselves towards the aquarium substrate. At the end of each power stroke, the feet converged medially, below the tail. During the "recovery stroke" (the portion of the stroke when the leg is brought forward), the toes and web were folded posteriorly, reducing resistance to the water. All species swam to the bottom with necks stretched forward. None of the species extended their wings for propulsion or stabilization while underwater.

Upon reaching the bottom, the birds maintained their location with leg strokes directed perpendicular to the water surface. The Lesser Scaup and Ruddy Ducks always used simultaneous leg strokes; the Canvasbacks, however, occasionally used alternate leg strokes. When foraging, the birds positioned their bodies at an angle to the substrate which varied among species (see next section). When its body was angled away from perpendicular to the substrate, the power stroke moved the bird forward and also prevented the bird from floating toward the water surface. All species moved forward along the bottom with the power stroke of the legs parallel to the axis of the body.

To return to the water surface, the birds stopped moving their legs and briefly (<1 sec) floated backwards, towards the water surface, until a power stroke and an upward motion of the head oriented the body towards the water surface. They floated to the water surface with little or no effort. The feet normally trailed behind the bird in a relaxed position with the webbing folded so that the legs and feet provided little resistance against the water. Occasionally, however, the birds moved their feet to change direction; e.g., to swing to the right, the bird extended the right foot laterally with its web spread open. As the birds neared the water surface, they extended both legs laterally and spread the foot webbing, which decreased their velocity. Occasionally, the birds adopted this posture to slow their upward velocity and maneuvered to grasp a food item.

The Ruddy Ducks floated to the water surface with the neck and bill slightly forward of the posture adopted when sitting on the surface. The Lesser Scaup and Canvasback arched the neck so the distal end of the bill was near or against the upper chest or lower neck. These positions were maintained until the head broke the water surface and the birds returned to the normal swimming position.

FORAGING BEHAVIOR

Ruddy Duck. When foraging on prey distributed in the substrate, the Ruddy Ducks inserted their bills at a 35 to 45° angle into the substrate to a point slightly distal to the nares. The birds swam forward and rapidly opened and closed the mandibles while also moving their heads in short, lateral arcs so that an area of about 1.5 times the bill width was searched for food. This mandibular movement caused substrate and associated benthos to be drawn into the bird's mouth when the mandibles were opened. Upon closing, substrate was forced out the sides of the bill while the lamellae retained items that were consumed. Often the birds stopped their forward movement and began very vigorous lateral head shaking movements in one spot. In these situations, the birds also oriented the body more perpendicular to the substrate.

The Ruddy Ducks did not appear to visually select individual prey; they did not direct bill movements towards prey that we could see on the bottom in the immediate vicinity of the feeding birds. Ruddy Ducks, however, often swam directly towards large aggregations of amphipods which appeared as dark patches on the bottom or walls of the aquarium. Ruddy Ducks also did not direct bill movements towards individual amphipods swimming in the water column. Instead, where dense aggregations of amphipods occurred, they strained them from the water column using bill and head movements similar to those used when foraging in the substrate.

Some amphipods aggregated on the artificial vegetation. To consume these, the Ruddy Ducks grasped a piece of the vegetation between the mandibles and then "dabbled" (rapid opening and closing of the mandibles) along the vegetation, ingesting amphipods that remained on the vegetation.

Lesser Scaup. The Lesser Scaup foraged in a similar manner to the Ruddy Ducks with one important difference: scaup appeared to visually locate both prey individuals and patches. When diving, the scaup frequently stopped and directed foraging movements of the bill towards amphipods that were swimming in the water column.

When foraging on prey distributed beneath the substrate surface, the behaviors of the Lesser Scaup (including bill movements, bill angle, and body angle) were the same as those described for the Ruddy Duck. Like Ruddy Ducks, scaup also consumed prey distributed on the artificial vegetation; but unlike them, they often pursued and consumed amphipods that would drop to the substrate when the vegetation was disturbed.

Canvasback. The body and bill of the Canvasbacks were oriented perpendicular to the substrate when they foraged on prey distributed in the substrate. The Canvasback used the bill as a probe to locate and extract food items from the substrate. When searching for corn kernels distributed beneath the substrate, Canvasbacks inserted their bills into the substrate using slight, lateral head shaking motions. The bill remained in the substrate for 1 to 2 sec; the birds then pulled the bill from the substrate and either inserted it somewhere else or returned to the water surface. When Canvasbacks encountered smaller food items, such as wheat grains, on or directly beneath the substrate surface, they held the bill at a 50 to 75° angle and used rapid opening and closing movements of the mandibles to sieve food items from the substrate; they rarely exhibited the rapid, lateral bill and head movements utilized by Ruddy Ducks and Lesser Scaup. We did not conduct any observations of Canvasbacks foraging on invertebrate prey.

DISCUSSION

The legs of Canvasbacks, Lesser Scaups, and Ruddy Ducks are located on the posterior portion of the body, an adaptation for efficient swimming and diving (Raikow 1970). During submersion, the legs of each species were abducted to a position near or above the horizontal body plane. This is the most efficient position for diving and is also exhibited by other species (e.g., loons [Gaviiformes] and grebes [Podicipediformes]) that are highly adapted for foraging underwater (Raikow 1970).

Several species of waterfowl, including steamer-ducks (Livezey and Humphrey 1984), Oldsquaws, *Clangula hyemalis* (Kelso 1922, Snell 1985), scoters, *Melanitta* spp., eiders, *Somateria* spp., and Harlequin Ducks, *Histrionicus histrionicus* (Brooks 1945; Humphrey 1957, 1958), use their wings for propulsion or stabilization during some portion of submergence. Canvasbacks, Lesser Scaups, and Ruddy Ducks, however, kept their wings folded against the body, similar to the wing position of Greater Scaups, *Aythya marila*, mergansers, *Mergus* spp., goldeneyes, *Bucephala* spp., and the Musk Duck, *Bi*- *ziura lobata* (Townsend 1909, Kelso 1922, Brooks 1945, Frith 1967).

All three species exhaled immediately prior to beginning a dive. This has been observed in another pochard, the Tufted Duck (Butler and Woakes 1979) and in steamer-ducks (Livezey and Humphrey 1984). This action likely reduces the buoyancy during submersion (Livezey and Humphrey 1984).

The Canvasback and Lesser Scaup returned to the water surface with the tip of the bill held against the anterior sternum, a posture similar to that described for the Surf Scoter, *Melanitta perspicillata* (Humphrey 1957), and the Common Eider, *Somateria mollissima* (Humphrey 1958). The Ruddy Duck returns to the water surface in a posture that is similar to that described for the steamer-ducks (Livezey and Humphrey 1984) with the head and neck stretched slightly forward of the position used when swimming on the surface.

The Canvasback's bill and skull shape are well adapted for probing the substrate for plant tubers. As Goodman and Fisher (1962) note, "the bill and cranium are relatively long, narrow, and low; the bill narrows moderately from base to tip which is unusual among the straining ducks. Thus, the skull is modified for probing, and the jaws are capable of a powerful gaping action." In this study, Canvasbacks foraged by inserting the bill into the substrate while the long axis of the body and the power strokes of the legs were perpendicular to the water surface. In this position, the Canvasbacks maximized the force necessary to insert the bill into the substrate to find buried tubers and maintained their position in the area that tubers were located. Pondweed tubers have a clumped distribution (Anderson and Jones 1976) and once a tuber has been located a foraging bird should continue to search in that general area for more tubers. Canvasbacks also differed from the other species in this study by occasionally using alternate foot strokes when feeding. This has been observed in Canvasbacks by other investigators (J. Takekawa, pers. comm.) and may permit the exertion of a more constant force with the bill while probing for tubers. Canvasbacks exhibited flexibility in their foraging behavior by also sieving epibenthic prey with rapid opening and closing of the mandibles, a behavior that is probably more efficient for juvenile and prelaying and laying female Canvasbacks, which consume large numbers of aquatic invertebrates (Bartonek and Hickey 1969).

Lesser Scaups and Ruddy Ducks have a bill morphology well adapted for straining food from the water column or soft substrate. Characteristics of a bill adapted for straining include a spatulate bill shape with closely spaced, bladelike lamellae (Goodman and Fisher 1962). In our study, Lesser Scaup foraged in the water column and on the surface of the substrate and vegetation. This species frequently consumes amphipods (Bartonek and Hickey 1969), which occur in any of these three sites and may differ in their visibility and availability to the foraging bird. Lesser Scaup foraging behavior varied according to prey location and visibility. In clear water, the scaup visually located and directed grasping movements of the bill towards amphipods encountered in the water column and individual prey in aggregations. This species also employed a foraging strategy that utilized only tactile location of a food item. Lesser Scaup used the bill to sieve through the substrate in search of food using lateral movements of the head and bill similar to those used by Ruddy Ducks. Depending on the conditions present in the wetland where the scaup are foraging, any combination of these behaviors could be employed.

Although Ruddy Ducks and Lesser Scaup have similar underwater postures and behaviors, their foraging behavior differs in one important aspect: the Ruddy Duck rarely directed grasping movements of their bills towards prey. The most commonly consumed prey of the Ruddy Duck is benthic chironomid larvae, which are located in very fine bottom ooze. This type of substrate clouds the water when disturbed, making visual detection of prey impossible; tactile location of food is much more efficient in turbid water.

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