Feeding ecology and behavior of postbreeding male Blue-winged Teal and Northern Shovelers

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This study examined foraging strategies in male Northern Shovelers (*Anas clypeata*) and Blue-winged Teal (*Anas discors*). Differences in time–activity budgets and esophageal contents between the two species indicated major differences in the degree of foraging specialization. Preflightless male Northern Shovelers spent 84.2% of time foraging, with dabbling in the water column as the principal foraging mode (83.4%), while postflightless male shovelers spent 81.6% of time foraging (78.7% dabbling). Preflightless male Blue-winged Teal spent 68.6% of time foraging, with dabbling in mud (32.5%) and picking in vegetation (29.4%) as the two principal modes, whereas postflightless male bluewings spent 85.9% of time foraging (dabbling in mud 40.6%, and picking 34.2%). Most male Northern Shoveler food items were cladocerans (85.5%) or chironomid pupae (12.9%); this was related to the specialized foraging method employed by shovelers. Male Blue-winged Teal food items were principally gastropods (44.3%), culicids (29.2%), seeds and vegetation (15.5%), and chironomids (5.6%), which corresponded to the plastic feeding behaviors of bluewings. Examination of esophageal items revealed that male Northern Shovelers did little feeding during the summer flightless period, while male Blue-winged Teal fed throughout the period.

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Les stratégies alimentaires des mâles du Canard souchet (*Anas clypeata*) et de la Sarcelle à ailes bleues (*Anas discors*) ont fait l'objet d'une étude. Les différences dans les budgets temps–activité et les contenus oesophagiens entre les deux espèces reflètent des différences majeures de degré de spécialisation dans la recherche de la nourriture. Les mâles du Canard souchet avant la période sans vol passent environ 84,2% de leur temps à la recherche de nourriture et le principal mode de recherche (83,4% du temps) consiste à barboter et à fouiller dans la colonne d'eau, alors qu'après la période sans vol, les mâles passent 81,6% de leur temps à chercher leur nourriture (78,7% par barbotage en surface). Avant la période sans vol, les mâles de la Sarcelle à ailes bleues, passent 68,6% de leur temps à chercher leur nourriture en fouillant dans la boue (32,5%) ou dans la végétation (29,4%), alors qu'après la période sans vol, les mâles consacrent 85,9% de leur temps à la recherche de leur nourriture (40,6% en fouillant dans la boue et 34,2% en se nourrissant dans la végétation). La nourriture du Canard souchet se compose surtout de cladocères (85,5%) ou de nymphes de chironomides (12,9%), ce qui s'accorde avec leur méthode de recherche de nourriture; la nourriture de la Sarcelle à ailes bleues contient surtout des gastropodes (44,3%), des culicidés (29,2%), des graines et de la végétation (15,5%) et des chironomides (5,6%), ce qui correspond aussi aux comportements plastiques de recherche de nourriture des Sarcelles à ailes bleues. L'examen des contenus oesophagiens a révélé que les Canards souchets mâles se nourrissent peu durant la période sans vol de l'été, alors que les mâles de la Sarcelle à ailes bleues continuent de se nourrir durant toute cette période.

[Traduit par le journal]

Introduction

The Northern Shoveler (*Anas clypeata*) and the Blue-winged Teal (*Anas discors*) belong to a group of seven species of dabbling ducks commonly known as the blue-winged ducks (Delacour 1956; McKinney 1970), distinguished by blue patches on the upper wing coverts. These seven species constitute four "shoveler-like" and three "teal-like" species. Of them, the Northern Shoveler is a common Holarctic species of waterfowl that exhibits a high degree of morphological and feeding specialization (Goodman and Fisher 1962; Lack 1974; Palmer 1976), whereas the Blue-winged Teal is found only in the Western Hemisphere and is considerably smaller with a more typical, although slightly elongated, dabbling-duck bill (Delacour 1956). The only other species of blue-winged duck found in North America is the Cinnamon Teal (*Anas cyanoptera*), which is primarily a South American species; however, populations occur in Central America and up the west coast of North America as far as southern British Columbia and Alberta, where they are only marginally sympatric with the other two species. The Blue-winged Teal and Northern Shoveler are common and sympatric during the breeding season over much of temperate North America, and the evolution of a highly specialized foraging morphology may have resulted from selection decreasing interspecific competition or favoring the occupancy of an underutilized niche (Olney 1965; Hespenheide 1973).

Unlike most species of dabbling ducks (tribe Anatini), the Northern Shoveler has a highly developed bill ideally suited for sieving small swimming crustaceans from the water. The bill is elongated, widened distally, and spatulate, and it has a conspicuous series of comblike lamellae along the lateral edges. Previous studies (summarized in Bellrose 1976 and Palmer 1976) have shown that Northern Shovelers feed primarily by holding the bill in the water while swimming and straining out small invertebrates by continually dabbling. In contrast, other studies (Swanson, Meyer, and Serie 1974; see also Palmer 1976) have shown the Blue-winged Teal to have generalized foraging and food habits.

The main objective of this study was to compare adaptive strategies of two closely related, but morphologically distinct and ecologically dissimilar, species of waterfowl, one of which (Northern Shoveler) is a feeding specialist, and the other (Blue-winged Teal) with more generalized food and foraging habits. Other objectives included an analysis of foods and feeding behaviors of the two species. I decided to examine only adult males of each species because that sex does not participate in incubation or brood rearing. Moreover, females have time and

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energy budgets which may vary considerably, depending on the number of eggs laid and whether or not the brood is reared successfully (McHenry 1971; Afton 1977).

Methods

This study was conducted during 1977–1979 on the Delta Marsh along the southern edge of Lake Manitoba in south-central Manitoba. The marsh is a complex series of interconnected large open water areas interspersed with dense stands of *Phragmites*, *Typha*, and *Scirpus*. North and south of the marsh are a series of intermittent wet and dry meadows containing numerous small potholes and sloughs. The vegetation and physiography of the marsh have previously been described by Hochbaum (1944), Sowls (1955), and Anderson and Jones (1976).

Time budgets of the two species were determined by observing wild birds. During the breeding season, birds were observed along the Assiniboine River Floodway (Portage Diversion) and Manitoba Provincial Road No. 240. After deserting their mates, males were studied at the Delta Waterfowl Research Station and at other locations on Delta Marsh. Days were divided into 3-h bouts from sunrise until dusk. Study sites were randomly chosen, and the birds at that site were watched for the entire 3 h. With the use of a metronome, behaviors of the birds were recorded every 30 s. Recorded behaviors included resting, sleeping, feeding, swimming, preening/comforting, and alert, aggressive, and courtship activities.

Food habits analyses were modeled after those of Swanson, Meyer, and Serie (1974). During spring or fall, a bird was observed feeding for at least 10 min before it was collected, and a description of its feeding behavior was recorded. The breeding status of the bird was determined whenever possible; a bird was said to be paired if it was observed with a mate, or, in the case of Northern Shovelers, if it was defending a territory. After collection the bird was weighed on a hand-held spring scale to the nearest 5 g. During summer when the birds became flightless and secretive, they could not be observed prior to collection. Most flightless birds were collected by night-lighting from an airboat (Young 1977). Other birds were collected using an airboat during daylight. Immediately after collection, the esophagus and proventriculus were removed, and the contents were washed into a labeled vial with 80% ethanol. This immediate preservation prevented postmortem digestive breakdown of food items.

Habitat characteristics, including swimming invertebrates, benthic invertebrates, aquatic vegetation, distance from emergent vegetation, and water depth were measured at the last observed point of feeding. Swimming invertebrates were sampled using a 20.3 × 45.7 cm (8 × 18 in.) nylon sweep net. A 61-cm (2-ft) sweep was taken just below the water surface for an effective volume measurement of 57 L (2 ft^3). In cases where water depth was under 20 cm (the depth of the sweep net) an adjustment was made in calculations to bring the sample to the equivalent volume. Invertebrates were preserved in 80% ethanol in a labeled jar. Core samples for benthic invertebrate analysis were taken by a sampler with a diameter of 10 cm. The entire mud column was placed in a labeled plastic bag for transport to the lab.

Upon return to the lab, benthic invertebrates were separated from the mud by using the sucrose flotation technique (DuBowy 1980). The sample was placed in a pan, and enough supersaturated sucrose solution (2:1 sucrose to hot water by volume) was poured in to cover the sample. The sample was stirred and, because the specific gravity of the invertebrates is less than the specific gravity of the solution, the former floated to the surface. They then were collected, placed in a labeled vial, and preserved in 80% ethanol.

Aquatic invertebrates from the esophagus and habitat samples were removed from preservative and soaked overnight in tap water to return the organisms to their original volume and weight (Donald and Paterson 1977). They then were sorted into various taxa by using keys in Pennak (1953), and wet weights were determined. They were placed in a drying oven at 90°C for at least 24 h and then reweighed to determine moisture-free dry weight.

Wet weights of the esophagus samples were used to determine the food habits of the two duck species. Methods were modified from those of Swanson, Krapu et al. (1974). Percent occurrence, aggregate percent, and percent wet weight of each food item were determined from wet weights of the invertebrates rather than their volume. This was done because the volume of many of the smaller taxa could not be taken reliably. Aggregate percent for each food taxon is defined as the mean of gravimetric percentages for all birds examined, and aggregate wet weight is simply the percentage of the total wet weight constituted by each taxon. Percent occurrence is the proportion of birds examined in which the prey taxon occurred.

Food selectivities of individual birds were determined by running a series of χ^2 tests on food taxa in the esophagus versus the habitat. Invertebrate taxa used in these tests represent the region (whether the water column or the mud) from which the duck had obtained its prey items. A duck was said to be selecting a given prey taxa if the proportion of that prey taxa was higher in the esophagus sample than in the habitat sample. Conversely, the bird was said to be selecting against a potential prey item if the proportion was less in the esophagus sample than in the habitat sample.

Results

Male Northern Shovelers remain paired longer than most species of North American dabbling ducks (Poston 1974; Seymour 1974; Afton 1977), often well into the prebasic molt. Males in late prebasic molt were observed on territories in mid-June. By late June males had deserted their mates and formed all-male flocks of 10 to 40 birds; females, presumed to be nonbreeding, were occasionally found in the flocks. Little aggression (<0.1%) was observed in these social flocks, and the birds spent most of the day (84.2%) feeding by mainly dabbling in the water column (83.4%) while swimming back and forth on a pond as a unit (Table 1). Increases in food consumption and fat deposition were recorded during this time (DuBowy 1980). These flocks tended to be stable in nature, remaining together in flight and alighting as a unit on another area of the marsh when disturbed. In early July small flocks (6–10 individuals) were observed flying from the Delta Marsh due north over Lake Manitoba, presumably to molting areas, but most birds molted locally.

Once the birds became flightless they were solitary and secretive. Unlike species of dabbling ducks (e.g., Gadwall (*A. strepera*) and American Wigeon (*A. americana*)) that remained in open water (Oring 1964, 1969) and unlike other *Anas* species which were active nocturnally, male Northern Shovelers remained near or hidden in emergent vegetation even at night. When frightened they frequently went ashore or into vegetation rather than out into open water. Male Northern Shovelers fed little during the flightless phase (DuBowy 1980), and their remaining hidden in the vegetation was probably related to these reduced rates of feeding. Flightless birds that were collected contained little or no food in the proventriculus, gizzard, or intestines, and the birds lived off stored reserves during this time (DuBowy 1980).

After regaining flight in early to mid-August, male Northern Shovelers again formed small flocks in the marsh and spent most time feeding (81.6%), predominantly by dabbling (78.8%). These flocks left the marsh and began their fall migration by early September, much earlier than females or young birds. I observed few adult male Northern Shovelers on Delta Marsh after 1 September of each year. Aerial surveys and the results of hunter bag checks showed that very few adult male Northern Shovelers were present during the hunting season (late September to November). Additionally, during the 1977 hunting season only one adult male Northern Shoveler was observed shot on the Delta Marsh after 17 October.

Blue-winged Teal males also remained with their mates

TABLE 1. Time–activity budgets of postbreeding male Blue-winged Teal and Northern Shovelers

	Northern Shovelers		Blue-winged Teal	
	Preflightless	Postflightless	Preflightless	Postflightless
Feeding activities	0.842	0.816	0.686	0.859
Dabbling	0.834	0.788	0.325	0.406
Tipping up	0.007	0.026	0.065	0.109
Picking	0.001	0.002	0.294	0.342
Diving	0.000	0.000	0.002	0.002
Nonfeeding activities	0.158	0.194	0.314	0.141
Resting/sleeping	0.014	0.012	0.081	0.037
Being alert	0.000	0.001	0.005	0.004
Swimming	0.092	0.110	0.089	0.050
Preening/comforting	0.052	0.071	0.106	0.041
Aggression/courtship	0.000	0.000	0.033	0.009

well into incubation (McHenry 1971; Stewart and Titman 1980), but males deserted their mates by mid-June. Like Northern Shovelers, Blue-winged Teal also formed all male aggregations, but these were not nearly as social as those of shovelers. Male Blue-winged Teal spent most time resting at loafing sites, and aggressive encounters between males or chases after lone females or mated pairs were occasionally observed (3.3%). Additionally, male Blue-winged Teal spent less time foraging than male shovelers (68.6%). Presumably, most male Blue-winged Teal molted locally (McHenry 1971), but some birds undertook a molt migration.

Like Northern Shovelers, male Blue-winged Teal were solitary during the flightless period. They remained secretive during the day but were also found in open water. Oring (1964) found that flightless adults moved to open water when disturbed. At night, however, flightless male Blue-winged Teal were active and found long distances (up to 200 m) from cover. Based on collected birds, male Blue-winged Teal, unlike Northern Shovelers, fed extensively during the flightless period, but, because of their secretive nature, behaviors could not be quantified.

After they regained flight in mid- to late August, male Blue-winged Teal formed small flocks and began fall migration. Postflightless male bluewings spent more time foraging (85.9%) than preflightless birds. Most adult males left by early September. Adult males made up 7.3% of the Blue-winged Teal harvested on the Delta Marsh during the 1st week of the 1977 hunting season (3–8 October) and then were not present afterwards.

In this study, it would be difficult to quantify feeding behavior of male Blue-winged Teal as foraging mode was a function of habitat physiography; however, dabbling in the bottom mud and picking in the vegetation were the two most prevalent feeding modes observed in both pre- and post-flightless birds, with dabbling in deep water, tipping up, and diving only occasionally observed (Table 1). "Gleaning" (Palmer 1976) and "hawking" (Connelly 1977) (both of which refer to picking invertebrates off submerged or floated vegetation) and dabbling in shallow water have been described as the two most common feeding behaviors of Blue-winged Teal.

As suggested by their bill morphologies, Northern Shovelers and Blue-winged Teal had different principal modes of feeding (Goodman and Fisher 1962; Palmer 1976; Bellrose 1976; Connelly 1977). All adult male Northern Shovelers that were observed to be feeding before being collected had been dabbling along the surface of the water, straining small swimming invertebrates and seeds from the water. Northern Shovelers, however, also may occasionally dive or tip up to feed underwater (Kear and Johnsgard 1968; M. G. Anderson, personal communication). This specialization in feeding habits was reflected in food items that made up the diet of adult male Northern Shovelers (Table 2). The largest proportion of the diet was made up of cladocerans (*Daphnia* and related genera). These small crustaceans occurred in dense numbers and were easy for Northern Shovelers to feed on by straining the water column. The large number of chironomid pupae found was primarily the result of feeding by one individual that was collected while it was feeding on a dense concentration of floating pupae during a midge hatch. Previous feeding by Northern Shovelers on midge larvae was reported by Preble and McAtee (1923).

TABLE 2. Esophageal food items of adult male Northern Shovelers (N = 25)

Food item	Aggregate wet weight[a]	Aggregate %[b]	% occurrence[c]
Conchostraca	0.21	*tr*[d]	4
Cladocera	85.49	68.6	76
Hydracarina	0.01	tr	8
Hemiptera			
Corixidae	0.42	4.7	28
Coleoptera			
Dytiscidae larvae	TR[e]	*tr*	4
Diptera			
Culicidae pupae	0.01	0.1	4
Chironomidae larvae	0.23	2.3	28
Chironomidae pupae	12.90	4.0	12
Ephydridae larvae	TR	*tr*	4
Gastropoda			
Physidae	0.02	*tr*	8
Seeds	0.69	22.3	72
Vegetation	0.01	0.1	12

[a]The percentage of the total wet weight constituted by each taxon.
[b]The mean of gravimetric percentages for all birds examined.
[c]The proportion of birds examined in which the prey taxon occurred.
[d]*tr*, < 0.1.
[e]TR, < 0.01.

The large percentage of seeds in the diet (aggregate percent method) of male Northern Shovelers reflected a curious phenomenon. In mid-summer when birds were flightless, they apparently reduced feeding considerably. During this period, they were secretive and remained hidden in the emergent vegetation during the day and rarely ventured from the vegetation at night (DuBowy 1980). Because the birds remained hidden, it was impossible to observe their behavior, but of the 21 adult male flightless Northern Shovelers collected, only two had been actively feeding prior to collection. The other 19 birds, which had been collected during all stages of the day or night, had only an occasional seed or some grit in the esophagus, proventriculus, or gizzard. Consequently, not all flightless birds were included in the food-habit analyses. Therefore, those birds that had only a few seeds for the entire food sample greatly inflated the aggregate percent of seeds in the total. Aggregate wet weight shows a much more realistic figure for food items in the diet of adult male Northern Shovelers during spring and summer.

Food items of male Blue-winged Teal (Table 3) are evidence of the different foraging strategy employed by that species. Rather than having a single stereotyped feeding behavior, adult male Blue-winged Teal exhibited several different feeding modes (Table 1). Depending on physiography, especially water depth and amount of submerged aquatic vegetation, Blue-winged Teal altered their feeding behavior. In shallow water (depth less than about 10 cm), the birds would dabble in the mud below the water. By doing so, they tended to feed mainly on chironomid and culicid larvae and pupae and seeds. In deeper water, with fairly dense stands of aquatic vegetation, Blue-winged Teal usually were observed swimming and picking snails or seeds off vegetation. Birds occasionally tipped up in deeper water, presumably to feed at or near the bottom on chironomids and culicids. In deeper water with little or no aquatic vegetation, birds were occasionally observed dabbling along the surface of the water. When doing so they generally fed on cladocerans in much the same way as Northern Shovelers; however, Blue-winged Teal, owing to their less specialized bill morphology, were much less efficient at feeding in this way. Wet weights of esophageal contents of Blue-winged Teal that had been feeding principally by dabbling in open water were less than those of Northern Shovelers that had been feeding for the same length of time. Blue-winged Teal also were observed diving and presumably feeding on the bottom, but this was a rare behavior. Diving also has been reported in Blue-winged Teal by Kear and Johnsgard (1968).

Owing to their plastic feeding behaviors, Blue-winged Teal utilized a wide range of food resources. If cladocerans and corixids, two abundant taxa of very small or very quick invertebrates, are eliminated from the spectrum of potential prey items determined by the sweep and bottom habitat samples, 70% of the Blue-winged Teal sampled fed on the most abundant (biomass determined by wet weight) invertebrate taxa. Of the remaining 30%, two-thirds (20%) fed mainly on seeds or vegetation, which were usually quite abundant, and only one-third (10%) did not primarily feed on the most abundant invertebrate taxa or vegetation, although the invertebrates that those birds did feed on were also fairly abundant.

Discussion

Previous food-habit studies have found Northern Shovelers to feed primarily on vegetation or seeds (McAtee 1922; Korschgen 1955; Anderson 1959; Stewart 1962; McGilvrey 1966). It should be noted, however, that most of these studies examined gizzard contents, often after they were left intact in the duck for long periods of time. Consequently, most of the small crustaceans and other invertebrates would have been broken down or partially digested by then, which would bias the food items towards those that resisted digestion or were not broken down by the mechanical action of the gizzard, especially seeds or vegetation. Swanson and Bartonek (1970) found about three times as much animal food in esophagi as in gizzards of Blue-winged Teal, and unless the birds were collected in the process of feeding and the food items were immediately preserved, many of the soft bodied invertebrates were rapidly digested in the esophagus. Other studies that found a preponderance of animal matter in the diet of Northern Shovelers include those of Wetmore (1917), Preble and McAtee (1923), Dementiev and Gladkov (1967), and Swanson et al. (1979). With improved methods of food data collection (Swanson, Meyer, and Serie 1974), estimated percent animal matter of Northern Shovelers food will probably increase.

Previous studies indicated that up to 70% of the food items of Blue-winged Teal are seeds, tubers, or vegetation (Mabbott 1920; Bennett 1938; Korschgen 1955; Anderson 1959; Stewart 1962). These findings were not borne out by this study, which showed that vegetation and seeds made up only 15.5% by aggregate wet weight or 43% by aggregate percent of the total food items. My findings are more in agreement with those of Swanson, Meyer, and Serie (1974) who found that vegetation and seeds made up 21% of the diet of Blue-winged Teal. Vegetation, seeds, or both occurred in all esophageal food samples and made up the entire diet of two birds; however, in

TABLE 3. Esophageal food items of adult male Blue-winged Teal[a] (N = 30)

Food item	Aggregate wet weight	Aggregate %	% occurrence
Cladocera	1.84	5.4	40.0
Ostracoda	0.02	1.0	6.7
Amphipoda	0.83	2.4	6.7
Odonata	0.23	0.6	6.7
Hemiptera			
Gerridae	0.07	0.2	3.3
Notonectidae	0.01	0.1	3.3
Corixidae	0.52	1.1	33.3
Coleoptera			
Haliplidae larvae	0.06	1.3	6.7
Dytiscidae larvae	0.30	0.1	3.3
Dytiscidae adults	0.11	*tr*	3.3
Hydrophilidae larvae	0.46	0.1	6.7
Hydrophilidae adults	0.46	0.4	3.3
Helodidae adults	0.01	*tr*	3.3
Diptera			
Tipulidae larvae	0.01	*tr*	3.3
Culicidae larvae	27.54	5.5	10.0
Culicidae pupae	1.61	0.3	10.0
Chironomidae larvae	4.21	15.4	43.3
Chironomidae pupae	1.36	2.0	26.7
Ceratopogonidae larvae	0.01	*tr*	3.3
Stratiomyiidae larvae	0.42	1.3	6.7
Tabanidae larvae	0.02	*tr*	3.3
Syrphidae larvae	0.12	0.1	3.3
Gastropoda			
Planorbidae	16.04	5.4	30.0
Physidae	25.35	13.7	33.3
Lymnaeidae	2.94	0.4	3.3
Seeds	11.02	32.1	93.3
Vegetation	4.43	10.9	36.7

[a] For definitions, see footnote to Table 2.

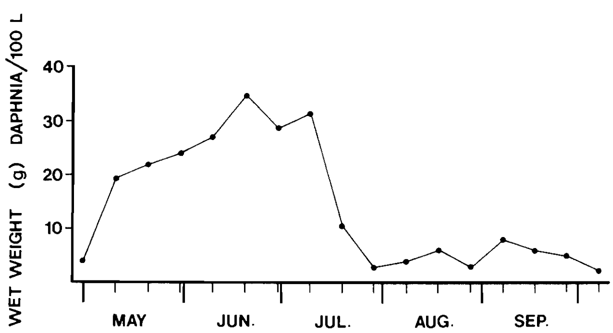

FIG. 1. Seasonal change in cladoceran biomass (grams wet weight per 100 litres water) during 1978 in the Delta Marsh, Manitoba.

many cases seeds or vegetation made up only a small percentage of the total array of food items. Swanson, Meyer, and Serie (1974) reported that Blue-winged Teal apparently began switching over to higher proportions of animal matter in the diet by mid-May, and Dirschl (1969) reported that animal foods reached a peak (81.2%) in July, after which Blue-winged Teal switched back to more plant matter in the diet in late summer. The findings of this study did not contain any food-habit data which corroborate these earlier studies; however, morphological changes in the digestive tract in late summer may indicate an increase in the amount of fibrous material (vegetation and (or) seeds) in the diet of Blue-winged Teal during that time (DuBowy 1980).

The unusual seasonal dynamics of feeding in male Northern Shovelers can best be explained by an examination of the seasonal dynamics of cladocerans, the major food item of Northern Shovelers (Fig. 1). Northern Shovelers are usually one of the last species of dabbling duck to arrive on the breeding grounds in spring (Sowls 1955; Poston 1974), possibly waiting until cladoceran levels have built up sufficiently to allow the birds to feed almost exclusively on them. However, cladocerans undergo a midsummer decline in population levels on a Northern Hemisphere-wide basis throughout the breeding range of Northern Shovelers (see Threlkeld 1979 for a review of this phenomenon; also Collias and Collias 1963 and Allan 1977). This predictable summer decline in cladoceran numbers apparently has affected the evolution of a long-term foraging optimization strategy in male Northern Shovelers.

Behavioral data for preflightless Northern Shovelers and Blue-winged Teal are similar to those found by Poston (1974) and Stewart and Titman (1980), except that preflightless male Northern Shovelers fed more and rested less than territorial males, and preflightless male Blue-winged Teal fed less and had more intraspecific interactions than territorial males. Hyperphagia exhibited by preflightless male Northern Shovelers resulted in significant increases in fat and protein depots and organ weights, notably liver, kidney, and pancreas. In contrast, male Blue-winged Teal exhibited a significant increase only in fat index during this same period of time (DuBowy 1980).

In early summer, after abandoning their mates, male Northern Shovelers form small all-male flocks and spend most time feeding. Feeding heavily during this period of cladoceran abundance allows the birds to gain weight rapidly. With these stored fat reserves, the birds are prepared for the upcoming midsummer decline in cladoceran numbers. When the decline does occur, adult male Northern Shovelers are able to utilize stored fat reserves for energy requirements rather than switch to less profitable prey items. An energy-based computer simulation model (in preparation) has demonstrated that molting male Northern Shovelers with adequate fat reserves can successfully fast for up to 2 weeks. As population levels begin to increase after the midsummer decline, male Northern Shovelers are able once again to begin feeding on cladocerans. Similar long-term foraging optimization strategies have been advanced for birds by Katz (1974) and Craig et al. (1979).

It has often been postulated that the territorial breeding system of Northern Shovelers is primarily due to a necessary and defendable food resource, because shovelers are inefficient feeders and require long periods of time to ingest all the energy necessary for breeding, egg production, and incubation (Siegfried 1965; McKinney 1970). This hypothesis is not consistent with the facts, which show adult male Northern Shovelers feeding very efficiently on *Daphnia*, indeed so efficiently that when the *Daphnia* populations crash males live off stored reserves rather than switch to another, less efficient, mode of foraging. Alternatively, I propose that specialization on a ubiquitous and very dense food resource has allowed Northern Shovelers to evolve a territorial strategy. Conversely, other dabbling duck species with more ephemeral or patchily distributed prey may not be able to defend territories large enough to meet the energetic needs of laying females.

In contrast, Blue-winged Teal, with their many different foraging options, are not tied to any single food resource, and, hence, are not affected by seasonal trends in the population dynamics of any particular prey species. As such, no mechanism for long-term foraging optimization apparently has evolved for Blue-winged Teal, except for premigratory fattening. An analysis of the data (DuBowy 1980) shows that Blue-winged Teal actually increase body weight and stored fat during the flightless period, which indicates that foraging opportunities are not diminished during that period of time.

The plastic feeding behaviors of Blue-winged Teal bring up the interesting possibility that, rather than switching food patches when prey are depleted (or simply not available) (MacArthur and Pianka 1966; Royama 1970), the birds are simply switching foraging behavior to obtain a different food resource in the same patch. This apparently does happen, at least part of the time, with the evidence coming from observations of several different foraging methods (e.g., picking, tipping up, or dabbling on the bottom) at the same locale and from analyses of esophageal contents, which show a wide variety of food items in some individuals that could only have been obtained by foraging in several different ways. Switching foraging mode has not been considered in models of optimal foraging theory and may prove to be an important process by which birds maximize prey yield per unit effort. Current models of optimal foraging theory, especially models of diet selection, assume the same mode of prey acquisition for all taxa of potential prey. This simplifying assumption overlooks the ability of some species to change foraging modes, thereby allowing species to increase diet breadth while, in fact, increasing yield per unit effort.

Consequently, long-term foraging optimization has evolved in male Northern Shovelers as a response to the potential need of switching to less profitable prey items during the seasonal decline of the preferred food item. Blue-winged Teal are able to circumvent this problem by being able to forage efficiently on several different prey items. If any particular food item undergoes a seasonal decline in population numbers, bluewings still have a large selection of food items to choose from.

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