Feeding ecology of Pintail, Gadwall, American Widgeon and Lesser Scaup ducklings

by Lawson G. Sugden

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Perspective

The prairies and parklands of southern Canada are dotted with millions of water areas where more than half the continent's waterfowl are produced. To the casual observer the myriad of wetlands might seem unlimited but this is not so. Each year some wetlands are permanently lost through man's activities. As wetlands are eliminated from the landscape, ducks also disappear. If we wish to maintain duck populations at present-day levels, then we must learn to produce several ducks where one is now produced.

A detailed understanding of wetlands and how ducks use them is needed to do this. Ducks require food, water, cover and space to reproduce successfully. My objectives dealt with food of ducklings, an aspect that had been neglected until recent years. I studied the Pintail, Gadwall, American Widgeon and Lesser Scaup and have shown how the diet of each species changes as they grow and how these changes are related to shifts in feeding methods and habitat use. These features also differ among species. A diverse habitat will produce the greatest variety and probably the greatest number of ducks.

Abstract

Objectives were to determine the diet of flightless young Pintails (*Anas acuta*), Gadwalls (*A. strepera*), American Widgeons (*Mareca americana*) and Lesser Scaups (*Aythya affinis*); investigate factors which influence food use; and determine nutritional composition of duck foods. Diet was determined from dry weight of esophagus-proventriculus contents from 144 Pintails, 167 Gadwalls, 129 Widgeons and 135 Scaups.

Up to 5 days, Pintails ate mostly insects captured on the water surface. Older ducklings ate aquatic invertebrates and plants. Pintails ate a variety of invertebrates; gastropods, chironomid larvae and cladocerans were most important. Diet during the prefledgling period contained 33 per cent plants, chiefly seeds of Gramineae and Cyperaceae.

Gadwalls first ate chiefly surface invertebrates. As they grew, they ate proportionately more aquatic invertebrates and plants, and by 3 weeks, were essentially herbivorous. Most important animal foods were chironomid larvae and adults, corixids, coleopterans and cladocerans. The prefledgling diet comprised 90 per cent plants, the most important being leaves of *Potamogeton pusillus*, Cladophoraceae and *Lemna minor*.

Prefledgling Widgeons ate 89 per cent plant food. Despite similar diets, feeding methods, feeding habitat and seasons of use, Widgeons and Gadwalls had sufficient food and did not compete.

Young Scaups ate 96 per cent invertebrates of which amphipods, chironomid larvae and gastropods contributed 52, 16 and 16 per cent, respectively. As they grew, Scaups ate relatively more amphipods and fewer bottom larvae, because broods moved to larger ponds where amphipods were more prevalent.

Changes in methods and sites used by dabbling ducklings paralleled and confirmed diet changes. Diet data indicated that extensive surface feeding observed in newly-hatched Scaups was inefficient compared with diving for food. Feeding Pintails favoured the shallows near shore, Gadwalls and Widgeons fed mostly over submersed plants and Scaups preferred deeper water.

A comparison of food available with food eaten showed ducklings ate the most available invertebrates, considering the ducks' characteristic feeding adaptations. Gastropods were an exception and though often available, were seldom eaten. Use of plants was determined more by preference. Ducks sought a mixed diet and this may be related to selection of foods which provided a nutritionally balanced diet. Few of 21 duck foods analysed would provide the nutrient requirements of ducklings in adequate proportions. Chironomid larvae, *Gammarus* and corixids contained the highest quality protein in terms of amino acid requirements of chicks.

Résumé

Nos objectifs étaient de déterminer le régime des jeunes Canards pilets (*Anas acuta*), Canards chipeaux (*A. strepera*), Canards siffleurs d'Amérique (*Mareca americana*) et Petits Morillons (*Aythya affinis*) pendant la période précédant leur premier vol, d'étudier les facteurs qui influent sur le choix de leur nourriture, et de déterminer la composition nutritive de l'alimentation des canards. La détermination de la nourriture a été faite par analyse du contenu (poids anhydre) de l'oesophage et de l'estomac glandulaire de 144 Canards pilets, 167 Canards chipeaux, 129 Canards siffleurs et 135 Morillons.

Les Canards pilets ayant jusqu'à cinq jours se sont nourris surtout d'insectes attrapés à la surface de l'eau. Les plus âgés ont absorbé des invertébrés aquatiques et des plantes. Ces canards se sont alimentés d'une variété d'invertébrés dont la majorité était constituée de gastéropodes, de larves de chironomes et de cladocères. Pendant la période où les Canards pilets n'étaient pas encore en état de voler, leur alimentation se composait de 33 pour cent de plantes, principalement de graines de graminées et de cypéracées.

Les Canards chipeaux mangeaient d'abord des invertébrés happés à la surface des eaux. En grandissant, ils absorbaient de plus en plus d'invertébrés aquatiques et de plantes et, au bout de trois semaines, ils étaient devenus exclusivement herbivores. Leur principale nourriture animale était constituée de larves de chironomes et de chironomes adultes, de corisides, de coléoptères et de cladocères. Pendant la période où le Canard chipeau ne volait pas, 90 pour cent de sa nourriture se composaient de plantes, dont les plus importantes étaient des feuilles de *Potamogeton pusillus*, de cladophorées et de *Lemna minor*.

Quant au Canard siffleur, sa nourriture était à 89 pour cent végétale. Malgré la similarité des régimes, des manières de se nourrir, des lieux d'approvisionnement et des périodes d'utilisation, le Canard siffleur et le Canard chipeau avaient assez de nourriture et ne se faisaient pas de concurrence.

Chez les jeunes Morillons, les amphipodes, les larves de chironomes et les gastéropodes constituaient respectivement 52 pour cent, 16 pour cent et 16 pour cent des invertébrés, dont ils se sont nourris dans une proportion de 96 pour cent. À mesure qu'ils se sont développés, les Morillons mangeaient relativement plus d'amphipodes et moins de larves de fond parce qu'ils avaient déménagé sur de plus grands étangs où les amphipodes étaient plus répandus.

Les changements de méthodes et de lieux d'alimentation des canardeaux qui appartiennent aux espèces "de surface" ont coïncidé avec les changements de régime et les ont confirmés. Certaines données indiquent que la manière de se nourrir en surface (observée chez des Morrillons nouvellement éclos) est inefficace par comparaison à la plongée. Le Canard pilet préférait chercher sa nourriture dans les endroits peu profonds, près du rivage tandis que le Canard chipeau et le Canard siffleur se nourrissaient surtout de plantes submergées. Les Morillons aimaient s'alimenter dans des eaux plus profondes.

Une comparaison entre la nourriture accessible et la nourriture absorbée montre, compte tenu des adaptations alimentaires caractéristiques des canardeaux, que ces derniers mangeaient les invertébrés qu'ils pouvaient attraper en plus grand nombre, exception faite des gastéropodes qu'ils pouvaient trouver souvent mais qu'ils mangeaient rarement. Il a été déterminé que la consommation de plantes était plutôt une question de préférence. Les canards recherchaient une nourriture mixte ce qui peut avoir un rapport avec une sélection d'aliments constituant une nutrition équilibrée. L'analyse des aliments que 21 canards avaient absorbés a démontré que peu de ces aliments permettraient de répondre aux besoins nutritifs des canardeaux en proportions satisfaisantes. Les larves de chironomes, les *gammarus* et les corisides contenaient la protéine de la plus haute qualité, relativement aux besoins en acides aminés des oiseaux fraîchement éclos.

АБСТРАКТ

Целью работы является определение режима питания нелетающих молодых шилохвостей (**Anas acuta**), серых уток (**Anas strepera**), американских диких уток (**Mareca americana**) и нырков американских (**Aythya affinis**), исследование факторов, влияющих на выбор пищи, и определение питательного состава пищи уток. Рацион определялся по сухому весу пищевода железистого желудка у 144 шилохвостей, 167 серых уток, 129 американских диких уток и 135 американских нырков.

До возраста 5 дней шилохвости питались преимущественно насекомыми, пойманными на поверхности воды. Утята постарше поедали водных беспозвоночных и растения. Шилохвости питались весьма разнообразными беспозвоночными; наиболее важными являлись брюхоногие, личинки хирономид и кладоцеры (**cladocerans**). В течение периода до начала оперения их рацион составляет 33% растений, преимущественно семян травянистых и осокоцветных растений.

Серые утки сначала питались преимущественно наземными беспозвоночными. По мере их роста они постепенно переходили на водяных беспозвоночных и растения, и к концу третьей недели они питались преимущественно растениями. Наиболее важной животной пищей являются личинки хирономид и взрослые особи, жесткокрылые и кладоцеры. В период до оперения еда состоит из 90% растений, особенно листьев **Potamogeton pusillus**, **Cladophoraceae** и **Lemma minor**.

В период до оперения американские утки питались на 89% растительной пищей. Несмотря на похожий режим питания, способы питания, среду питания и сезон американские дикие утки и серые утки находили достаточно еды и не препятствовали друг другу.

Молодые американские нырки питались на 96% беспозвоночными, из которых амфиподные, личинки хирономид и брюхоногие составляли соответственно 52%, 16% и 16%. По мере своего роста американские нырки переходили больше на питание амфиподными, чем личинками на дне, так как выводки перемещались в более крупные пруды, где амфиподных было больше.

Изменения в методах поведения и местности только что вылупившихся утят соответствуют и подтверждают изменения в их режиме питания. Данные режима питания свидетельствуют о том, что преимущественное питание с поверхности вылупившихся американских нырков мало эффективно по сравнению с нырянием за пищей. Для поисков корма шилохвости предпочитали мели вблизи берегов, серые утки питались преимущественно погруженными растениями, а американские нырки предпочитали более глубокие воды.

Сравнение состава доступной пищи с принятой пищей показало, что утята поедали наиболее доступных беспозвоночных, если принять во внимание характерные адаптации методов питания уток. Брюхоногие являлись исключением; хотя они и были зачастую доступными, утки их поедали редко. Потребление растений регулировалось скорее предпочтением. Утки выбирали смешанный режим питания, и это можно считать причиной того, что разнообразие их пищи предоставляет питательно сбалансированный режим питания. Немного из 21 проанализированных образцов пищи уток обеспечило бы требования питательного баланса утят. Личинки хирономид, рачки-бокоплавы и жесткокрылые содержали белок наивысшего качества (в смысле потребности цыплят в аминокислотах).

Introduction

An understanding of the food requirements of any wildlife species is basic to its management and the need for such knowledge grows as management becomes more intensive. As hunting regulations suggest, the supply of North American waterfowl no longer exceeds demand. Increased demand helped to create this situation, but loss of habitat is potentially more serious. Various authors in *Waterfowl Tomorrow* (Linduska, 1964) stressed the need not only to preserve existing waterfowl habitat but also to make it more productive. Despite programs to create and preserve wetlands, the number dwindles because of competing land uses. To maintain waterfowl populations similar to those of the 1960's, future management must involve habitat manipulation, and this must be based on a knowledge of each species' requirements. One major requirement is food for growing young. What does each species eat? How do diets change with age of ducks? How adaptable is each species to changes in available food? How much energy in the various foods is available to ducks? What kinds of ponds produce adequate food? Answers to such questions will provide guidelines for improved habitat acquisition and development.

Waterfowl biologists do not know enough about diets of ducks, particularly flightless young. There are numerous brief accounts of foods eaten by ducklings, but many are of doubtful value because they include results based on small samples and on gizzard material which causes serious bias (Dillon, 1959; Perret, 1962). Only four significant studies of duckling diets have been reported. Chura (1961) discussed foods found in esophagus-proventriculus-gizzard samples from 94 young Mallards (*Anas platyrhynchos*) collected at Bear River Refuge, Utah. The sample included ducklings less than 1 week old through to flying age. Immediately after hatching, the birds ate chiefly terrestrial insects but took more aquatic invertebrates and plant food as they grew. After 18 days, they ate few terrestrial insects. The proportion of plant foods continued to increase until, at flying age, the ducklings were eating almost 100 per cent plants. The change in diet was accompanied by a change in feeding methods.

Perret (1962) analysed esophagus-proventriculus contents of 62 young Mallards collected during 3 years near Minnedosa, Manitoba. There, invertebrates dominated the diets of all ages of flightless young and animal foods made up 91 per cent of the total diet. Flying young ate significantly more plant food, principally grain. Perret (1962) measured availability of foods and concluded that, to a large extent, Mallards ate those most available.

Esophageal contents of 86 young Canvasbacks (*Aythya valisineria*), 37 Redheads (*A. americana*) and 25 Lesser Scaups (*A. affinis*) from southwestern Manitoba were reported by Bartonek and Hickey (1969a). Canvasbacks ate larger proportions of plant food as they grew. Canvasbacks and Redheads tended to select bottom fauna, whereas amphipods were most important for Scaups. Bartonek and Hickey (1969b) studied selective feeding by the same sample of juvenile Canvasbacks and Redheads.

Bartonek and Murdy (1970) analysed esophageal contents of 38 flightless young Lesser Scaups collected near Yellowknife, Northwest Territories. The ducks had eaten almost 100 per cent invertebrates. In late July and early August they had eaten mostly Culicidae larvae and pupae, and Conchostraca. Amphipods, odonate naiads and corixids were the most important items eaten by Scaups collected in early September. The authors suggested that the difference in diets may reflect a tendency for older ducklings to feed at greater depths.

My study, carried out from 1963 through 1967, involves four species: Pintail (*Anas acuta*), Gadwall (*A. strepera*), American Widgeon (*Mareca americana*) and Lesser Scaup. Objectives were to determine the diet of the four species from hatching to flying; to investigate factors which influence food selection and to determine nutritional composition of natural foods.

The four species were chosen for several reasons. All are relatively common on the prairie breeding grounds and are important game ducks in terms of numbers shot. Little was known about their food habits. The four species often use different parts of the same ponds. Pintails prefer the shallow edges; Gadwalls and Widgeons are intermediate and are seen more often away from the shore; Scaups, being diving ducks, favour the deeper areas. Thus the four are a good combination for comparative study.

The study area

The study area is a north-south rectangle about 10 by 22 miles (16 by 35 km) surrounding Strathmore, Alberta (51°02′N, 113°23′W). The block coincides with the main part of the Western Irrigation District. Elevation at Strathmore is 3,192 feet (972.9 m) above sea level.

The area lies within the Dark Brown Soil Zone (Wyatt et al., 1942). Soils vary from sandy to light loam in texture. Topography is undulating to gently rolling. According to Moss (1944, 1955) vegetation of the region is characterized by a *Stipa-Bouteloua* climax association. However, Coupland (1961) stated that the grassland of the Dark Brown Soil Zone is of the Mixed Prairie Association dominated by a *Stipa-Agropyron* Faciation. Probably no part of the area has been undisturbed. Poston (1969) gave percentages of 1966 land use on a 2,726-acre (1,103-hectare) block within my study area as: pasture 66, grain 14, alfalfa 9, summerfallow 2, roads and farmyards 2, brush and trees 2 and water 5 per cent. For the entire study area, I estimate there was 5 to 10 per cent more acreage in grain and correspondingly less in pasture.

Annual precipitation averages about 15 inches (38 cm). Using 29°F (−1.7°C) as the limit of a killing frost, Wyatt et al. (1942) reported that the area averaged about 115 frost-free days.

Water areas ranged in size from less than 1 acre (0.4 ha) to 2,880 acres (1,165 ha). Approximately 20 exceeded 50 acres (20 ha). The number of water areas fluctuated from year to year and usually water levels and pond numbers declined throughout summer. Most water areas drying up each summer were under 1 acre (0.4 ha) in size. George Freeman, Ducks Unlimited (pers. comm.) collected water area data each year from a 25-mile (40.2-km), east-west transect bisecting my study area and sampling 6.25 sq miles (16.19 km^2). During the 5-year period, the density of mid May water areas averaged 9.8 ± 1.5 (SE) per sq mile (3.8/km^2). The mid July average was 8.4 ± 1.2 water areas per sq mile (3.2/km^2). Ducks Unlimited (Canada) had modified several of the permanent lakes and recharged them with irrigation water each summer. The ponds seldom exceeded 48 inches (1.2 m) in depth. Mean maximum depth in July and August of 50 water areas used for duck collections was 23 inches (0.58 m) with a range of 8–54 inches (0.2–1.4 m). Average mean depth was 16 inches (0.4 m) with a range of 5–45 inches (0.13–1.14 m).

Type and abundance of vegetation varied widely among the water areas. Table 1 shows the per cent occurrence of plants on 52 water areas used for duck collections. None of the areas sampled was without some emergent and submersed plants. Trees were restricted to irrigation ditches and canals and farm windbreaks. Common trees along the watercourses were poplars (*Populus* spp.) and willows (*Salix* spp.). A variety of grasses and forbs grew on pastures. Commonest shrubs were wolfberry (*Symphoricarpos occidentalis*), silverberry (*Elaeagnus commutata*) and common rose (*Rosa Woodsii*). I placed specimens of plants collected on the study area in the CWS Herbarium, Saskatoon, and the Intermountain Herbarium, Utah State University, Logan.

Table 1
Percentage occurrence of plants on 52 water areas used for collecting ducks

Item	Per cent occurrence
Cladophoraceae	48
Characeae *Chara* sp.	2
Musci	6
Equisetaceae *Equisetum arvense* L.	2
Typhaceae *Typha latifolia* L.	13
Sparganiaceae *Sparganium eurycarpum* Engelm.	8
Zosteraceae	
Potamogeton vaginatus Turcz.	8
P. pectinatus L.	73
P. pusillus L.	63
P. gramineus L.	2
P. Richardsonii (Ar. Benn.) Rydb.	21
Zannichellia palustris L.	6
Juncaginaceae *Triglochin maritima* L.	25
Alismataceae *Sagittaria* sp.	10
Hydrocharitaceae *Elodea canadensis* Michx.	6
Gramineae	
Puccinellia Nuttalliana (Schultes) Hitchc.	40
Glyceria grandis S. Wats.	31
Scolochloa festucacea (Willd.) Link	2
Distichlis stricta (Torr.) Rydb.	38
Hordeum jubatum L.	79
Calamagrostis canadensis (Michx.) Nutt.	15
Alopecurus aequalis Sobol.	11
Spartina gracilis Trin.*	2
Beckmannia syzigachne (Steud.) Fern.	36
Cyperaceae	
Eleocharis acicularis (L.) R. & S.	8
E. macrostachya Britt.	79
Scirpus americanus Pers.	38
S. validus Vahl.	35
S. paludosus Nels.	13
Carex spp.	75
Lemnaceae	
Lemna trisulca L.	13
L. minor L.	36
Juncaceae	
Juncus tenuis Willd.	2
J. balticus Willd.	60
Polygonaceae	
Rumex spp.	29
Polygonum spp.	29
Ceratophyllaceae	
Ceratophyllum demersum L.	10
Ranunculaceae	
Ranunculus subrigidus W. B. Drew	15
R. Cymbalaria Pursh	23
R. Gmelini DC.	2
Haloragaceae *Myriophyllum exalbescens* Fern.	71
Hippuridaceae *Hippuris vulgaris* L.	13
Umbelliferae *Sium suave* Walt.	13
Labiatae *Mentha arvensis* L.	10

*Specific name from Hitchcock (1950).

Methods and materials

Nomenclature and definitions

Nomenclature for vascular plants follows Fernald (1950). I have followed the common usage of the term "seed" as it usually includes the entire fruit of a plant. Borror and DeLong (1964) was used for Insecta and Pennak (1953) for other invertebrates. Names of birds are taken from American Ornithologists' Union (1957).

Some definitions of terms used here are needed because of the vast array of ecological terms referring to aquatic organisms and their habitats. I distinguish among three groups of invertebrates depending on where they are usually taken by feeding ducks. Bottom fauna are those associated with the bottom mud and the solid-liquid interface. Planktonic invertebrates are those occurring in the free water whether or not plants are present. Collectively, bottom fauna and planktonic invertebrates make up aquatic invertebrates. Surface invertebrates are those forms not normally occurring below the water surface and include terrestrial forms. When measuring proportions of aquatic and surface invertebrates eaten by ducks, I arbitrarily divided unidentified animal material proportionately between the two. The calculated proportion of invertebrates taken from the surface represents minimum figures because many aquatic forms such as Corixidae, Culicidae larvae and Dytiscidae are sometimes captured at the surface. Amphipods are often associated with bottom fauna. In this study I consider them plankton or, more properly, nektoplankton which are motile plankton (Hutchinson, 1967). They regularly occurred throughout the entire planktonic zone. Hutchinson (1967:696) cited studies which showed that *Gammarus pulex* lived as nektoplankton in closed Tibetan lakes which lacked fish.

I have departed from an apparent tradition by not including Trichoptera larval cases in the analysis. Some cases may contribute a minor amount of food but most are valueless. By eliminating cases, the weight of Trichoptera included is more realistic. The exclusion of cases makes a greater difference when the food is measured by weight rather than by volume because of the high specific gravity of much case material. In a sample of 159 Leptoceridae, larvae made up 20 per cent of the combined dry weight of larvae and cases. All these cases appeared to be made of fine sand.

Food of ducklings

Collection and treatment of material

We collected ducks for food study on the study area from 1963 through 1967. Most were shot and the rest were captured on land by a retriever dog. A usable specimen was one that contained at least 1 mg dry weight of food in the combined esophagus and proventriculus. In the first year most ducks were taken in early morning or evening, but enough were collected during midday to demonstrate a diurnal feeding pattern as reported by Chura (1963). The proportion of specimens with food (37 per cent) was significantly ($P < 0.01$) lower in those taken between 7:00 A.M. and 7:00 P.M. After 1963, no midday collections were made. Near the end of the study, as samples increased in number, we noted that a higher proportion of usable specimens were collected in evening than in morning (88 vs. 76 per cent; $P < 0.01$). The best evening collections were made at dusk on clear warm days. Ducks fed more throughout cool and overcast days and their activity did not peak at dusk, except on calm evenings preceded by wind and rain. After such storms considerable feeding activity was evident.

To ensure the highest possible proportion of usable specimens, I tried to collect only feeding ducks. Although this method increases the number of usable ducks, it does not guarantee food above the gizzard. I tried to restrict each collection to two to four ducklings. Sometimes one duck, collected and examined immediately, was not usable, so I took no further specimens. Generally, if one contained nothing, other members of the brood would be the same. Because the study involved a comparison of food used by four species, we collected more than one species at the same time and place when possible. Certain ponds proved more productive than others. Collections on these were restricted so that no pond contributed more than one-half of any species' plumage class, as defined by Gollop and Marshall (1954).

To eliminate post-mortem digestion that may take place in the digestive tract (Koersveld, 1951; Dillery, 1965), we injected about 50 drops of 10 per cent formaldehyde into the gullet with a rubber-tipped syringe within 10 minutes of the kill. Usually within 1 hour specimens were refrigerated or the digestive tracts were removed and frozen.

Specimens were weighed on a triple-beam balance and aged according to plumage classes (Gollop and Marshall, 1954). Lengths of culmen and tarsus were measured to the nearest millimeter (Dzubin, 1959). Although plumage classes were used as a guide to age of ducklings while collecting, they were not used in the final analysis because the time intervals[1] for each class vary among species, making quantitative comparisons difficult. Moreover, I found that I tended to overage specimens in the hand when using the technique which was developed for field observations. I used age categories based on weight as shown in Tables 2 to 5. The age-weight data are based on estimated growth curves. The Gadwall curve was derived from six ducks raised from hatching to flying in an outside pen. The results agreed well with weights of wild Gadwalls of comparable plumage classes and were similar to those of Oring (1968) who presented data for a small number of hatchery-raised Gadwalls. I obtained the age-weight figures for Pintails and Widgeons from growth curves based on weight at hatching (Smart, 1965), mean weight of Class III ducks collected during the study and the assumption that the growth pattern is similar to that of Gadwalls. The Lesser Scaup growth curve was derived from aver-

[1] Gollop and Marshall, 1954. See tables 15, 17, 18, 19 of this report for age ranges of Pintails, Gadwalls, American Widgeons, Lesser Scaups in each plumage class.

Table 2
Pintail data. By age group for weights; numbers of specimens, collections and collecting sites; animal and plant food dry weights; and the largest percentage contribution of one collection to each food type. (The number of specimens in each collection is shown in parentheses.)

	Age, days							
	0-5	6-10	11-15	16-20	21-30	31-40	41+	Totals
Weight, g	to 50	51-120	121-220	221-350	351-560	561-670	671+	
Usable specimens	10	25	18	14	38	14	25	144
Collections	5	14	10	12	23	12	18	77
Different sites	5	14	9	12	19	9	17	54
Total animal food, g	0.894	3.529	4.345	1.984	9.693	8.881	13.518	42.844
Total plant food, g	0.020	0.132	0.407	0.447	15.383	0.834	13.321	30.544
Avg wt of total food, g/duck	0.091	0.146	0.264	0.174	0.660	0.694	1.074	0.510
Range in food wt, g/duck	0.002–0.297	0.002–1.175	0.024–0.926	0.011–0.659	0.011–2.118	0.001–7.547	0.003–10.214	0.001–10.214
Largest % contribution of one collection:								
animal food	33(1)	55(3)	39(2)	31(1)	21(1)	79(1)	72(1)	39(2)
plant food	*	30(1)	57(3)	49(2)	66(3)	64(1)	86(2)	37(2)
total food	32(1)	54(3)	38(2)	27(1)	49(3)	78(1)	52(2)	24(2)

* Insufficient material.

Table 3
Gadwall data. By age group for weights; numbers of specimens, collections and collecting sites; animal and plant food dry weights; and the largest percentage contribution of one collection to each food type (The number of specimens in each collection is shown in parentheses.)

	Age, days							
	0-5*	6-10	11-15	16-20	21-30	31-40	41+	Totals
Weight, g	to 45	46-100	101-165	166-280	281-510	511-650	651+	
Usable specimens	22	32	35	31	15	14	18	167
Collections	11	16	14	12	8	8	9	60
Different sites	8	14	10	10	8	8	9	32
Total animal food, g	0.445	0.878	2.010	0.967	0.050	0.303	0.066	4.719
Total plant food, g	0.027	0.631	0.839	3.652	2.279	6.131	7.372	20.931
Avg wt of total food, g/duck	0.021	0.047	0.081	0.149	0.155	0.460	0.413	0.154
Range in food wt, g/duck	0.001–0.086	0.001–0.253	0.001–0.589	0.001–0.496	0.007–0.591	0.009–1.345	0.002–1.547	0.001–1.547
Largest % contribution of one collection:								
animal food	27(3)	48(4)	78(4)	49(3)	†	94(3)	†	32(4)
plant food	†	61(2)	35(4)	45(7)	57(3)	44(3)	21(1)	13(2)
total food	26(3)	28(2)	65(4)	36(7)	56(3)	56(3)	21(1)	12(3)

* Weight of 0- to 3-day-old ducks estimated to 33 g; 4- to 5-day-old ducks, 34 to 45 g.
† Insufficient material.

Table 4
American Widgeon data. By age group for weights: numbers of specimens, collections and collecting sites; animal and plant food dry weights; and the largest percentage contribution of one collection to each food type (The number of specimens in each collection is shown in parentheses.)

	Age, days							
	0-5	6-10	11-15	16-20	21-30	31-40	41+	Totals
Weight, g	to 44	45-90	91-150	151-255	256-460	461-590	591+	
Usable specimens	8	29	13	12	20	25	22	129
Collections	3	16	8	7	9	15	14	58
Different sites	3	11	8	6	8	14	14	38
Total animal food, g	0.780	2.392	0.965	0.083	0.043	0.065	0.156	4.484
Total plant food, g	0.005	0.065	0.114	1.541	2.301	4.787	3.210	12.023
Avg wt of total food, g/duck	0.098	0.085	0.083	0.135	0.117	0.194	0.153	0.128
Range in food wt, g/duck	0.047–0.216	0.001–0.373	0.005–0.239	0.010–0.371	0.004–0.497	0.003–0.779	0.001–0.908	0.001–0.908
Largest % contribution of one collection:								
animal food	51(3)	26(2)	41(2)	*	*	*	94(3)	14(2)
plant food	*	*	47(1)	54(3)	29(4)	32(3)	57(3)	21(4)
total food	51(3)	26(2)	37(2)	54(3)	29(4)	32(3)	54(3)	15(4)

* Insufficient material.

Table 5
Lesser Scaup data. By age group for weights; numbers of specimens, collections and collecting sites; animal and plant food dry weights; and the largest percentage contribution of one collection (The number of specimens in each collection is shown in parentheses.)

	Age, days							
	0-5	6-10	11-15	16-20	21-30	31-40	41+	Totals
Weight, g	to 45	46-90	91-150	151-230	231-395	396-535	536+	
Usable specimens	19	22	15	16	24	23	16	135
Collections	7	10	9	9	12	15	11	45
Different sites	7	10	7	7	11	10	7	24
Total animal food, g	0.716	1.059	1.092	4.085	4.760	13.786	7.198	32.696
Total plant food, g	0.004	0.006	0.017	0.008	0.439	0.228	0.409	1.111
Avg wt of total food, g/duck	0.038	0.048	0.074	0.256	0.217	0.609	0.475	0.250
Range in food wt, g/duck	0.001–0.151	0.002–0.195	0.002–0.567	0.001–0.621	0.005–2.459	0.005–3.155	0.003–1.361	0.001–3.155
Largest % contribution of one collection:								
animal food	57(3)	45(3)	52(1)	49(4)	52(1)	48(3)	35(3)	20(3)
plant food	*	*	*	*	79(3)	51(1)	56(2)	42(4)
total food	57(3)	45(3)	51(1)	49(4)	47(1)	42(1)	33(3)	19(3)

* Insufficient material.

age weights of 13 ducks reared in the outside pen. Comparisons with weights and plumages of wild Scaups indicated similar growth rates. I collected flying young only in Pintails and assigned these to the oldest age group regardless of weight. To calculate the composition of the prefledgling diet, I assumed 50 days represented the flightless period for the four species.

In the laboratory, contents of esophagi and proventriculi were sorted separately[2] into weighing pans, identified, oven-dried for 12 to 18 hours at 80°C and weighed to the nearest 0.1 mg on a Type H4 Mettler balance. Grit was not included. Because of bias caused by different rates of digestion of different foods in the gizzard (Dillon, 1959; Perret, 1962), gizzard material was not used. James Bartonek (pers. comm.) believed that similar bias could result from use of proventriculus material and for that reason I tabulated data for esophagus and proventriculus contents separately and compared them with results for combined samples.

Sample size

Davison (1940) and Hanson and Graybill (1956) have discussed methods for determining sample size in food habit studies. As in most waterfowl diet studies, practical considerations rather than statistical requirements dictated sample sizes in this study. After the first season it was apparent that amounts and composition of food recovered from ducks were so variable that one would have to make serious inroads upon the duck population of the study area to satisfy acceptable statistical standards. Probably no species' population on the area could sustain the rate of collection needed to obtain an adequate sample in 5 years. Thus, for each species, I set an arbitrary objective of a minimum of 10 ducks, each with at least 10 mg dry weight of food, for each of the seven plumage classes (Gollop and Marshall, 1954). These would be in addition to usable specimens containing less than 10 mg. At the other extreme, an arbitrary objective was set to collect enough birds so that no collection contributed more than 35 per cent of the total food weight in any plumage class. More often than not, this objective was not met.

Samples meeting the above quota would permit, among the various plumage classes, such comparisons as plant vs. animal foods, surface invertebrates vs. aquatic invertebrates, etc.

Expression of results

Hartley (1948) and Bartonek (1968) have reviewed methods for measuring diet composition. Because moisture in duck foods varies widely — from about 10 to 90 per cent — I chose to oven-dry and weigh them and express results as percentage of dry weight. This also facilitated conversion of data into terms of gross energy. I also calculated percentage of occurrence of each food item because, in combination with weight data, this method can reveal bias caused by inadequate samples. It may also show which items are eaten regularly but incidentally to more important foods. Although not considered a problem here, differential digestion rates of foods influence percentage of occurrence data less than volumetric or gravimetric data. For comparative purposes, diet composition is also expressed in terms of percentage of calorific (gross) energy contributed by each food. Calorific values were obtained for the more important foods in connection with nutritional analyses. Values for other items were taken from averages compiled by Cummins and Wuycheck (1971). Ideally, the relative importance of different foods would best be expressed in terms of metabolizable energy contributed. However, reliable values for wild waterfowl foods are not available.

I calculated the composition of the prefledgling diet by weighting the percentage of weight data according to the total estimated percentage of food actually eaten by each subsample or age group. This compensated for unequal numbers of specimens in different age groups and the fact that food intake did not increase with age at the same rate as average weight of food recovered from ducks. (For example, a 40-day-old duck ate about four times as much as a 10-day-old duck, but average[3] weight of food recovered was about eight times greater.) Thus, if diet composition changes with age — one aspect under study — the two factors could bias unweighted diet estimates for the entire prefledgling period. Estimates of the food consumption are based on intake of a commercial diet eaten by captive Lesser Scaups (Sugden and Harris, 1972), and the scant information in the literature (Sincock, 1962; Penney and Bailey, 1970). Scott and Holm (1964) concluded that basic food requirements were the same for diving and dabbling ducks, so the use of Scaup data seems justified for all species. A peak in food intake, which accompanies the latter stages of exponential growth at 5 to 7 weeks, has been found in Mallards (Jordan, 1953), Black Ducks (*Anas rubripes*) (Penney and Bailey, 1970), and Lesser Scaups (Sugden and Harris, 1972), but does not appear in figures 1 to 4. The fact that a knoll is not shown in the food intake curves, should not significantly affect estimates for the prefledgling diet composition.

Factors affecting food use

Feeding behaviour

In early morning and in evening when activity was highest, I observed feeding broods to determine methods and locations used by different ages of each species. These observations were not associated with birds collected for food analysis. I observed a brood for 10 minutes (min.) at a time, if possible, and for not more than 30 min. during 1 day. After each 1 min. of observation I recorded activity of the majority of the brood, their feeding method, water depth at the feeding site and the type of plants — emergent or submerged. Feeding methods were categorized as follows: diving, dabbling in mud (including tipping up), surface feeding, subsurface feeding in water, pecking at

[2] In 1963, contents of esophagi and proventriculi were not separated.

[3] Weights of food recovered from Widgeons and Pintails differed less.

Figure 1. Changes in plant and animal food intake by young Pintails.

Figure 2. Changes in plant and animal food intake by young Gadwalls.

Figure 3. Changes in plant and animal food intake by young American Widgeons.

Figure 1

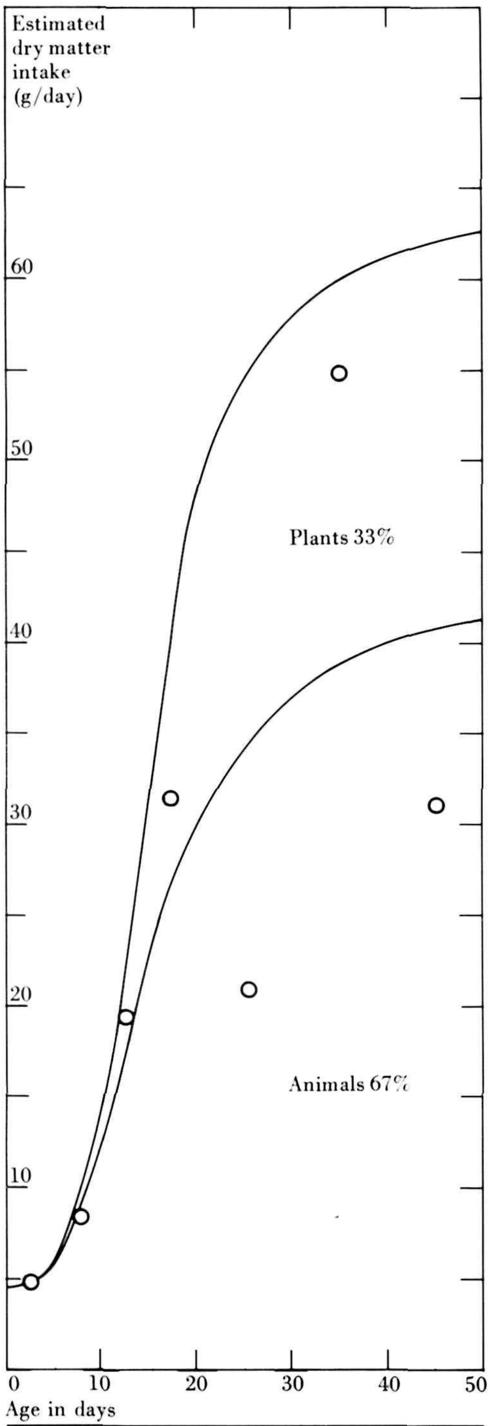


Figure 2

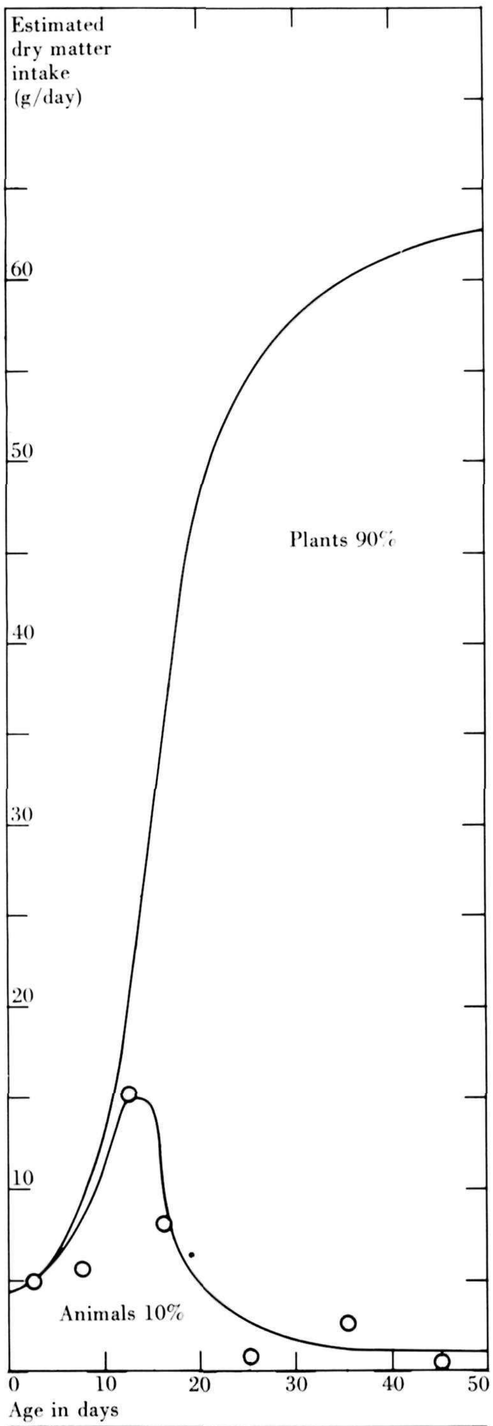


Figure 3

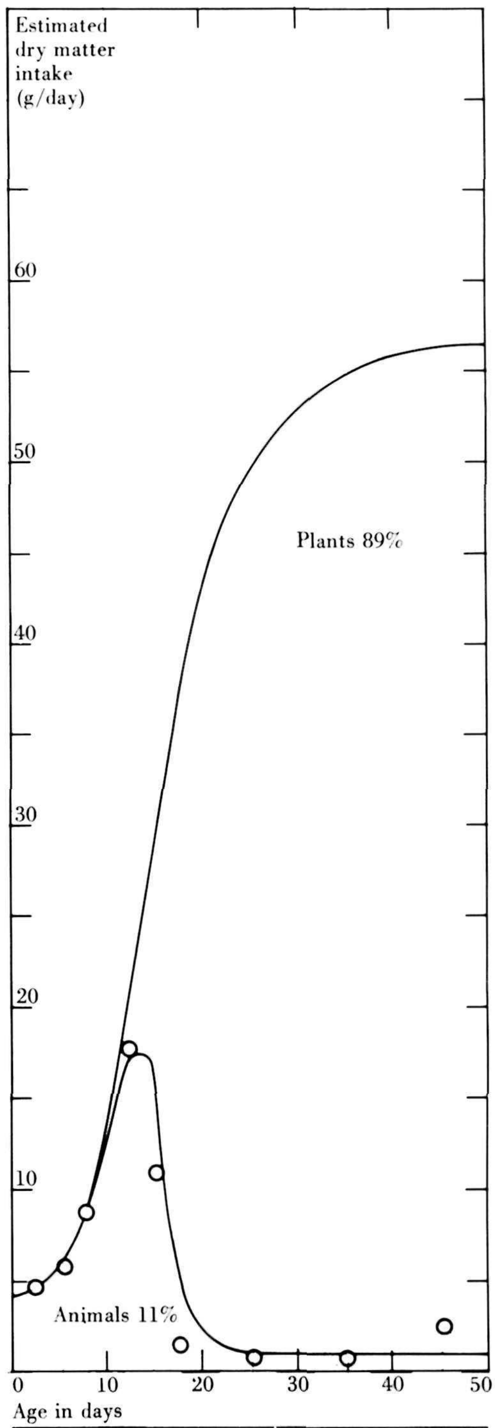
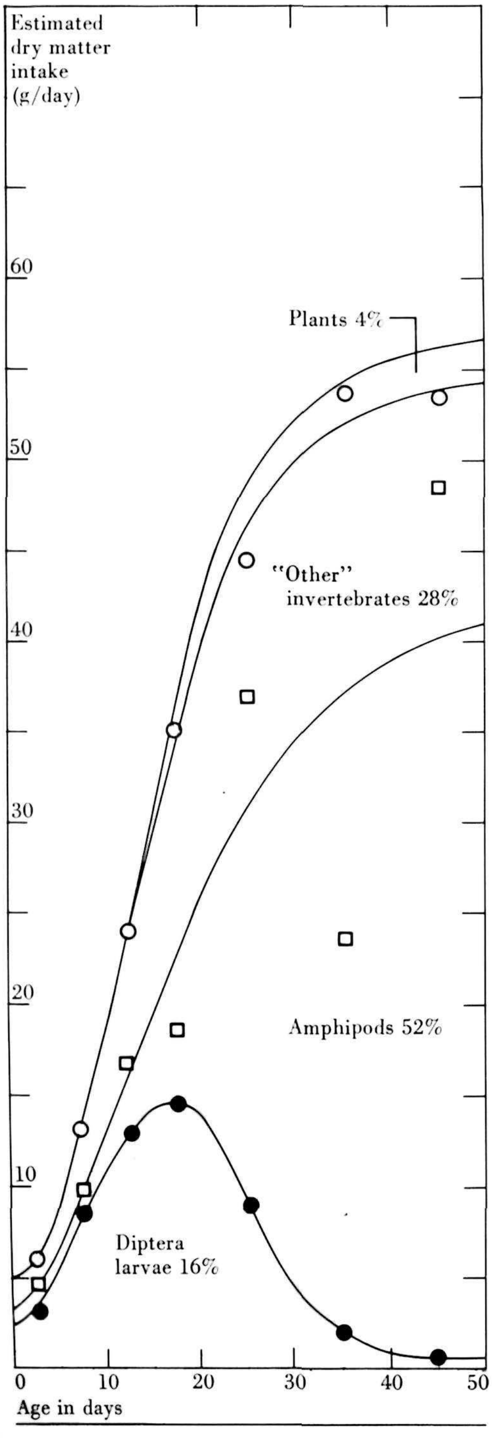


Figure 4. Trends in the diet of average Lesser Scaup ducklings.

Figure 4



emergent plants, feeding on mud flats and chasing flying insects. Water depth and plants were checked after the 10-minute observation period if not obvious at the time.

The categories of feeding methods are largely those associated with the different feeding zones — above water, water surface, subsurface water, bottom mud and mud flat — and do not always reflect the method of ingesting food. Goodman and Fisher (1962:35) divided anatids into two groups, based on feeding methods. One group uses a *grasping-action* to secure most of its food and includes grazers, such as Widgeons. The second group, which includes Scaups, uses the *straining-action* that involves a rapid opening and closing of the jaws. Both groups use a *gaping-action* at times — "...an opening and closing of the jaws that is simultaneous with the forward thrust of the head, to move large pieces of food back into the pharynx and possibly to enlarge the pharyngeal cavity." At a distance I could seldom determine which method a duck was using when it fed below the surface.

To increase the number of usable observations, I arbitrarily assigned 5 minutes to each observation when details could be noted but when it was not possible to watch a brood for any length of time, e.g., when broods became frightened and stopped feeding shortly after being sighted. This was justified because observations had shown that the features being measured changed little over a 30-minute period.

The feeding activity data were weighted to obtain averages for the prefledgling period in the same way as diet data. To do this, I assumed that different foraging methods were equally efficient. The assumption is not entirely valid; however, differences should not be great enough to obscure broad comparisions.

To supplement field data, I observed Lesser Scaup ducklings feeding in an aquarium. In addition to general observations on Scaup feeding behaviour, I made six tests using different pre-counted live aquatic invertebrates. The ducks were allowed to feed for a predetermined time, after which the uneaten items were counted. The relative selection rate was measured.

Food sampling

To compare foods in the diet with foods in the habitat, I sampled aquatic invertebrates at each site where ducks containing significant amounts of animal foods had been shot. It was possible to sample within 15 minutes of most collections. The two methods used to sample invertebrates available to ducks are similar to those described by Bartonek and Hickey (1969b). I sampled planktonic organisms with a mesh cone having an 8.3 inch (21 cm) opening. A piece of nylon mesh was fastened to the small end to collect each sample. A *sweep* consisted of passing the cone through 10 feet (3 m) of water which sampled about 35 cubic feet (1 m^3). I tried to sample those zones available to ducks, considering the species, age and characteristic method of feeding. When sampling for dabbling ducks which had been feeding on or close to the surface of deep water, I sampled close to the surface including some of the surface zone. Conversely, samples for Scaups were taken by making an arcing sweep from surface to bottom to surface.

I sampled bottom fauna with a 6-sq-inch (15.2-cm^2) Eckman dredge during the first 3 years, and later I took sweep samples which included mud bottom. Initially, and with little success, I tried to separate organisms from the bottom debris by immersing the sample in a sugar solution with a specific gravity of 1.12 (Anderson, 1959). Most samples were preserved in their entirety and sorted by screening and hand-picking in the laboratory. Invertebrate samples were oven-dried and weighed in the same way as samples of food recovered from ducks. I pooled the weight data from samples for each collection site and expressed the composition of invertebrates in percentage of dry weight. Usually four samples were taken at a collection site although it varied from one to 16. A comparison of food in the diet with food available could be no better than the data gained from the duck specimens, so more intensive food sampling would add little precision.

I obtained data on available plant foods in two ways. Each of 52 water areas randomly selected from the 95 collecting sites was thoroughly searched and plant species present recorded. This provided an estimate of the percentage of occurrence for each species on the study area.

To measure plant cover where collected ducks had been feeding I used a 1-foot-square (30-cm-square) frame (divided into 100 equal squares with a wire grid) placed at about 1-yard (1-meter) intervals along a transect crossing the area occupied by the ducks, usually from shore part way out. The percentage of area covered by each plant species was used for comparison with plant foods found in the ducks. When ducks have been feeding on plants it is difficult to set limits for measuring the food available to them. Whether one samples the entire pond or only the vicinity of the feeding site can make a considerable difference in the ratios of *available* plant foods. I sampled the vicinity of the feeding site, and that seems to have been the best approach, though occasionally I missed an item eaten by the ducks.

Selection categories

To measure the degree to which ducks selected different items, I compared diet composition and relative abundance of foods sampled at collecting sites. Animal and plant foods were compared separately. To obtain food rankings, data from several collections are customarily pooled but this is justified only when the various features — the collecting period, collecting area and species' food niches — are relatively restricted. My study did not meet these conditions. I collected ducks over a 5-year period at many different sites, often containing different foods and in varying proportions. Each duck species used several feeding zones and classes of foods. I used different methods to sample bottom fauna, planktonic fauna and plants. The results from these different measurements are not comparable in terms of density or availability of foods. Also, significant correlations between food present in the habitat and food eaten for a single collection may be obscured when data are pooled. Consequently, I chose to calculate food ranks based on individual collections and, rather than pool original data, combined individual results. In each collection for which there were usable specimens as well as food measurements, I assigned each major item in the ducks and field samples to a selection category based on the ratio of the item in the diet to the item in the field samples as follows:

$$\frac{\text{Per cent of item in diet}}{\text{Per cent of item as available}}$$

Percentage of dry weight was used for eaten samples and samples of available aquatic invertebrates, and percentage of all cover measured along the transect was used for available plant samples. I arbitrarily chose nine categories with the following ranges: (1) 0.01–0.22, (2) 0.23–0.44, (3) 0.45–0.66, (4) 0.67–0.88, (5) 0.89–1.14, (6) 1.15–1.52, (7) 1.53–2.27, (8) 2.28–4.55 and (9) 4.56–100.00. Since 1.00 was to occupy a central position, there would be 4.5 categories below it and 4.5 above. Using percentages no lower than 1, there are 99 possible values below 1.00 (i.e., 0.01 to 0.99, inclusive), or a range of 0.22 per category; hence the ranges shown above. Ranges for categories above 1.00 are the reciprocals of corresponding values below it. Thus if a selection rating of 0.25 (20 per cent in diet/80 per cent in field sample) were reversed, the value becomes 4.00 (80 per cent in diet/20 per cent in field sample). The first value in this sample falls in category (2) the second in (8). To give the results greater significance, I ranked only those items occurring in either ducks or field samples in proportions greater than 3 per cent. A separate category (0) was used to designate those items present (over 3 per cent) but not eaten. Higher categories reflect positive selection on the part of the ducks. Average selection ratings were calculated by weighting the observation on the basis of category numbers, i.e., a rating falling in category (9) carried the weight of 9, one in category (8), the weight of 8, etc.

Feeding overlap

To measure overlap between two species, one must compare their diets quantitatively as well as such factors as feeding sites, feeding methods and season of use (MacArthur, 1958). Using the method of Horn (1966) and Orians and Horn (1969), I calculated for each combination of two species, overlap of diets, methods of feeding, range of water depths at feeding sites and the feeding sites (emergent plants, submerged plants, open water, mud flat).

Diet overlap between two species, X and Y, in which the percentage of food *i* in each is represented by x_i and y_i, respectively, is calculated from the formula:

$$\text{Overlap} = \frac{2\underset{i=1}{\Sigma}xy}{\underset{i=1}{\Sigma}x^2 + \underset{i=1}{\Sigma}y^2}$$

Overlap calculated this way can vary from 0, with no overlap, to 1.00, with complete overlap. When feeding methods, water depths and feeding sites used by each species are reduced to percentages, overlap for these factors can be calculated in the same way. If proportions of food items obtained from the different sites or habitats are estimated, total overlap between two species can be calculated (Orians and Horn, 1969). My data are insufficient for this purpose.

Nutrient composition of duck foods

Foods for chemical analysis were collected from the field in a fresh state. Prior to drying, invertebrates were placed in a 1 per cent solution of boric acid for about 5 hours to reduce loss of nitrogen (Alex Dzubin, pers. comm.). Foods were oven-dried at 65°C for 24 hours, or, in the case of some plant material, air-dried in the sun. Proximate analyses for moisture, crude protein (nitrogen x 6.25), crude fat (ether extract), crude fibre, ash, calcium and phosphorous were contracted to the Provincial Analyst,

Results

University of Alberta. The nitrogen free extract (N.F.E.) part of the carbohydrate content was calculated by subtracting the sum of percentages for protein, fat, fibre, moisture and ash from 100. The Department of Animal Science, University of Alberta, measured gross energy by oxygen bomb calorimeter. The Chemistry Department, Utah State University, made amino acid determinations.

Food of ducklings

Source of material

In 5 years I collected 175 Pintails, 213 Gadwalls, 153 American Widgeons, and 165 Lesser Scaups. Specimens containing usable amounts of food comprised 82 per cent of Pintails, 78 per cent of Gadwalls, 84 per cent of Widgeons and 82 per cent of Scaups. The lower average for Gadwalls resulted from those taken in 1963 (60 per cent of 91 were usable) before improved techniques were developed. After 1963, 92 per cent of the Gadwalls were usable. Larger birds contained more food on the average so more older than younger ducklings were usable, though the difference was slight. Males made up 49 per cent in Pintail, 47 in Gadwall, 52 in Widgeon and 53 in Scaup.

Ducks were collected from 95 sites (water areas). The numbers of usable specimens and collecting sites for each species are shown in Tables 2 to 5. All four species were collected (not necessarily simultaneously) on each of 4 sites, three species on 13 sites, two on 22 sites and one on 56 sites. Seven was the maximum number of collections for one species from one site during the study (Table 6). For a single year, the maximum number of collections from one site was four each for Pintail and Gadwall, three for Widgeon and five for Scaup. Collecting periods for each species' age groups (Table 7) do not necessarily represent the actual dates when each category of duckling was most abundant because collections were sometimes selective.

Sources of error

Excessive amounts of one food

In his study of surface feeding ducks, Coulter (1955) found a major source of error in the occurrence of a few specimens containing large amounts of one food. Such distortions occurred in all species in the present study. There was also a marked similarity of food composition in all specimens from any one collection; thus an entire collection could be considered a sampling unit. This illustrates the group behaviour characteristic of many vertebrates (Etkin, 1964).

Table 6
Frequency of collections from different sites for usable specimens

Number of collections per site	Number of sites for Pintail	Gadwall	Widgeon	Scaup
1	39	19	26	11
2	6	8	8	8
3	4	2	3	3
4	2	1		1
5		3		1
6	1			
7			1	
Total sites	52	33	38	24

The influence of excessive amounts of one food was measured in terms of the maximum percentage contribution of a single collection to the various food-type–age-group situations (Tables 2–5). More often than not, the largest contribution exceeded the arbitrary 35 per cent objective. Not all such collections caused distortions in final results because some involved items which were commonly found in the ducks in question. Some individual collections did, however, have a significant influence on the final breakdown of diet composition (Table 8). This indicates the large samples needed to obtain accurate estimates in waterfowl diet studies.

Proventriculus material

Comparisons of several items found in esophagi, proventriculi and the two combined are made in Table 9. Items chosen for comparison are those that would be expected to reflect differences in digestion rates between the two organs should they occur. That is, soft material would disappear first and therefore occur in lower proportions in the proventriculi if more digestion took place there. The distribution of items in the esophagus and proventriculus was similar in all species. Proportionately more seeds occurred in the proventriculi. These were mostly nutlets of *Scirpus*, *Potamogeton*, *Myriophyllum*, *Carex* and *Eleocharis*. Diptera larvae were also highest in that organ. Conversely, gastropods tended to be proportionately lower in proventriculi. Per-

Table 7
Collecting periods for seven age groups of four duckling species

Age group in days	Pintail	Gadwall	American Widgeon	Lesser Scaup
0– 5	June 2–June 30	July 9–July 29	June 29–July 30	July 9–Aug 11
6–10	June 2–July 17	July 10–July 30	June 25–Aug 12	July 7–Aug 13
11–15	June 2–July 6	June 30–July 30	July 6–July 26	July 20–Aug 22
16–20	June 8–July 26	July 9–Aug 15	July 5–July 28	July 24–Aug 18
21–30	June 21–Aug 16	July 26–Sept 1	July 18–Aug 13	July 29–Sept 3
31–40	July 7–Aug 23	July 26–Sept 13	Aug 2–Sept 6	Aug 3–Sept 15
41+	June 29–Aug 12	Aug 8–Sept 14	Aug 4–Sept 11	Aug 21–Sept 15

Table 8
The influence of some individual collections on percentages of certain food items in the diets of four duckling species shown by comparing values before and after the collections have been excluded (tr < 0.5%)

Species	No.* of Collections	No.* of Specimens	Food item	% of total dry food Before	% of total dry food After†
Pintail	1	2	Gastropoda	36	15
	1	2	*Hordeum vulgare*	9	0
	1	3	*Puccinellia* seeds	6	1
Gadwall	2	2	Cladocera	2	tr
	1	4	Coleoptera larvae	3	tr
	1	2	Cladophoraceae	19	12
	1	3	*Beckmannia* seeds	10	1
	1	3	*Potamogeton pusillus*	34	28
	1	3	*Ceratophyllum demersum*	3	0
Widgeon	1	3	*Carex lanuginosa*	9	0
	1	3	Cladophoraceae	18	11
	1	4	*Potamogeton pusillus*	47	39
Scaup	1	3	Gastropoda	16	4

*Total numbers of usable specimens and collections are given in Tables 2 to 5.

†Percentages would vary if more than one collection were eliminated.

centages of adult Coleoptera differed little between the two organs.

Because one would not use proventriculus contents alone for food study, but rather esophagus material alone or the combined samples, proportions for the latter are included for comparison. Necessarily, differences are less than those between esophagus and proventriculus proportions. For the most part, minor items are involved. A higher proportion of an item in the proventriculus does not prove that other items disintegrated faster. It may simply mean that certain items — nutlets in particular — pass down the esophagus into the proventriculus faster. Seeds were higher by percentage of dry weight in the proventriculus, but gastropods and adult beetles were similar or lower in that organ. Such hard-bodied invertebrates are among the most resistent to gizzard digestion (Perret, 1962), so they should also occur in higher proportions in the proventriculus if differential digestion is a fact. Moreover, dipterous larvae — principally chironomids — were equal or even higher in the proventriculi and since these would be among the most susceptible to digestion, the observed ratios indicate an absence of differential digestion. If seeds do move down the esophagus faster than other items, then not including proventriculus material could introduce bias. But if the accumulation of seeds in the proventriculus is caused by their slower passage into the

Table 9
Comparison of some food proportions in esophagi and proventriculi, separately and combined in Pintail, Gadwall, Widgeon and Scaup ducklings.

Item, %	Pintail (141)* Esoph.	Proven.	Comb.	Gadwall (117) Esoph.	Proven.	Comb.	Widgeon (120) Esoph.	Proven.	Comb.	Scaup(127) Esoph.	Proven.	Comb.
Plant food	33.7	34.3	33.8	80.0	83.6	81.6	70.6	74.4	72.5	1.0	6.5	3.4
Scirpus nutlets	0.8	7.5	1.9									
Potamogeton nutlets	0.3	2.2	0.6									
All seeds	32.4	33.1	32.5	3.0	7.8	5.2	3.1	6.6	4.8	0.3	4.5	2.1
Gastropods	37.5	21.6	35.0	0.2	0.1	0.1				25.1	16.3	21.3
Coleoptera adults	0.8	1.3	0.9	0.8	0.7	0.8	0.8	1.3	1.0	0.4	0.4	0.4
Diptera larvae, pupae	14.2	25.6	16.0	2.5	3.7	3.1	5.1	4.7	4.9	13.5	17.0	15.0
Total dry weight of food, g	52.2	9.7	61.9	12.1	10.2	22.3	7.6	7.5	15.1	18.5	14.0	32.5

* Number of specimens.

gizzard, then proventriculus material would add bias, though not because of differential digestion. Furthermore, it is possible that the injection of preservative into the gullet helped to flush small items into the proventriculus.

For these reasons and because differences between esophagus and combined proportions were small and involved minor items, there was no justification for excluding proventriculus material. Including it increased the food weight and number of usable specimens, respectively, by 19 and 22 per cent in Pintail, 84 and 27 per cent in Gadwall, 98 and 28 per cent in Widgeon, and 75 and 55 per cent in Scaup. The relatively small contribution of Pintail proventriculus material is probably because the Pintail's longer neck provides relatively more storage capacity in its esophagus.

Pintail foods

During the first 5 days Pintails ate chiefly surface invertebrates and, as they grew, consumed greater proportions of aquatic invertebrates and plants (Table 10). Surface invertebrates made up about 4 per cent of the prefledgling diet. Altogether, Pintails ate more than half animal food on the average (Table 10, Fig. 1), though the ratio was extremely variable. I estimated the average intake of animal food during the first 50 days as 67 per cent of the total diet (dry weight). Proportions of animal and plant foods eaten by Pintails during each of their first five 10-day periods (Table 11) were calculated from figure 1 with a dot grid. All Pintails ate some animal food during their first 15 days and two-thirds continued to do so during the last 20 days of the flightless period (Table 12). The use of plant food was almost the reverse.

Pintails ate many kinds of invertebrates, though a few accounted for most of the animal diet (Table 13). Gastropods made up 36 per cent by weight of the total diet, but as one collection contributed so much of the gastropod weight (Table 8), the estimate is too high. Moreover, the contribution of gastropods to a duck's nutrition tends to be

Table 10
Percentages of surface invertebrates (SI), aquatic invertebrates (AI), and plant foods (PF) eaten by different age groups of four duckling species (tr < 0.5%).

Age group, days	Pintail (144)*			Gadwall (167)			American Widgeon (129)			Lesser Scaup (135)		
	SI	AI	PF	SI	AI	PF	SI	AI	PF	SI	AI	PF
0– 3	73	25	2	74	26	0	79	20	1	3	96	1
4– 5				41	48	11						
6–10	14	83	3	24	34	42	62	35	3	3	97	tr
11–15	19	72	9	56†	15	29	55	34	11	tr	98	2
16–20	2	80	18	2	19	79	3	2	95	1	99	tr
21–30	4	35	61	tr	2	98	1	1	98	1	91	8
31–40	1	91	8	3	2	95	1	1	98	tr	98	2
41+	tr	50	50	tr	1	99	4	tr	95	0	95	5
Prefledgling avg.	4	63	33	5	5	90	7	4	89	1	95	4

* Number of specimens.
† Curculionid larvae in four ducks made up 88 per cent of total surface invertebrates.

Table 11
Percentage dry weight intake of animal and plant food by 10-day periods in four duckling species (tr < 0.05%)

Age period, days	Percentage of 50-day intake											
	Pintail (144)*			Gadwall (167)			Widgeon (129)			Scaup (135)		
	Animal	Plant	Total	Animal	Plant	Total	Animal	Plant	Total	Animal	Plant	Total
0 –10	3.3	0.1	3.4	2.3	1.1	3.4	3.2	0.1	3.3	5.0	tr	5.0
11–20	10.3	3.9	14.2	5.6	8.5	14.1	5.5	8.8	14.3	14.9	0.1	15.0
21–30	15.9	9.5	25.4	0.6	24.8	25.4	0.5	24.8	25.3	22.2	2.0	24.2
31–40	18.1	9.8	27.9	1.3	26.7	28.0	0.4	27.7	28.1	27.0	0.4	27.4
41–50	19.0	10.1	29.1	0.3	28.8	29.1	1.3	27.7	29.0	26.9	1.5	28.4
Totals	66.6	33.4	100.0	10.1	89.9	100.0	10.9	89.1	100.0	96.0	4.0	100.0

*Number of specimens.

Table 12
Frequency of animal and plant foods occurring in seven age groups of four duckling species.

Age group, days	Percentage with animal food				Percentage with plant food			
	Pintail	Gadwall	Widgeon	Scaup	Pintail	Gadwall	Widgeon	Scaup
0 – 5	100	100	100	95	50	23	25	26
6 –10	100	94	100	95	76	72	37	14
11–15	100	86	100	100	89	71	77	33
16–20	93	100	83	100	93	90	100	31
21–30	92	73	65	96	95	100	100	58
31–40	71	71	48	91	93	100	92	70
41+	60	67	45	94	96	95	96	75
Sample size	144	167	129	135	144	167	129	135

Table 13
Diet composition of young Pintails (P), Gadwalls (G), Widgeons (W), and Scaups (S), expressed as percentages of dry weight, frequency of occurrence and gross energy (tr < 0.5%)

	Dry weight				Occurrence				Gross energy			
Item	P	G	W	S	P	G	W	S	P	G	W	S
Nematoda*	tr		tr		5		8		tr		tr	
Hirudinea*	tr	tr		1	2	1		7	tr	tr		1
Crustacea												
Cladocera*	4	2	tr	1	26	26	6	9	3	1	tr	1
Podocopa*	tr	tr	tr	tr	13	5	1	4	tr	tr	tr	tr
Eucopepoda*	tr	tr	tr		1	2	1		tr	tr	tr	
Amphipoda*	tr	tr	tr	52	3	2	1	34	tr	tr	tr	56
(Crustacea subtotal)	(4)	(2)	(tr)	(53)	39	30	9	41	(3)	(1)	(tr)	(57)
Insecta												
Collembola*	tr	tr	tr		6	9	3		tr	tr	tr	
Ephemeroptera adults†	tr	tr	1		3	2	4		tr	tr	tr	
Ephemeroptera naiads*	tr	tr	tr	tr	2	1	1	7	tr	tr	tr	tr
Anisoptera naiads*	1			tr	8			1	2			tr
Zygoptera adults†	tr	tr	1	tr	4	2	4	1	tr	tr	1	tr
Zygoptera naiads*	1	tr	tr	3	10	5	2	19	2	tr	tr	4
Thysanoptera†		tr		tr		1		1		tr		tr
Orthoptera†	1				2				2			
Mallophaga†	tr				1				tr			
Hemiptera*†	tr	1	1	3	23	34	26	44	tr	1	1	4
Homoptera†	tr	tr	tr	tr	10	2	5	3	tr	tr	tr	tr
Coleoptera adults*†	1	tr	tr	tr	37	28	23	18	2	1	tr	1
Coleoptera larvae*†	1	3	tr	1	37	22	6	20	2	4	tr	2
Trichoptera adults†	tr	tr	1	tr	10	5	12	2	tr	tr	1	tr
Trichoptera larvae*	2			2	14			20	3			4
Lepidoptera adults†			tr				4				tr	
Diptera adults†	2	2	4	tr	40	45	38	15	4	2	5	tr
Diptera larvae, pupae*	16	2	1	16	66	59	37	57	22	2	1	18
Hymenoptera†	tr	tr	tr	tr	5	7	5	5	tr	tr	tr	tr
Unidentified Insecta*†	tr	tr	tr	tr					tr	tr	tr	tr
(Insecta subtotal)	(26)	(8)	(9)	(26)	86	85	71	86	(39)	(11)	(11)	(33)
Arachnoidea												
Araneida†	tr	tr	tr		8	1	1		tr	tr	tr	
Hydracarina*	tr	tr	tr	tr	10	7	4	10	tr	tr	tr	tr
Gastropoda*	36	tr	2	16	35	4	2	16	10	tr	tr	4
Unidentified animal food*†	tr	tr	tr	tr					tr	tr	tr	tr
Total animal food	67	10	11	96	88	88	74	96	53	12	11	95
Cladophoraceae	tr	19	18	tr	7	23	16	2	tr	16	16	tr
Characeae *chara* sp.												
foliage		3				2				3		
oögonia				1				1				1
Cyanophyceae	tr	tr		tr	3	1		1	tr	tr		tr
Musci	tr	tr	tr		1	1	1		tr	tr	tr	
Equisetaceae *Equisetum* sp. stem	tr				1				tr			

cont'd

Item	Dry weight				Occurrence				Gross energy			
	P	G	W	S	P	G	W	S	P	G	W	S
Typhaceae *Typha* sp. seeds	tr				1				tr			
Zosteraceae												
Potamogeton pectinatus												
foliage		1	1			3	2			1	1	
spikes		tr	1			4	3			1	1	
tubers	tr	tr	tr		1	1	2		tr	tr	tr	
Potamogeton pusillus												
foliage	tr	34	47		3	31	32		tr	33	46	
spikes		3	tr			3	2			3	tr	
buds	tr	tr	tr		3	2	2		tr	tr	tr	
Potamogeton Richardsonii												
foliage		tr	tr			1	2			tr	tr	
spikes		tr	3			2	2			tr	4	
Potamogeton sp.												
foliage	tr	tr	tr	tr	1	5	2	2	tr	tr	tr	tr
nutlets	1	tr	tr	tr	18	5	9	10	1	tr	tr	1
Zannichellia palustris foliage, seeds	2	2	1	tr	10	11	2	1	2	2	tr	tr
Juncaginaceae *Triglochin* sp. seeds	1				1				1			
Gramineae												
Puccinellia Nuttalliana seeds	6	tr	2	tr	6	1	5	1	8	tr	2	tr
Glyceria sp. seeds	tr				1				tr			
Distichlis stricta seeds	tr				6				tr			
Agropyron sp. seeds	tr				3				tr			
Hordeum jubatum seeds	2	tr	tr	tr	13	1	1	4	3	tr	tr	tr
Hordeum vulgare grain	9				1				12			
Agrostis sp. seeds	tr	tr			3	1			tr	tr		
Alopecurus aequalis seeds	tr	1			2	2			tr	1		
Beckmannia syzigachne seeds	1	10	tr		5	2	3		2	11	tr	
Unidentified Gramineae												
seeds	tr	tr			2	1			tr	tr		
foliage	tr	tr			1	1			tr	tr		
(Gramineae subtotal)	(19)	(11)	(2)	(tr)	21	4	9	4	(25)	(12)	(2)	(tr)
Cyperaceae												
Eleocharis sp. nutlets	4	tr	tr	tr	15	3	1	1	6	tr	tr	tr
Scirpus spp. nutlets	3	2	1	tr	57	10	8	8	5	tr	tr	tr
Carex lanuginosa perigynia, nutlets			9				2				11	
Carex spp. nutlets	1	tr	tr	tr	28	2	7	1	1	tr	tr	tr
(Cyperaceae subtotal)	(8)	(2)	(10)	(tr)	60	13	13	10	(12)	(tr)	(11)	(tr)
Lemnaceae												
Lemna trisulca		tr	1			5	4			tr	1	
Lemna minor	tr	7	4		4	13	7		tr	7	4	
Juncaceae *Juncus balticus* seeds	tr				3				tr			
Polygonaceae												
Eriogonum sp. seeds	tr				3				tr			
Rumex maritimus achenes	tr	tr		tr	5	1		1	tr	tr		tr
Polygonum spp. achenes	tr	tr		tr	8	1		1	tr	tr		tr

cont'd

Item	Dry weight P	G	W	S	Occurrence P	G	W	S	Gross energy P	G	W	S
Ceratophyllaceae												
Ceratophyllum demersum foliage		3	tr			2	1			3	tr	
Chenopodiaceae *Chenopodium* sp. seeds	tr	tr		tr	16	2		6	tr	tr		tr
Leguminosae *Medicago* sp. seeds	tr				1				tr			
Ranunculaceae												
Ranunculus subrigidus foliage		1		tr		2		1		1		tr
Ranunculus Cymbalaria foliage			tr				2				tr	
Haloragaceae												
Myriophyllum exalbescens												
foliage	tr	tr	tr	tr	3	7	5	6	tr	tr	tr	tr
spikes		tr				2				tr		
nutlets	1	tr	tr	2	18	1	1	23	2	tr	tr	3
Caprifoliaceae												
Symphoricarpos sp. nutlets	tr				3				tr			
Compositae												
Cirsium sp. achenes	tr				1				tr			
Sonchus sp. achenes		tr				1				tr		
Taraxacum sp. achenes	tr	tr	tr		4	1	1		tr	tr	tr	
Unidentified foliage	1	1	1	tr					1	2	1	tr
Unidentified seeds	tr	tr	tr	tr					tr	tr	tr	tr
Total plant food	33	90	89	4	88	78	78	44	47	88	89	5
Number of specimens	144	167	129	135	144	167	129	135	144	167	129	135

* Aquatic invertebrates.
† Surface invertebrates.

overrated when presented on a gravimetric basis because of their relatively high ash content. This relationship is apparent when weight and calorific percentages are compared in Table 13.

Insects made up 26 per cent of the total diet. Most important were dipterans which contributed 18 per cent.[4] Of that, larvae and pupae made up 16 per cent. A breakdown of insect orders shows that Chironomidae (15 per cent) was the dominant Diptera family (Table 14). Insect orders of lesser importance were Odonata (2 per cent), Coleoptera adults and larvae (2 per cent) and Trichoptera larvae (2 per cent) (Table 13).

Cladocerans were the only crustaceans eaten in significant amounts (4 per cent) by young Pintails.

Three downy Pintails collected by Munro (1944) in British Columbia contained 99 per cent Zygoptera naiads by volume.

[4] Unless otherwise specified, percentage of total prefledgling diet.

Most plant foods in Pintails less than 15 days old were seeds that the ducks probably had ingested accidentally while feeding on invertebrates, particularly bottom fauna. There appeared to be no deliberate selection of plant foods during the first 2 weeks. As they grew, Pintails selected more plant material as evidenced by relatively large amounts that could not have been swallowed accidentally. Plants made up 33 per cent of the diet and of that, seeds and nutlets comprised 30 per cent (Table 13). Grass (Gramineae) seeds contributed 19 per cent. The 9 per cent estimate for barley (*Hordeum vulgare*) is probably high as it was all found in two specimens (Table 8). *Puccinellia* seeds made up 6 per cent of the diet, *Hordeum jubatum* 2 per cent and *Beckmannia* 1 per cent. Grass seeds formed a major part of the diet of Pintails wintering in Louisiana (Glasgow and Bardwell, 1962). At Gem, Alberta, Keith (1961) examined stomach contents of 19 adult Pintails, 9 flying young and 33 flightless young. Seeds of aquatic plants made up the bulk of the identifiable material in the three groups and very few grass seeds had been eaten. Munro (1944) reported on stomach contents of 45 fall and winter adult Pintails collected in British Columbia — 25 from the interior and 20 from the coastal region. In a few specimens grass seeds constituted a minor part of the recovered food.

Fallen seeds from previous years made up about 10 per cent of the Pintails' diet in this study. Cyperaceae contributed 8 per cent of these seeds as follows: *Eleocharis* 4, *Scirpus* 3 and *Carex* 1 per cent. Because such hard-coated fruits are not easily digested (Bartonek, 1968), their nutritional value may be much less than indicated by consumption rate.

A variety of items, foliage and attached seeds of *Zannichellia* and winter buds of *Potamogeton pusillus* predominating, made up the remaining 3 per cent of plant food.

Seven of the 41+ day group Pintails were flying young — six taken in late July and one in early August. They had eaten essentially the same as flightless ducks of the same age group. Perret (1962) found significantly more plant food in a sample of eight young Mallards which could fly (early August) than in their flightless counterparts. He attributed it to their greater access to fields. Flying adult and young Pintails in the Strathmore area characteristically fed on sites similar to those used by flightless ducks. Several times they were seen feeding together. I observed no field feeding by ducks in July or August during this study; however, there was relatively less land in grain in the Strathmore area. Significantly, the only two Pintails that had eaten cultivated barley were flightless. They were taken from a roadside ditch and had apparently eaten spilled barley.

In summary, Pintails ate about 67 per cent invertebrates during the prefledgling period. Although a wide variety was eaten, gastropods and dipterous larvae accounted for half the total diet. Surface invertebrates comprised 73 per cent of the diet during the first 5 days but gradually were replaced by aquatic invertebrates and plants. Seeds and nutlets dominated the plant portion of the diet and accounted for 30 per cent of the prefledgling diet. Most prevalent were seeds of Gramineae and Cyperaceae.

Gadwall foods

Gadwalls showed a trend from a predominantly invertebrate diet immediately after hatching to an almost exclusive plant diet after 3 weeks of age (Table 10, Fig. 2). None of six ducks considered less than 3 days old contained plant material. The frequency of plant food increased with age and after 3 weeks, over 90 per cent had eaten plants (Table 12). Chura (1961) reported a trend from an animal to plant food diet for young Mallards at Bear River Refuge, Utah, though the transition was not as rapid. The comparison is not entirely valid because Chura used gizzard material and Dillon (1959) and Perret (1962) have shown that the practice overrates plant proportions. The fact that the plant food in Chura's Mallards was mostly seeds of aquatic plants further indicates distortion. Although the proportion of animal food in the Gadwall diet decreased as the ducks grew, the actual intake of animal food would not start to decrease until about 2 weeks of age due to the rapidly increasing food intake (Fig. 2). Close to 80 per cent of the prefledgling animal food was eaten during the first 20 days, with about half taken in the 11- to 20-day period (Table 11). Intake of plant food increased until about 3 weeks of age when it levelled off. Altogether, Gadwalls ate 10 per cent animal and 90 per cent plant food.

Animal food eaten by Gadwalls during their first 3 days was mostly surface invertebrates (Table 10). After 3 days of age, the ducklings ate more aquatic invertebrates. Although invertebrates make only a small contribution to the prefledgling diet, ducklings depend on them almost entirely during their first few days. Close to 80 per cent of the animal food eaten by Gadwalls was insects (Table 13), primarily Diptera and Coleoptera. One dipterous family, Chironomidae, was dominant and made up about one-third of the animal food (Table 14). The families Curculionidae, Dytiscidae and Haliplidae accounted for most of the Coleoptera eaten by Gadwalls. Four ducks contained unusually large numbers of curculionid larvae (Table 8) that had infested immature spikes of *Myriophyllum* and *Potamogeton* which were also eaten. The contribution of Coleoptera larvae may thus be overrated. Corixidae comprised most of the Hemiptera eaten by Gadwalls.

Cladocera made up about 16 per cent of the animal food. Most of the Cladocera occurred in two specimens (Table 8), and the high frequency in Gadwalls (Table 13) resulted from trace amounts in many. The ingestion of such minor amounts — sometimes a single ephippium — probably occurred incidentally to swallowing other foods.

Gadwalls ate proportionately more plant food as they grew and plants made up 90 per cent of the diet (Table 13). *Potamogeton* foliage was the most important item and of that, *P. pusillus* contributed 34 per cent. Leaves of aquatic plants were also important in the autumn diet of Gadwalls in Utah (Gates, 1957). In that study, Gadwalls ate *P. pectinatus*, *Ruppia maritima* and *Zannichellia palustris*. Keith (1961) examined stomach contents of 12 adult, 3 flying young and 3 flightless young Gadwalls collected near Gem, Alberta. He believed that foliage of *Potamogeton pusillus* and *P. Friesii* were among the most important foods eaten by those specimens.

Green alga (Cladophoraceae), at 19 per cent, was the second most important plant food in the Strathmore Gadwall diet, followed by *Beckmannia* seeds (10 per cent) and *Lemna minor* (7 per cent). The percentage for *Beckmannia* may be too high because one duck contained most of the seeds recovered (Table 8). Single collections contained considerable quantities of some items: leaves of *Chara*, *Ceratophyllum* and *Ranunculus;* current seeds of *Alopecurus;* and immature spikes of *Potamogeton pectinatus* infested with curculionid larvae. Leaves and attached seeds of *Zannichellia* and *Scirpus* nutlets each contributed 2 per cent to the diet.

To recapitulate, Gadwalls ate chiefly surface invertebrates during their first few days. These were replaced by aquatic invertebrates and plants as they grew. By 3 weeks of age the ducks were essentially vegetarian. Insects dominated the animal diet, with chironomid larvae being the most important. *Potamogeton pusillus* foliage and Cladophoraceae were the most important plants and contributed 34 and 19 per cent, respectively. I estimated the average prefledgling Gadwall diet as containing 10 per cent animal and 90 per cent plant food.

American Widgeon foods

Animal foods dominated the Widgeon diet at first but were largely replaced with plants by 3 weeks of age (Table 10, Fig. 3). About 80 per cent of the animal food was taken during the first 20 days of the flightless pe-

Table 14
Some invertebrate families and their percentage of dry weight contribution to the total diets of four duckling species (tr < 0.05%)

Item	Pintail		Gadwall		Widgeon		Scaup	
Hemiptera		(0.136 g)*		(0.255 g)		(0.234 g)		(0.986 g)
Corixidae		0.1		0.6		0.6		2.9
Notonectidae				tr				0.1
Gerridae		tr		tr				
Miridae						tr		
Lygaeidae		tr		tr		tr		
Saldidae		tr		tr		tr		tr
Mesoveliidae		tr						
	adults	larvae	adults	larvae	adults	larvae	adults	larvae
Coleoptera	(0.656 g)	(0.633 g)	(0.189 g)	(1.467 g)	(0.135 g)	(0.188 g)	(0.117 g)	(0.340 g)
Carabidae	tr		tr					
Haliplidae	tr	tr	tr	0.1	0.1	tr	0.1	0.7
Dytiscidae	0.3	0.6	0.1	0.1	tr	tr	0.2	0.3
Noteridae	tr							
Gyrinidae	tr							
Silphidae		0.1						
Hydrophilidae	0.1	0.1	tr	tr	tr		0.1	tr
Staphylinidae	tr		tr					
Elateridae	tr							
Malachiidae								
Heteroceridae	tr							
Coccinellidae	tr							
Anthicidae							tr	
Scarabaeidae	tr		tr					
Curculionidae	0.6		0.3	2.7	0.1	0.2	tr	
Trichoptera (larvae)		(1.053 g)						(0.904 g)
Phryganeidae								0.1
Limnephilidae		0.1						tr
Leptoceridae		1.5						2.4

cont'd

riod (Table 11). By 30 days, the food intake had almost levelled off and comprised mostly plants. As they grew, fewer Widgeons ate animal food and more ate plants (Table 12).

The ratio of surface invertebrates to aquatic invertebrates declined with age of ducks, though the former remained more important throughout the flightless period (Table 10). The diet contained 11 per cent animal food—7 per cent surface and 4 per cent aquatic invertebrates. The animal food eaten by Widgeons was 82 per cent insects (Table 13). Diptera—adults, pupae and larvae—made up 48 per cent of the animal food; no other insect order contributed more than 10 per cent. Chironomids were the most common adult dipterans, ceratopogonids (chiefly pupae) and chironomids the most common immature dipterans (Table 14).

Gastropods comprised 14 per cent of the animal diet but only three of 129 ducks ate them; thus, the percentage may be too high. Widgeons ate trace amounts of crustaceans.

Munro (1949) reported that 10 stomachs of downy American Widgeons collected in British Columbia contained 88 per cent (by volume) animal matter, chiefly insects.

The Widgeon diet contained 89 per cent plant material and the composition of the plant diet did not change as the ducks grew. Older birds contained a greater variety because they ate more plants more frequently. *Potamogeton pusillus* foliage, the most important item, made up 47 per cent of the total diet, followed by Cladophoraceae at 18 per cent (Table 13). The 9 per cent for *Carex lanuginosa* is probably too high since three ducks from one collection accounted for all of it (Table 8). Other plants that contributed at least 1 per cent were: *Lemna minor* and *L. trisulca*, *Potamogeton Richardsonii* and *P. pectinatus* (principally spikes), *Puccinellia* seeds, *Zannichellia* foliage and seeds and *Scirpus* nutlets.

Item	Pintail		Gadwell		Widgeon		Scaup	
	adults	1 + p†	adults	1 + p	adults	1 + p	adults	1 + p
Diptera	(1.670 g)	(11.133 g)	(0.563 g)	(0.896 g)	(1.121 g)	(0.812 g)	(0.035 g)	(4.947 g)
Tipulidae		0.8	tr					
Psychodidae		tr						
Culicidae	tr	0.2	tr	tr		tr		0.1
Ceratopogonidae	tr	0.2	tr	0.2	0.1	0.8		
Chironomidae	2.0	13.6	1.5	1.6	3.8	0.5	0.2	15.3
Mycetophilidae			tr					
Stratiomyidae	tr	0.5			tr			0.1
Tabanidae		0.3	0.1					
Dolichopodidae	tr		tr		tr			
Sepsidae					tr			
Syrphidae	tr	0.5						
Otitidae			tr					
Ephydridae	tr	0.5	tr	tr	tr	tr		
Chloropidae	tr		tr		tr			
Anthomyiidae	0.1		0.1		0.1			
Gastropoda		(21.806 g)		(0.027 g)		(0.286 g)		(7.510 g)
Physidae		31.6		0.1				1.9
Lymnaeidae		3.9				1.1		13.7
Planorbidae		0.4		tr		0.4		tr

* Weight of identified material. † l = larvae, p = pupae.

Keith's (1961) opinion concerning the importance of *Potamogeton* foliage to Gadwalls apparently also held for a similar number of Widgeon specimens pooled with the Gadwall sample. In interior British Columbia, Munro (1949) found that stomachs of 38 adult Widgeons collected during autumn contained 6 per cent (by volume) animal matter, 29 per cent alga and 65 per cent *vegetation*. Major foods included *Potamogeton, Utricularia, Ceratophyllum, Elodea* and *Chara;* the last four were insignificant or absent in this study.

In summary, invertebrates dominated the Widgeon diet up to 2 weeks. By 3 weeks, they were eating over 90 per cent plants, and an estimated 89 per cent of the prefledgling diet comprised plants. Surface invertebrates were more important than aquatic invertebrates throughout the flightless period, particularly during the first 10 days. Insects made up 82 per cent of animal food. The major plant items were *Potamogeton pusillus* and Cladophoraceae which contributed 47 and 18 per cent, respectively, to the total diet.

Lesser Scaup foods

Flightless Scaup ducklings in this study ate principally animal food (Tables 10, 11, Fig. 4) as did young Scaups in Manitoba (Bartonek and Hickey, 1969a) and near Yellowknife, Northwest Territories (Bartonek and Murdy, 1970). Animal food—entirely invertebrates—comprised 96 per cent of the Strathmore Scaup diet. More than 90 per cent of Scaups in all age groups ate animal food (Table 12). Unlike the three dabbling species, Scaup ducklings did not make heavy use of surface invertebrates in early life, though they did spend considerable time surface feeding. This disparity will be discussed under *Feeding behaviour*. Figure 4 shows diet changes with ages of Scaups. As they grew, the ducks ate higher proportions of amphipods, mostly at the expense of dipterous larvae. Cause of the change is discussed under *Food selection*.

The most important item in the diet of Scaups was Amphipoda which made up 52 per cent (Table 13). Insects contributed 26 per cent, with dipterous larvae being most important (16 per cent). Chironomids were the principal dipterans eaten (Table 14). Other insect orders eaten in significant amounts were Hemiptera (3 per cent and chiefly corixids), Zygoptera naiads (3 per cent) and Trichoptera larvae (2 per cent, mainly leptocerids). Coleoptera, principally haliplids and dytiscids, made up 1 per cent. Gastropods formed 16 per cent of the diet (12 per cent from one collection). Cladocerans were eaten in appreciable amounts by three Scaups from two collections and made up 1 per cent of the diet.

Scaup ducklings of all ages ate only 4 per cent plant food (Tables 10, 13). Most of the plant material came from six ducks in two collections which contained *Chara* oögonia and *Myriophyllum* nutlets, respectively.

Strathmore Scaups ate food similar to that of 25 young collected in Manitoba by Bartonek and Hickey (1969a). There, amphipods, gastropods and Tendipedidae (chironomid) larvae formed 49, 39 and 8 per cent by volume, respectively, of all food eaten. Amphipods and chironomid larvae were the most important items in 14 adults in the same study. The diet of 39 adult

Scaups from the Manitoba pothole area was also dominated by amphipods (Rogers and Korschgen, 1966). Similarly, Munro (1941) found chiefly amphipods in stomachs of 15 young and 9 adult Lesser Scaups collected in British Columbia. Amphipods were also major items eaten by 108 adults from the Saskatchewan River Delta (Dirschl, 1969). However, Dirschl noted seasonal differences and during the July to September period amphipods were secondary to other foods, principally Hirudinea and *Nuphar*. Bartonek and Murdy (1970) reported that 19 Class Ia–IIa Scaups collected during late July and early August in the Northwest Territories ate mostly culicid larvae and pupae (54 per cent by volume) and Conchostraca (30 per cent), and 19 Class IIa–III Scaups collected in early September had eaten mostly amphipods (57 per cent), odonate naiads (17 per cent) and corixids (11 per cent). In contrast to these results, amphipods were insignificant in stomachs of 17 juveniles collected by Cottam (1939) in the Prairie Provinces; the bulk of the food was insects. Cladocerans, which comprised 1 per cent of the Strathmore Scaup diet, were not found in Manitoba Scaups by Bartonek and Hickey (1969a) though trace amounts of cladoceran ephippia were found in a few. In the Northwest Territories, cladocerans contributed 8 per cent of the food in 23 adult Scaups, but only trace amounts in 38 juveniles (Bartonek and Murdy, 1970). Three of 39 adults examined by Rogers and Korschgen (1966) had eaten significant amounts of adult Cladocera.

In summary, Scaups ate 96 per cent invertebrates. Dipterous larvae were important to early age classes but older ducklings ate more amphipods. Altogether, amphipods contributed 52 per cent; insects 26 per cent; and gastropods 16 per cent.

Table 15
Feeding activity by Pintail broods. Figures show percentage of observations (tr < 0.5%)

	Age class						
	Ia	Ib	Ic	IIa	IIb	IIc	III
Age in days*	1-5	6-12	13-18	19-23	24-33	34-43	44-51
Number of broods	12	11	9	11	5	10	10
Total observations†	165	148	97	207	52	124	135
Feeding method							
Surface	84	51	28	tr			
Subsurface:							
bill-dip	14	7	21	24		10	
head-duck		1	24	25	37	10	34
tip-up						25	
Bottom:							
head-duck						22	5
tip-up		30	15	44	63	33	57
Diving	1	9		6			4
Peck at emergent plant	tr	tr				tr	
On mud flat	1	1	12				
Chase flying insect	tr	1					
Maximum depth at site							
0– 6 in. (0–16 cm)	26	32	20	27	10	32	50
7–12 in. (17–31 cm)	47	42	33	47	90	30	16
13–18 in. (32–46 cm)	23	24	35	12		22	23
19–24 in. (47–62 cm)	4	2		9		16	11
25–30 in. (63–77 cm)				5			
31–36 in. (78–92 cm)			12				
Feeding site							
Open water	36	56	36	23	60	9	48
Emergent plants	48	27	21	48	13	36	19
Submerged plants	15	16	31	29	27	55	33
Mud flat	1	1	12				

* From Gollop and Marshall (1954).
† One observation per minute.

Factors affecting food use

Feeding behaviour

Pintail feeding

Young Pintails used a variety of methods to secure food (Tables 15, 16). They frequently fed among emergent plants where they were not readily observed so I may have underestimated the amount of activity there. Class Ia ducks fed mostly by pecking items from the water surface. This is the gaping-action of Goodman and Fisher (1962). Surface feeding was not observed in Class IIb and older Pintails. Diet data (Table 10) show, however, that older Pintails ate some surface invertebrates. Subsurface feeding either by dipping the bill, ducking the head or tipping up, and bottom feeding by head-ducking or tipping, gradually replaced surface feeding.

Of 68 Pintail broods on which I made feeding observations, seven included ducklings that were diving for food. I cannot recall seeing them diving during numerous unrecorded observations in the past. Johnsgard (1965) and Kear and Johnsgard (1968) reported that mature Pintails frequently dived for food, though Smith (1966) did not observe any diving during a 3-year study. The abundance of shallow water and submerged vegetation in the Strathmore areas used by Pintails may have reduced the incidence of diving.

As expected, water under 12 inches (31 cm) deep was favoured by feeding Pintails. Virtually all bottom feeding occurred there. Feeding activity was about evenly distribu-

Table 16
Feeding activity by four duckling species. Figures show percentage of observations weighted on the basis of prefledgling food intake (tr < 0.5%)

	Pintail	Gadwall	Widgeon	Scaup
Feeding method				
Surface	5	12	22	1
Subsurface	39	86	74	0
Bottom	53	2	3	0*
Diving	2	0	0	99
Miscellaneous	1	tr	1	tr
Maximum depth at surface				
0– 6 in. (0– 16 cm)	29	8	12	0
7–12 in. (17– 31 cm)	45	29	28	0
13–18 in. (32– 46 cm)	17	44	19	11
19–24 in. (47– 62 cm)	8	11	35	60
25–30 in. (63– 77 cm)	tr	7	5	23
31–36 in. (78– 92 cm)	1	1	1	2
37–42 in. (93–107 cm)	0	0	0	2
43–48 in. (108–122 cm)	0	0	0	2
Feeding site				
Open water	37	6	7	53
Emergent plants	26	6	10	tr
Submerged plants	36	87	82	46
Mud flat	1	tr	tr	0

*An unknown amount of bottom feeding would be recorded as *diving*.

ted among sites with no vegetation, sites with emergent plants and sites with submersed plants. Surface feeding appeared unrelated to the presence of vegetation, but caution must be used when relating feeding activity to such features as depth and vegetation because other factors such as the proximity of escape cover and the feeding behaviour of the hen also influence duckling distribution.

The manner in which Pintail ducklings obtained grass seeds illustrates their adaptability in securing food. Most *Hordeum jubatum* was apparently taken from the pond bottom while the ducks fed on other items. In at least one collection, *Beckmannia* seeds were also taken by bottom feeding. In other cases, I assumed that seeds floating on the water had been strained out by the ducks. *Beckmannia* on the study area usually grew tall and in most cases the spikes would be out of reach of a duckling. Pintails apparently strip the seeds from *Puccinellia* and, possibly, *Alopecurus*. I have not seen them do this, but duck tracks, dislodged seeds and stripped spikes evinced this method. Nowhere have I seen enough fallen seeds to account for large quantities sometimes eaten. Evidently Canada Geese (*Branta canadensis*) commonly strip grass seeds from plants, particularly *Poa* (Hanson, 1965).

Gadwall feeding

Class Ia–Ib Gadwalls fed most often from the water surface (Table 17). The rest of the time they fed just below the surface, principally by the bill-dip method. There is little difference between surface feeding and bill-dipping below the surface and often a brood used both methods. The high incidence of surface feeding by Class I ducklings explains the dominance of surface invertebrates in their diet. The ducks largely replaced surface feeding with subsurface feeding as they grew. This change paralleled the diet change from invertebrates to plants.

About 73 per cent of Gadwall feeding occurred where water was 7 to 18 inches (17 to 46 cm) deep (Table 16). The data do not show any trends with changing age of ducks. Whether the depths over which Gadwalls fed reflect random use of existing depths is unknown. However, the 8 per cent use shown for the 0- to 6-inch (0- to 16-cm) zone is considerably less than the actual area occupied by that zone in the ponds so it appears they tended to avoid the shallow zone.

Feeding sites (emergent plants, submersed plants and open water) varied with age of ducks. Class Ia and Ib Gadwalls fed at random at least with regard to open water and submersed plants, the per cent use being similar to proportions estimated from vegetation transects. This kind of use would be expected for ducks which eat chiefly surface invertebrates. As the ducks grew and ate more aquatic invertebrates and plants, they fed less on open water and more over submersed aquatics. Such plants attract and provide habitat for aquatic invertebrates (Moyle, 1961; Sculthorpe, 1967) and, perhaps more significantly, are selected as food, particularly by older Gadwalls.

I estimated that 16 per cent of the animal food eaten by Class I Gadwalls was chironomid larvae. Though usually considered bottom fauna, these slow-moving larvae were invariably collected in sweep samples in water; similarly they could be captured by ducklings. I conclude that most chironomid larvae eaten by small Gadwalls were taken from the water near the surface. The complete absence of Trichoptera larvae in Gadwalls in contrast to Pintails and Scaups also indicates little bottom feeding.

American Widgeon feeding

Surface feeding, prevalent in the early Widgeon age classes, was replaced largely by subsurface feeding and bottom feeding was negligible (Table 18). My observations confirm data which showed that Class Ia Widgeons ate mostly surface insects while older age classes concentrated on aquatic

Table 17
Feeding activity by Gadwall broods. Figures show percentage of observations (tr < 0.5%)

	Age class						
	Ia	Ib	Ic	IIa	IIb	IIc	III
Age in days*	1-6	7-14	15-18	19-27	28-38	39-44	45-50
Number of broods	9	7	10	8	8	8	10
Total observations†	122	120	115	110	80	132	144
Feeding method							
Surface	94	76	44		9		7
Subsurface:							
bill dip	6	24	22	60	71	48	30
head-duck			8	26	20	22	5
tip-up				14		30	58
Bottom:							
head-duck			26				
Peck at emergent plant						tr	
Chase flying insect		tr					tr
On mud flat							tr
Maximum depth at site							
0– 6 in. (0–16 cm)	3		26	18			15
7–12 in. (17–31 cm)	26	54	24	18	28	48	19
13–18 in. (32–46 cm)	50	17	33	36	72	36	24
19–24 in. (47–62 cm)	13	17		15		8	28
25–30 in. (63–77 cm)	8	12		13		8	14
31–36 in. (78–92 cm)			17				
Feeding site							
Open water	16	23	8	4	4		13
Emergent plants	7	4	1			19	14
Submerged plants	77	73	91	96	96	81	73
Mud flat							tr

*From Gollop and Marshall (1954).
†One observation per minute.

plants. In a Michigan study of duck broods, Beard (1964) reported that American Widgeon ducklings at first fed mostly by surface feeding and dabbling (bill-dipping?). After 4 weeks of age they also began tipping for food, but Beard did not say whether it involved bottom feeding. Tipping in this study involved both subsurface and bottom feeding, though the former was more prevalent.

Feeding Widgeons tended to avoid the shore. Munro (1949) commented on this preference for areas free of emergent plants and suggested it was an adaptive behaviour related to the species' commensal association with diving ducks and coots. He stated that the commensal association began soon after the Widgeons hatched, though the amount of food obtained during summer in this way was much less than that obtained in autumn and winter. I suggest that the Widgeon's preference for water free of emergent plants is primarily an adaptation to its plant diet. Plants sought by Widgeons are not restricted to the shallow margins of ponds and, moreover, occur less frequently among emergent plants. Thus, it is to the species' advantage to seek food over the entire pond. The two characteristics—preference for plant food and preference for open water—have permitted the Widgeon to develop the commensal association with diving ducks. Such an association was not observed in this study, probably because the principal diving duck, Lesser Scaup, was carnivorous. Also, plants eaten by Widgeons were readily available.

As the ducks grew, they fed more over submersed plants. Again, the feeding sites changed as the diet changed from surface insects to aquatic plants. Younger ducklings tended to feed more at random, indicating that their food was more or less distributed throughout the entire pond habitat. Indeed, it was not uncommon to see members of a Class I brood scattered widely over a pond (e.g., up to 10 acres [4 ha]), simultaneously surface feeding on areas of open water, submersed plants, emergent plants and a variety of water depths.

Lesser Scaup feeding

After 1 week of age, Scaups obtained virtually all their food by diving (Table 18). Although I did not observe it, diet samples showed that Class II Scaups occasionally took surface insects. Scaup ducklings could make dives of short duration within a day or so after hatching. Dives by Class Ia ducks usually lasted 3 to 4 seconds and most were apparently shallow. Bartonek and Hickey (1969b) observed a 3-day-old Scaup remain submerged in a tank for 9 seconds. Dives by Class II and III Scaups averaged about 6 seconds in this study. Duration of dives appeared related to water depth and perhaps the mode of feeding. Deeper water and bottom feeding are probably associated with longer dives. On one occasion, Class IIb ducks, known to be bottom feeding in about 4 feet (1.2 m) of water, averaged 14 seconds per dive. Those were the longest dives timed and occurred on one of the deepest ponds. Maximum depth measured on each of 17 Scaup collecting sites varied from 18 to 54 inches (0.46 to 1.37 m) and averaged 29 inches (0.74 m). Bartonek and Murdy (1970) found diet differences between Class I–IIa and IIa–III Scaups and suggested that the older ducks may have fed at greater depths. Sites used by feeding Scaups in that study averaged about 4 feet (1.2 m) in depth.

The diet of Class Ia Scaups and their observed methods of feeding showed little correlation. Over 40 per cent of their feeding took place on the surface, yet less than 5 per cent of their food contained items that occurred there. That this disparity resulted from different ingestion rates was evident on several occasions when ducklings which had been actively surface feeding were collected, only to find little or no food in them. Generally, ducklings which had been diving contained more food. The observed feeding activity was not a reliable index to food intake in this case and surface feeding was less efficient than diving for food.

Feeding Scaups preferred deeper areas of ponds probably because plants were sparse or absent in those areas. Data from vegetation surveys showed there was a high probability that open water occurred in the deeper zones of ponds. The feeding site data in Tables 16 and 19 suggest that the absence of submersed plants is not why deeper areas are choosen. However, during observations it was seldom possible to evaluate densities of submersed plants and, if any plants were in the vicinity of the ducks, they were simply recorded as present. Such a crude measurement would not reveal patches of open water present on many ponds. Whether or not the ducks were diving among submersed plants was a rather subjective consideration.

Bartonek and Hickey (1969b) reported that most of the lymnaeid and physid snails eaten by Canvasbacks and Redheads were crushed and the shell material washed away. Scaups in my study did not do this and gastropods were intact when removed from the esophagi and proventriculi. This was also true for the three dabbling duck species.

Table 18
Feeding activity by American Widgeon broods.
Figures show percentage of observations (tr < 0.5%)

	Age class						
	Ia	Ib	Ic	IIa	IIb	IIc	III
Age in days*	1-7	8-12	13-18	19-26	27-35	36-41	42-50
Number of broods	12	10	8	6	6	6	7
Total observations†	152	155	112	100	102	102	142
Feeding method							
Surface	75	79	57	13	34	10	3
Subsurface:							
bill-dip	14	21	36	62	42	33	48
head-duck	1			12	8	43	38
tip-up				13	13	2	11
Bottom:							
tip-up					3	12	
Peck at emergent plant		tr	7				tr
Chase flying insect	10		tr				tr
On mud flat				tr			
Maximum depth at site							
0– 6 in. (0–16 cm)	tr			50	3	12	
7–12 in. (17–31 cm)	3	11	32	23	3		75
13–18 in. (32–46 cm)	38	23	28	12	20	29	11
19–24 in. (47–62 cm)	30	56	31	15	74	39	11
25–30 in. (63–77 cm)	11	10				20	3
31–36 in. (78–92 cm)	18		9				
Feeding site							
Open water	35	25	30	13			3
Emergent plants	24	20	9	15	17	5	2
Submerged plants	41	55	61	72	83	95	95
Mud flat				tr			

*From Gollop and Marshall (1954).
†One observation per minute.

Food selection

To understand why ducks eat certain foods and not others, one must first compare the food they eat with that which is available. The comparison is made under the assumption that food sampling data reflect the relative availability of items present. The assumption is not always valid because standard sampling methods fail to duplicate activities of a feeding duck. So-called indexes of preference must be interpreted with this in mind. Probably the greatest shortcoming occurs when foods must be sampled by more than one method because more than one feeding zone or category of food is involved. How much area of water surface is equivalent to a cubic meter below the surface in terms of available food? How much mud bottom must be sampled to equal a cubic meter of water? How does one compare availability of floating *Lemna* with a stand of seed-bearing *Puccinellia*? Thus, though precise measurements of available foods can be made, it is impossible to escape some subjective interpretation of results.

In determining food selection by ducks in this study, I did not combine animal and plant food data because of the difficulty of comparing availability. When because of age or species characteristics, the ducks were either essentially carnivorous or vegetarian, this posed no problem. However, there were times when invertebrates were obviously selected over plants and vice versa. No satisfactory method was devised to sample surface insects so that valid comparisons with aquatic invertebrates could be made. Nor did I attempt to compare availability of grasses with that of submersed and floating plants. By and large, comparisons are most valid for those items of like habit. Because the ratings are relative, the presence of other items will influence the rating for a given item. When

Table 19
Feeding activity by Lesser Scaup broods. Figures show percentage of observations (tr < 0.5%)

	Age class						
	Ia	Ib	Ic	IIa	IIb	IIc	III
Age in days*	1-6	7-13	14-20	21-28	29-33	34-42	43-50
Number of broods	17	6	7	7	12	6	6
Total observations†	193	70	105	120	185	110	95
Feeding method							
Surface	41	1	tr				
Chase flying insect	3						
Diving	56	99	100	100	100	100	100
Maximum depth at site							
13–18 in. (32– 46 cm)	21			17	5	14	16
19–24 in. (47– 62 cm)	45	57	76	67	46	68	53
25–30 in. (63– 77 cm)	18	43	24	4	27	18	31
31–36 in. (78– 92 cm)	8				11		
37–42 in. (93–107 cm)	8			12			
43–48 in. (108–122 cm)					11		
Feeding site							
Open water	66	70	71	33	68	53	37
Emergent plants	10					1	
Submerged plants	24	30	29	67	32	46	63

*From Gollop and Marshall (1954).
†One observation per minute.

Table 20
Average selection categories* of invertebrates available to the young of four duck species. (Number of collections shown in parentheses.)

Item	Pintail (43)	Gadwall (26)	Widgeon (16)	Scaup (34)
Hirudinea	9.0 (1)	2.5 (4)		6.0 (3)
Anostraca	0 (2)			
Cladocera	1.5 (25)	3.2 (16)	0 (6)	0.7(14)
Podocopa	3.3 (3)	7.0 (1)		
Eucopepoda		0 (1)		0 (1)
Amphipoda	4.5 (2)	0.2 (5)	0.5 (2)	6.0 (15)
Collembola		9.0 (2)	9.0 (1)	
Ephemeroptera naiads	0 (1)	0 (2)	0 (2)	4.0 (5)
Anisoptera naiads	6.0 (6)		0 (2)	5.0 (1)
Zygoptera naiads	1.8 (9)	0.3 (4)	0.3 (4)	2.4 (14)
Hemiptera	1.6 (20)	3.2 (23)	4.3 (13)	3.5 (25)
Coleoptera adults, larvae	6.7 (20)	7.4 (14)	3.3 (7)	8.1 (9)
Trichoptera larvae	7.6 (5)			9.0 (4)
Diptera larvae, pupae	7.4 (30)	7.7 (21)	6.6 (12)	5.7 (24)
Hydracarina		0.3 (3)	1.0 (2)	2.0 (2)
Gastropoda	1.6 (34)	0.1 (20)	0 (12)	1.4 (26)

*Highest selection indicated by category 9; no selection indicated by 0.

the available food includes mostly unimportant items measured in the habitat, other items will be given a higher rating. Despite its shortcomings, I believe the method does provide a useful guide with which to interpret diet results.

Pintail food selection

Pintails appeared to select those items most available to them in terms of their characteristic feeding adaptations (Table 20). The diversity of the Pintail diet further suggests that they ate what was available. This was also evident in individual ducks, some of which had eaten as many as 25 different kinds of animal and plant items. All of the more common invertebrates were selected at least occasionally by Pintails. Considering only those items available in at least four collections (Table 20), highest selection was shown for Trichoptera larvae, Diptera larvae, Coleoptera, and Anisoptera naiads. Lower selection was evident for Zygoptera naiads, Hemiptera, Gastropoda and Cladocera. On the basis of diet analysis and field samples, surface invertebrates were evidently selected over aquatic forms when the former were relatively abundant and available. Low selection of gastropods is believed to reflect low preference rather than availability. Otherwise selection values appeared related to availability. Because Pintails did much of their feeding in shallow areas close to shore and in the mud bottom, organisms characteristic of those zones had highest selection ratings.

I did not attempt to rank plant foods eaten by Pintails because the plant diet varied widely and was obtained from different zones: nutlets from the mud bottom, rooted and unrooted foliage from water and grass seeds from bottom, surface and land. I believe most of the nutlets taken from the bottom were ingested accidentally while the ducks fed on bottom fauna. They were seldom taken in quantities which would indicate that they represented selected items. The frequency of plants on 52 sites (Table 1) provides a measure of abundance with which to compare diet data (Table 13). The following common plants occurred on at least one site from which Pintails over 20 days old were collected and Pintails showed little or no tendency to select them: Cladophoraceae, *Potamogeton*, *Triglochin*, *Distichlis*, *Lemna*, *Juncus*, *Rumex*, *Polygonum*, *Ranunculus* and *Myriophyllum*. Evidence from two collections indicated that Pintails had selected winter buds of *Potamogeton pusillus*. Some preference was also shown for *Zannichellia*, seeds of *Puccinellia*, *Beckmannia* and perhaps *Alopecurus*. Generally, if *Zannichellia* was present, it was almost always found in usable specimens. Such was not the case with the grass seeds which were taken sporadically. Data for *Hordeum jubatum* are not conclusive. It comprised a significant amount of the food eaten but seldom occurred in large quantities. It was also one of the most common plants at collecting sites, so it may have been taken largely through accident. Pintails apparently ate little grass seed in Keith's (1961) study. This is significant because, of the grasses for which Pintails in my study showed some preference (*Puccinellia*, *Beckmannia*, and *Alopecurus*), the last two were not recorded in Keith's plant surveys and *Puccinellia* occurred infrequently on his study area.

Pintails ate a wide variety of foods—animal and plant—and demonstrated an ability to exploit markedly different food resources. Perret (1962) found this was the case with young Mallards. Pintails did show high selection for invertebrates associated with the shallow areas close to shore which they most frequently used. Much of their food was taken from the mud bottom, and their long neck is considered an adaptation for bottom feeding (Olney, 1964). It would also be an advantage when stripping seeds from grasses.

Gadwall food selection

Selection ratings for invertebrates eaten by Gadwalls (Table 20) do not include surface invertebrates. During periods of emergence when they were abundant, adults of Diptera, Trichoptera and Ephemeroptera were obviously selected over aquatic invertebrates and that depressed values for the latter. As previously discussed, surface invertebrates were most frequently eaten by ducks less than 15 days old.

Trends are apparent for some of the more common items. Gadwalls tended not to select Cladocera though there were two exceptions when cladocerans or their ephippia were apparently abundant enough to be selected. One duck had gorged itself on ephippia that had been concentrated along the shore by wind action. Keith (1961) collected an adult male Gadwall under similar circumstances. Another duckling that I examined had eaten immature cladocerans about 0.3 mm in diameter and contained an estimated 25,000 individuals. Collias and Collias (1963) tested Gadwall ducklings and concluded that they were inept at straining small items from the water.

Amphipods were seldom selected, apparently for a different reason. These mobile crustaceans occur throughout the entire pond, and ducks must pursue and capture them individually. Thus they are largely unavailable to non-diving ducks such as Gadwalls. The same is probably true of insect naiads which do not surface for air. Gadwalls tended to select Coleoptera adults and larvae and Diptera larvae and pupae. Most of the Coleoptera were probably captured when they surfaced for air. Most dipterous larvae were probably taken close to the surface.They move slowly and, hence, are easy prey. There was no trend shown in selection for Hemiptera, principally corixids. They were often present and selection ratings were distributed through all categories (0–9). Notonectids were virtually never taken and accounted for two category "0" ratings for Hemiptera. They are rapid swimmers and probably difficult to capture when they do surface. Gadwalls tended to ignore gastropods which were among the commoner invertebrates. This was clearly out of preference because most gastropods would be available given the feeding anatomy or behaviour of the ducks.

A change in the type of animal foods eaten by Gadwalls, from mainly surface invertebrates during the first few days, to mainly aquatic invertebrates in older birds, was described in the section on Gadwall foods. Chura (1961) reported a similar trend in young Mallards. Because only animal food is involved this comparison is probably valid. As with the Mallards, the change in Gadwall foods was associated with changing feeding methods. Perret (1962) found no such trend in the diet of young Mallards in Manitoba and believed that Chura's (1961) results, with regard to declining use of surface fauna and increasing use of plants, reflected a paucity of aquatic fauna in the habitat. That was not the case in this study and I conclude that the trend in Gadwall diet resulted from a normal change in food selection.

Gadwalls appeared to discriminate more among plant foods (Table 21). Ducklings can exercise more choice in selection of plants since these represent a more stable and uniform food resource. Thus, differ-

Table 21
Average selection categories* of plants available to young Gadwalls and Widgeons. (Number of collections shown in parentheses)

Item	Gadwall (22)	Widgeon (17)
Cladophoraceae	3.7 (7)	1.1 (7)
Chara sp.	9.0 (1)	
Musci	0.3 (3)	3.0 (1)
Potamogeton pectinatus foliage	0.2 (12)	0.2 (12)
Potamogeton vaginatus foliage	0 (1)	0 (1)
Potamogeton Richardsonii foliage	0.2 (4)	0 (1)
Potamogeton pusillus foliage	5.4 (12)	7.2 (10)
Zannichellia palustris foliage, seeds	6.0 (4)	
Lemna trisulca	4.5 (4)	7.5 (2)
Lemna minor	7.8 (5)	7.0 (4)
Ceratophyllum demersum	9.0 (1)	
Ranunculus subrigidus foliage	5.0 (1)	
Myriophyllum exalbescens foliage	0.2 (13)	0.2 (12)

*Highest selection indicated by category 9; no selection indicated by 0.

ences in selection ratings reflect preferences more than with invertebrates. Positive selection was evident for *Lemna minor*, *Zannichellia* and *Potamogeton pusillus*. *Lemna trisulca* and Cladophoraceae occupied an intermediate position and their degree of selection appeared to depend on what else was present. Gadwalls appeared to reject Musci, *Potamogeton pectinatus*, *P. Richardsonii* and *Myriophyllum*. Two cases where spikes of *Potamogeton pectinatus* and *Myriophyllum* were selected also involved beetle larvae.

The one time they were selected in large amounts, *Beckmannia* seeds were apparently taken from the water surface where they were readily available.

A selection hierarchy can be calculated based on food rankings from each collection, though a much larger sample is desirable. To illustrate, *Zannichellia* and Cladophoraceae occurred simultaneously at collection sites on four occasions and each time *Zannichellia* was selected over Cladophoraceae. Selection for Cladophoraceae usually occurred when such favoured foods as *Potamogeton pusillus*, *Zannichellia* and *Lemna* were absent. On two occasions when *Potamogeton pusillus* and *Lemna minor* were both present, the latter was apparently the preferred food. A selection ranking, based on this method, for the nine most common plants (Gadwall column, Table 21) does not differ significantly from the ranking based on the average selection ratings as given.

American Widgeon food selection

Invertebrate selection values for Widgeons are fewer (Table 20) but the pattern is similar to that of Gadwalls. One difference was the Widgeons' non-selection of cladocerans the six times these crustaceans were present in appreciable amounts. Apparently Widgeons are even less inclined than Gadwalls to strain small items. Only three items—Diptera, Hemiptera and Coleoptera—showed significant selection by Widgeons. In one collection, not included in Table 20 for lack of food samples, Widgeons apparently selected gastropods over other invertebrates. This appeared to be an exceptional case.

Selection of plant foods was also similar in Widgeons and Gadwalls. One possible difference was the lower rating for Cladophoraceae in Widgeon collections. In one collection three Class IIc Widgeons had eaten large amounts of combined perigynia and nutlets from *Carex lanuginosa* growing in shallow water. This was the only time that ducks were known to feed on standing Cyperaceae. Why it was selected in this case is not clear but it may be because the pond contained very little of the usual foods eaten by Widgeons.

Lesser Scaup food selection

The diet data indicated that food selection by Scaups changed as they grew (Fig. 4). The trend from predominantly bottom larvae to predominantly amphipods was related to movement of the broods to larger ponds. Generally, collections were random and lake size did not restrict collecting. I collected Class I Scaups from all types of water areas, including shallow, temporary ponds covered with emergent plants, and altogether on 16 ponds, of which eight were less than 2 acres (0.8 ha) in size. Older ducklings were seldom found on small ponds and, when they were, the pond was invariably deeper than average. Only three of 15 Class II–III (Scaup) ponds were less than 2 acres. Larger ponds were used by both Class I and older ducks. Low (1945), Smith (1953), Berg (1956), Evans and Black (1956), Keith (1961), Lokemoen (1966) and Wright (1968) have described a tendency for duck broods to move from small to larger water areas. Low (1945) and Lokemoen (1966) studied Redheads, but in the other studies dabbling ducks contributed most of the data. It is reasonable to assume that Lesser Scaups would show a greater preference than dabbling ducks, for large, deep, open water areas, though they might show less tendency to move overland than some. In the Strathmore area, irrigation ditches and canals facilitated movement by flightless ducks between ponds.

Amphipods also occurred more often in larger and deeper ponds based on invertebrate samples from 54 collecting ponds for all species—the nearest I have to a random sample. They were found in 29 per cent of 38 ponds in the 0- to 3-acre (0- to 1.2-ha) range 56 per cent of 9 ponds in the 4- to 11-acre (1.6- to 4.5-ha) range and all of 7 ponds over 11 acres. Little is known about the over-winter requirements of amphipods. Pennak (1953) implied that they need water, which would mean permanent water areas that do not freeze to the bottom. If that is true, and since water depth and permanency tend to be related to surface area, the observed distribution of amphipods was to be expected. As predictable from the distribution of Scaups and amphipods, the latter occurred more often in ponds used by older ducklings. They occurred in 44 per cent of 16 Class I (Scaup) ponds, and 73 per cent of 15 Class II–III ponds, the difference not being significant ($P > 0.05$). The difference between amphipod occurrence in the 15 Class II–III ponds and that in the 54 collecting ponds that were sampled (73 vs. 43 per cent) is not quite significant at the 5 per cent level ($\chi^2 = 3.29$ with Yate's correction). However, the 54 ponds were not a random sample of water areas since they were chosen because ducks—including older Scaups—were using them. Poston's (1969) data indicate that ponds of less than 3 acres were much more prevalent than the 70 per cent shown above (38 of 54 ponds). Thus there would be fewer amphipods in a random sample of water areas.

I believe Scaups shifted to larger ponds not to seek food but rather, for security and freedom from harassment on larger and deeper ponds. (At least one collection pond dried up before the Scaups would have reached flying age.) The food in small ponds was adequate. Moreover, older Scaups regularly used larger ponds (4 to 15 acres; 1.6 to 6.1 ha) which were without amphipods. There, they ate chiefly bottom larvae.

Considering only items which were available at least four times, Scaups' selection ratings were highest for Trichoptera larvae and Coleoptera adults and larvae (Table 20). These were followed by Amphipoda and Diptera larvae. Scaups of all ages tended to select amphipods when available and, generally, these were chosen over all other invertebrates. Selection of dipterous larvae was variable and often appeared to be influenced by the presence of amphipods. Only once did Scaups select larvae over amphipods. In contrast, larvae were available to some extent virtually every time amphipods were taken. Rogers and Korschgen (1966) also believed that adult Scaups selected amphipods over the more abundant dipterous larvae. They suggested that the amphipods may have been more conspicuous and therefore easier prey. Perhaps amphipods were more palatable to Scaups.

Data for individual collections showed that selection of Hemiptera, Ephemeroptera naiads and Zygoptera naiads was variable and probably reflected their relative availability. On the other hand, gastropods and Cladocera were often present but seldom chosen by Scaups (Table 20), indicating low preference.

Scaups selected a plant food, *Chara* oögonia, only once, on the only site where the plant was found. While this does not prove that *Chara* is a preferred food, it does indicate some preference for diversity. The two ducks which contained *Chara* had evidently strained the oögonia from the water or mud, as no other parts were ingested.

Results of six feeding tests made with various combinations of aquatic invertebrates in the aquarium indicate that ability of prey to escape influenced selection rate by Scaups in the wild. In the confined tank there was nowhere to escape to and the invertebrates were almost equally available. Although too few tests were made for statistical analysis, the selection pattern was consistent for most items. Assigning the value of 100 to the item with the highest selection rate, the following values were obtained from the feeding tests:

Hemiptera (Notonectidae)	100
Anisoptera naiad	100
Zygoptera naiad	90
Hemiptera (Corixidae)	65
Coleoptera (Dytiscidae l.)	60
Coleoptera (Dytiscidae a.)	60
Amphipoda (Gammaridae)	40
Gastropoda (Physidae)	25

The results show that the selection values derived from field data do not necessarily reflect preferences. Amphipods, frequently selected in the ponds, were among the last to be taken in the presence of other items in the tank. In contrast, Zygoptera naiads and notonectids were among the first taken in the tank, but had relatively low selection values in the wild. Gastropods, relatively available in both situations, were least preferred both in the tank and in the ponds.

In the tank, young Scaups tended to prey on the largest items first. Whether or not these attracted their attention first was not determined, but the impression gained from watching them was that size and movement did influence their choice. Where availability is equal, selection of larger items has obvious survival value. Less effort is expended for a given amount of food. I have no data on whether or not wild Scaups select larger items.

Dirschl (1969) concluded that seasonal changes in food selection by adult Lesser Scaups reflected changes in the relative abundance of foods. Bartonek and Murdy (1970) also detected seasonal differences in the diet of young Scaups. However, they suggested that the changes may have resulted from changing feeding methods (i.e., older ducklings may have been diving deeper) because their data did not reveal marked changes in relative food abundance.

In summary, Lesser Scaup ducklings tended to select the most available invertebrates, considering their feeding methods and capabilities. Gastropods were an exception and, though generally available, were not preferred. Apparently amphipods were most often selected because they were frequently the most abundant prey.

Table 22
Calculated overlap of diet, feeding methods, depth at feeding sites, and feeding sites (emergent plants, submerged plants, open water and mud flat), between combinations of four duckling species (tr < .005)

Species	Diet	Method	Depth	Site
Pintail vs. Gadwall	.05	.59	.77	.64
Pintail vs. Widgeon	.05	.61	.77	.69
Pintail vs. Scaup	.34	.03	.18	.88
Gadwall vs. Widgeon	.90	.98	.78	.99
Gadwall vs. Scaup	.02	tr	.35	.69
Widgeon vs. Scaup	.02	tr	.72	.71

Feeding overlap

Overlap indexes for diet, method of feeding, depth and feeding site for each combination of two species (Table 22) provide but a rough measure of total overlap between species because not all factors that influence it were measured. Distribution of food within the habitat should be measured (Orians and Horn, 1969) because food items are seldom randomly distributed. Time of use should also be considered (Pianka, 1969). For example, populations of certain invertebrates available to Pintails may be different from those available to Scaups—Scaups being 4 to 6 weeks later (Hochbaum, 1944; Keith, 1961; this study, Table 7). Some invertebrates, such as adult Ephemeroptera, are extremely temporary (2 to 3 days) and use of such food by two species with dissimilar hatching peaks would tend to reduce total overlap. Also, each species tended to choose a certain type of pond. While some ponds were used by all species, others were used little or not at all by one or more; Pintails and Scaups differed most in their choices. The indexes of depth overlap are valid only when the feeding methods are also considered. For example, a Scaup diving in deep water and a Widgeon surface feeding at the same place would have the same depth designation as used here but would be feeding from different zones. Rather broad taxa—orders and classes—were used in the animal food lists. That would bias overlap indexes upward because similarity of invertebrate orders in the diets does not necessarily mean species or even families were the same. Some differences are apparent in proportions given in Table 14, e.g., gastropods in Pintails and Scaups.

Two species combinations—Pintail–Scaup and Gadwall–Widgeon—had significant diet overlaps (Table 22). In the case of Pintail and Scaup, the low overlap for depth as well as factors discussed above would probably make the total overlap insignificant. The actual feeding method overlap between the two species is probably higher than the given estimate because some Scaup activity recorded as *diving*, undoubtedly involved bottom feeding. However, any similarity in foraging methods would not have much bearing on the total overlap between Pintails and Scaups because of the dissimilarity of their habitat use.

Gadwalls and Widgeons showed a high overlap in all factors measured, and I believe the total overlap would also be high. The significance of this will be considered under *Discussion*. Most of the diet overlap resulted from the similarity of their plant diets. Gadwalls ate a greater variety of plants than Widgeons, but the larger sample of Gadwalls (167 vs. 129) may be the reason. Even during the last year after most Gadwalls had been collected, I found new items in some. Thus a larger sample of Widgeons would also probably contain greater variety.

Another way to compare food selection by different species is to collect more than one species at the same time and place (Talbot and Talbot, 1963) so differences in food eaten reflect choice rather than availability. There were 11 mixed collections from which species comparisons could be made (Table 23). Some minor items have been omitted. Of the seven times Gadwalls and Widgeons were collected together, only twice had they eaten the same food in appreciable amounts. Overlap indexes cal-

Table 23
Comparisons of major foods eaten by two or more species collected at the same time and place. Figures show percentage of dry weight (tr < 0.5%)

		3 IIc–III Gadwalls (1.008 g)*	3 IIc–III Widgeons (0.127 g)
Potamogeton pusillus foliage		0	90
Ceratophyllum demersum foliage		71	tr
Lemna minor		29	8
		1 IIa Gadwall (0.175 g)	3 IIb Widgeons (0.684 g)
Cladophoraceae		99	98
		3 III Gadwalls (1.036 g)	3 III Widgeons (0.071 g)
Cladophoraceae		93	0
Potamogeton pectinatus foliage		3	96
Potamogeton pusillus foliage		3	0
Invertebrates		tr	4
		2 III Gadwalls (1.249 g)	3 IIc Widgeons (0.195 g)
Lemna minor		98	25
Chironomidae adults		2	75
		1 Ic Gadwall (0.346 g)	2 Ib Widgeons (0.022 g)
Cladophoraceae		73	0
Ranunculus Cymbalaria foliage		0	15
Trichoptera adults		0	38
Chironomidae adults		tr	18
Chironomidae larvae		26	12
Corixidae		0	16
		4 IIa Gadwalls (0.343 g)	3 IIa Widgeons (0.879 g)
Cladophoraceae		38	tr
Lemna minor		46	tr
Potamogeton pusillus foliage		5	90
Other plants		1	6
Invertebrates		9	4
	2 Ib Gadwalls (0.117 g)	2 IIb Widgeons (0.631 g)	6 IIa Scaups (0.810 g)
Cladophoraceae	0	97	0
Cladocera	88	0	46
Diptera larvae	9	1	51

cont'd

	1 IIc Widgeon (0.051 g)	5 IIa Scaups (0.735 g)
Potamogeton pusillus foliage	98	0
Hirudinea	0	30
Amphipoda	0	58
Other invertebrates	0	12
	2 Ic Widgeons (0.288 g)	4 Ib Scaups (0.168 g)
Amphipoda	0	68
Ephemeroptera naiads	0	6
Diptera larvae	0	16
Hemiptera	0	7
Gastropoda	98	0
	1 Ic Widgeon (0.076 g)	1 IIc Pintail (0.378 g)
Lemna trisulca	3	0
Scirpus nutlets	91	1
Carex nutlets	0	24
Alopecurus seeds	0	64
Diptera adults	6	0
Diptera larvae	0	9
	2 IIc Widgeons (0.465 g)	1 III Pintail (0.004 g)
Lemna minor	98	0
Diptera larvae	tr	87
Coleoptera larvae	tr	13

*Total dry weight of food.

culated for the Gadwall-Widgeon collections in order of appearance in Table 23 are .04, 1.00, .03, .33, .07, .08 and 0. The average of these is .22 which is considerably lower than the value of .90 (Table 22) calculated from diet lists. The difference in foods eaten by the two species collected at the same time and place is surprising considering the similarity of their diets. Age differences in one collection could have accounted for the dissimilar foods eaten. It is also true that the two species were not always taken from a mixed flock and that available food can vary considerably over a portion of a pond. That could account for some of the differences. However, in the first example (Table 23), both species were the same age and had been feeding at the same end of a small pond, yet had selected different foods. Perhaps a larger sample of mixed collections would show fewer differences in food selection by the two species.

There were fewer collections involving other species combinations. In one collection of Class I Gadwalls and Class II Scaups, both had eaten appreciable amounts of Cladocera. Widgeons and Scaups in three collections ate different foods, as did Widgeons and Pintails from two collections.

Nutrient composition of duck foods

Chemical and energy data for 21 duck foods are given in Table 24. Some samples were too small for complete analysis. Except for Corixidae and Coleoptera, each sample was taken from a single site. The calorific content of living organisms is influenced by genetic constitution, nutritive condition and life history which in turn may vary with season, species and environmental conditions (Golley, 1961). Thus, average values are good only for extensive surveys of biomass. By the same token, isolated samples may not be representative of average conditions. Variations in plant ash can be caused by calcareous deposits on the leaves in certain lakes (Sculthorpe, 1967). This was evident in the samples of *Potamogeton pusillus* (Table 24) in which leaves of two samples were visibly coated. Variations in the nutrient and calorific contents of a series of freshwater plants are summarized from the literature by Straškraba (1968). Cummins and Wuycheck (1971) have compiled an extensive list of calorific values for various animals and plants. Straškraba (1968) demonstrated some correlation between the chemical composition of plants and their ecological category—emergent, submerged and those with floating leaves. Variability of invertebrate composition is well illustrated by the ash content of *Daphnia*. Comita and Schindler (1963) reported no ash after combustion of cladocerans. Ash in Wisconsin *Daphnia* ranged from 2.6 to 25.8 per cent of dry matter (Welch, 1952; Wissing and Hasler, 1968). In my sample of Cladocera (mostly, if not all, *Daphnia*) ash made up 48 per cent.

The moisture content of natural duck foods is a rather meaningless variant and does not seem to influence food selection. Since the energy available in a food usually governs the amount eaten, those foods with a high water content are probably eaten in greater quantities (wet weight) than are the low-moisture foods. An exception would be when the latter are lower in digestibility. Pulliainen, Paloheimo and Syrjälä (1968) demonstrated this with Willow Grouse (*Lagopus lagopus*). Although *Vaccinium* berries had a higher digestibility than stems, the berries contained more moisture and the wet weight consumption of both was similar.

Evidently nutrient requirements of wild ducklings are similar to those of domestic ducklings (Holm and Scott, 1954; Scott and Holm, 1964). A comparison of these requirements (Dean and Scott, 1965) with the composition of foods in Table 24 shows

Table 24
The nutrient and energy content of some duck foods

	Dry matter		Composition on a dry basis, %						
			Crude	Crude		Crude			
Item	%	kcal/g	protein	fat	N.F.E.*	fibre	Ash	Ca	P
Cladophoraceae (cf. *Cladophora*)		3.57	16.0	0.2	41.3	22.4	20.1	2.9	0.6
Potamogeton pectinatus foliage	14	3.74	13.3	0.9	57.8	14.7	13.3	2.0	0.6
P. pusillus foliage	15†	3.99	13.7	1.6	56.7	11.4	16.6	1.2	0.8
P. pusillus foliage	15†		13.4	1.1	64.3	13.9	7.3	1.1	0.5
P. pusillus foliage	15†		15.0	1.2	53.3	17.1	13.4	2.7	0.6
P. pusillus winter buds	23	4.99	24.6						
Zannichellia palustris foliage, seeds	18†	4.06	20.3	9.2	47.6	1.3	21.6	1.5	0.7
Puccinellia Nuttalliana seeds	88	4.34	11.1	0.4	70.6	13.1	4.7	0.3	0.5
Glyceria grandis seeds	80†		6.0	1.4	76.1	7.9	8.5	0.3	0.5
Beckmannia syzigachne seeds	90†		7.0	6.5	59.6	20.0	6.9	0.5	0.4
Beckmannia syzigachne seeds	90†	4.73	8.9	4.9	53.3	27.4	5.5		
Scolochloa festucacea seeds	90	4.43	8.8	1.9	67.9	16.1	5.4	0.4	0.4
Alopecurus aequalis seeds	90†		15.5	9.1	51.6	15.5	8.3		
Carex lanuginosa perigynia, nutlets	90†		11.1	4.7	47.6	31.1	5.5		
Lemna trisulca	23	2.47	15.2	0.8	56.2	7.7	20.1	2.0	0.8
Lemna minor	9	4.09	37.1	4.2	37.1	8.8	12.8	1.2	1.2
Cladocera	13	2.71	31.8	1.5	10.9	7.3	48.4	11.8	1.2
Amphipoda *Gammarus* sp.	15	4.02	47.0	5.9	16.5	8.4	22.2		
Zygoptera naiads	19	5.72							
Hemiptera Notonectidae adults	21		62.9	9.4	12.8	9.0	5.9	0.4	1.3
Hemiptera Corixidae adults	20†	5.31	71.5	9.2	0.7	11.5	7.1	0.7	1.0
Coleoptera aquatic adults, larvae	24†	5.93							
Diptera Chironomidae larvae	16	4.30	56.0						
Gastropoda Lymnaeidae	17	0.92	16.9	0.7	5.8	12.4	64.2	26.1	0.3

* Nitrogen-free extract.
† Estimated.

that few foods by themselves would supply the basic nutrients in adequate proportions, though increased intake might compensate for certain deficient nutrients in some foods. The number of adequate foods would no doubt be smaller were other essential nutrients (amino acids, vitamins and additional minerals) considered. Apparently a mixture of foods is necessary to supply ducklings with a nutritionally balanced diet.

The little work which has been done on amino acid requirements of waterfowl (Demers and Bernard, 1950) and the fact that the protein requirement of ducks is similar to that of chicks (Anonymous, 1962) indicate that amino acid requirements of chicks and ducklings are similar. Consequently, I included the essential amino acid requirements of chicks (Bolton, 1963) in Table 25 for comparison. Tryptophan is an essential amino acid for chicks but was not measured in the duck foods, so is excluded. In chicks, requirements for some amino acids vary with the level of protein in the diet (Bolton, 1963), so any list must be interpreted with that in mind.

There is considerable variation in amino acid composition among the different foods. None of the plant foods meets all the requirements. Of all 13 foods, chironomid larvae, corixids and gammarids would appear to provide the most complete range of amino acids as based on chick requirements. The high quality protein provided by chironomid larvae is significant because these invertebrates seem important in the diets of most, if not all young ducks. Likewise, amphipods are the most important items in their diet. I believe corixids would be equally important were they similarly available. High glycine such as found in corixids can retard growth in chicks when nicotinic acid is inadequate (Bolton, 1963), and the same might occur in ducks not eating mixed foods.

Cladocera, *Zannichellia* and *Potamogeton pusillus* are deficient only in cystine and methionine, the sulfur amino acids essential for feather growth. They, as well as threonine, are also low in *Lemna minor*. *Potamogeton pectinatus* is low in arganine, cystine and methionine. Evidently a relatively high level of arganine is needed by the duck for rapid growth before feathering (Hegsted and Stare, 1945). The remaining five foods are deficient in most essential amino acids.

Table 25
Partial amino acid composition of 13 duck foods

		Amino acids on a dry basis, %							
	Dry matter	Alanine	Arginine	Asparagine*	½Cystine	Glutamic acid	Glycine	Histidine	Isoleucine
Chick requirements†			1.2		0.35‡		1.0	0.3	0.6
Chironomidae larvae	16	6.0	3.2	4.9	0.3	5.2	4.3	2.4	2.2
Corixidae adults	20	10.1	4.4	5.1	0.3	9.0	6.4	3.2	2.8
Gammarus sp.	15	5.5	2.2	3.3	0.3	5.0	4.3	1.4	1.5
Cladocera	13	1.7	1.3	1.3	0.2	3.1	1.4	0.6	0.9
Zannichellia palustris foliage, seeds	18	2.0	1.5	2.2	0.1	2.7	2.1	0.5	0.8
Potamogeton pusillus foliage	15	1.5	1.9	3.1	0.2	2.9	1.5	0.7	0.9
Lemna minor	9	1.5	1.7	4.3	0.1	3.4	1.4	0.5	0.9
Potamogeton pectinatus foliage	14	1.2	1.1	2.5	0.1	2.3	1.2	0.3	0.8
Scolochloa festucacea seeds	90	0.4	0.6	0.7	1.0	1.6	0.4	0.2	0.3
Cladophoraceae cf. *Cladophora*		0.7	0.7	1.7	0.3	2.1	0.8	0.1	0.4
Lemna trisulca	23	0.6	0.6	1.2	0.1	1.2	0.6	0.2	0.4
Puccinellia Nuttalliana seeds	88	0.5	0.6	0.6	0.1	2.0	0.4	0.2	0.3
Lymnaeidae	17	1.2	0.4	1.4	0.0	1.5	0.6	0.2	0.4

	Amino acids on a dry basis, %								
	Leucine	Lysine	Methionine	Phenyla-lanine	Proline	Serine	Threonine	Tyrosine	Valine
Chick requirements†	1.4	1.0	0.8§	1.4//			0.6		0.8
Chironomidae larvae	3.3	6.3	0.7	4.9	2.4	2.7	2.5	1.5	2.5
Corixidae adults	5.5	6.2	1.2	1.8	3.8	4.0	3.5	7.5	4.6
Gammarus sp.	2.7	4.3	0.8	1.5	2.6	2.1	2.0	2.9	2.2
Cladocera	1.8	1.7	0.4	2.1	1.2	1.0	0.8	2.0	1.1
Zannichellia palustris foliage, seeds	1.8	1.5	0.4	0.9	0.8	1.6	1.3	0.7	1.2
Potamogeton pusillus foliage	1.8	1.8	0.3	1.3	1.1	1.5	1.3	1.2	1.4
Lemna minor	2.0	1.5	0.4	1.2	1.2	1.2	0.5	0.9	1.2
Potamogeton pectinatus foliage	1.7	1.3	0.3	1.1	1.1	1.1	1.0	0.7	0.9
Scolochloa festucacea seeds	0.5	0.3	0.1	0.6	0.4	0.4	0.3	0.2	0.3
Cladophoraceae cf. *Cladophora*	0.7	0.6	0.1	0.6	0.8	0.4	0.6	0.5	0.6
Lemna trisulca	0.8	0.7	0.2	0.6	0.5	0.6	0.5	0.4	0.5
Puccinellia Nuttalliana seeds	0.6	0.4	0.1	0.5	0.5	0.4	0.3	0.3	0.4
Lymnaeidae	0.8	0.6	0.0	0.5	0.6	0.6	0.6	0.4	0.5

*Amide corresponding to aspartic acid.
†Essential amino acid requirements of chicks, 0–8 weeks old; 20 per cent protein in diet (Bolton, 1963:79). Tryptophan was not measured in duck foods so is omitted.
‡Given as *cystine*.
§Can be 0.45 per cent if cystine is 0.35 per cent.
//Can be 0.7 per cent if tyrosine is 0.7 per cent.

Discussion

This and other studies have shown that ducklings depend principally on invertebrate foods immediately after hatching. Moreover, during their first few days, dabbling ducks, at least, eat chiefly invertebrates which they capture on or close to the water surface. Veselovsky (1953) believed that during their first few days, ducklings took only items which they could see. Hochbaum (1944) stated that, although newly-hatched Canvasbacks could dive, they obtained most of their food from the surface during their first 2 weeks. During the first few days there was considerable overlap among the diets of the four species. The average diet of Scaups differed most, but the diet of some Scaups was indistinguishable from that of the three dabbling species.

The similarity of diets during the first few days is paralleled by a similarity in feeding behaviour and feeding apparatus. Veselovsky (1953) reported that at hatching the different duckling species have bills similar in structure. I examined a series of bills from each of the four species in this study and agree. The bill of a newly-hatched duckling is relatively unspecialized and appears adapted primarily for the gaping-action (Goodman and Fisher, 1962), common to all anatids. As a duckling grows its bill becomes more specialized. In the three dabbling species there was a concomitant change of feeding behaviour and diet with bill specialization. No doubt other changes occur which parallel the dietary transition. Increased size would bring more underwater food within reach. There may be physiological changes enabling older ducks to remain submerged longer. Muscles required for adult feeding methods (Goodman and Fisher, 1962) may be ineffective in small ducklings. The ability to digest plant foods may increase with age.

Unspecialized feeding apparatus and behaviour early in the life of ducklings could be considered an adaptation in itself. Because of their small size and buoyancy in the water, downy ducklings are largely confined to a narrow feeding zone close to the water surface and they must all share a limited supply of animal food. An overlap in diet by several species of young ducks using the same habitat at first appears to belie the concept of species' ecological niches. However the degree of overlap would be more apparent than real as it occurs when food intake is at a minimum. The need for adaptations that ecologically isolate species from one another becomes greater as the birds grow, eat more food and the potential for interspecific competition increases.

Although measurements are lacking, I believe surface invertebrates on the average study lake were not dense enough to sustain a duck beyond its first few days. Because surface feeding involves much moving about, the energy required to obtain food would increase with age (size). A comparison of the Scaup diet with feeding activity data indicated that surface feeding on invertebrates was inefficient for Scaups. Certainly terrestrial (flying) insects, which constitute most of the surface fauna available to ducks, were not a stable source of food when compared with aquatic invertebrates. During periods of emergence on calm days, adults of Chironomidae, Ephemeroptera and Trichopetera were abundant and taken in large numbers by ducks of all ages. But more often, and particularly on windy days, they were sparse on the water surface. When a duckling's energy requirements are minimum, it can obtain sufficient invertebrate food from the surface most of the time. But as its requirements increase, it soon reaches the point where it cannot secure enough food to meet its needs. Then it must either seek food in other zones or change to a diet of the more abundant plant foods. To varying degrees, both methods were used by the dabbling species studied.

Closely related bird species in the same area usually differ in habitat, food selection or other features which prevent competition for food (Lack, 1954). In this study, only the Gadwall and Widgeon showed sufficient feeding overlap to suggest possible competition. Similarity of diet does not mean that two species are competing for food (Crombie, 1947; Lack, 1954; Milne, 1961). Competition occurs when two or more animals use a resource which is insufficient to meet the needs of all. It also occurs when animals seeking a common resource harm one another in the process, despite an adequate supply (Birch, 1957) and when behavioural interactions prevent an animal from using an otherwise plentiful resource (Gibb, 1961). This latter aspect was not investigated, but casual observations suggest that it was unimportant. Gadwalls seemed tolerant towards Widgeons and vice versa. There was no evidence that Gadwalls and Widgeons were competing for food despite the similarity of their diets. The co-existence of sympatric species, of course, is dependent on the absence of competition (Lack, 1944; 1945). Generally there appeared to be an abundance of foods, plant foods in particular, and, except for the removal of seeds from a few grasses, nowhere could I find evidence of significant use of plants by ducks. Also, the overlap in the animal portion of their diets took place when food intake was minimum. It may be significant that the highest overlap occurred between two essentially herbivorous species. Data summarized from the literature by Moyle (1961) indicate that the standing crop of aquatic plants in lakes is several times greater than the invertebrate standing crop. Thus there would be more opportunity for herbivores to eat the same foods without competing. This is in keeping with the concept that herbivore populations are seldom limited by food resources (Hairston, Smith and Slobodkin, 1960).

In the Strathmore area, the way breeding pairs are spaced throughout the habitat (McKinney, 1965) results in populations of young which are well within the food carrying capacity. While the function of pair spacing may not be related to food of young, the effect is the same. Lack (1966) believed that limited food outside the breeding season was the most important density-dependent factor regulating numbers of wild birds. Most species share certain components of their ecological niches in varying degrees with other species. When a shared component is in good supply and, by itself, does not limit either species' population, then considerable overlap occurs as with foods of young Gadwalls and Widgeons. Absence of food competition between duckling species on my study area does not preclude interspecific competition in other habitats. The Strathmore area is probably atypical of prairie breeding habitat in that irrigation water helps to maintain water levels throughout the brood season. Ditches and canals also facilitate movement of ducks between water areas. The ratio of ponds available to broods to those available to breeding pairs would be higher than on most areas without irrigation. Thus the brood population in the Strathmore area would have access to more habitat than a similar population on prairie habitat with no irrigation.

My results show that both preference and availability influence ducks in their selection of food. Choice of invertebrates appears to depend more on availability than does choice of plants. Plants represent a more stable and usually more abundant source of food, so ducks have greater opportunity to exercise a choice when eating them. There is some evidence that ducks seek diversity in their diet. Because of varying supplies of available foods — particularly invertebrates — a mixed diet may have been imposed in some cases, whether or not it was preferred. However, there were times when each species selected certain foods for no apparent reason other than a preference for a change. The fact that gastropods or certain plants were sometimes selected but often ignored suggests a preference for diversity. Occasionally Pintails ate large quantities of grass seeds and there was every reason to believe they could have eaten these foods exclusively had they so chosen. Similar examples could be cited for the other species. The variety of foods sometimes found in ducks also suggested a preference for a mixed diet. Individual contents sometimes reflected an abrupt change in food selection. In three Pintails collected from a small pond, the esophagi were packed with food and contained *Puccinellia* seeds in the lower half and chironomid larvae in the upper half. The ducks seemed to have switched foods simply out of preference.

Other vertebrates prefer a mixed diet. Tinbergen (1960) reported that Great Tits (*Parus major*) did not restrict their diet to one prey, despite the fact it was abundant and readily available. He believed the birds preferred a mixed diet. Holling (1959) showed that *Peromyscus* preferred a mixed diet: although sawfly pupae were preferred and available, the mice continued to eat some of the alternate foods. Young (1940) concluded that white rats selected food on the basis of food eaten beforehand. He established that rats consistently preferred sugar to wheat when given a choice. However, when they were pre-fed sugar *ad libitum* and then presented with a choice, the original preferences were reversed.

Ducks that select a mixed diet have two obvious advantages. First, they can adapt readily to changing food resources and secondly, they are more apt to obtain a balanced diet. Chemical analyses showed that few foods by themselves would provide all the nutritional requirements of ducks. Behaviourially, seeking a mixed diet may be the same as selecting foods that provide a balanced diet (Dove, 1935; Young, 1941; Treichler, Stow and Nelson, 1946; Newton, 1964; Rodgers and Rozin, 1966; Miller, 1968). Scott and Verney (1947) tested rats with diets containing variable amounts of B vitamins, and concluded that the rats associated certain adequate diets with a certain flavour. That is, the appetite for the diet containing the needed vitamin was learned (associated with well-being), and not innate. Much the same conclusion was reached by Young (1948) in his rat studies.

It is tempting to compare food quality and food selection by ducks in this study because data suggest that preferred foods were also among the highest in quality as measured by crude protein in dry matter.

However, additional analyses are needed of both selected and non-selected foods before valid conclusions can be made. Moreover, I doubt if valid comparisons can be made from field data because other variables such as availability and palatability also influence selection. Stoudt (1944) and Spinner and Bishop (1950) pointed out that preference ratings of foods eaten by game animals during the hunting season may be biased when animals are forced into marginal habitat where they must subsist on low-preference foods. While this was not a factor in my study it does illustrate the type of variable encountered in field studies. Perhaps we are seeking the impossible when we try to correlate food selection with food quality when the latter is expressed in terms of crude protein or calorific energy. These tell nothing of the food value in terms of metabolizable energy, available amino acids, vitamins or minerals.

I did not compare the composition of duck diets throughout the season nor throughout the 5 study years because sample sizes for each species' age group were too small. However, changes in diets during the flightless period appeared largely due to changes in food selection as the ducks grew and not to changes in available food. Annual and seasonal differences in diets as found in young Mallards by Perret (1962) and in adult Lesser Scaups and Blue-winged Teals (*Anas discors*) by Dirschl (1969), respectively, could be expected if the foods available change over time. In the Strathmore area, there was greater variability of foods available among ponds at any one time, than throughout the season or between years for any one pond.

This study has reaffirmed the importance of invertebrates as food for small ducklings and, in particular, the dependence of ducklings on chironomids for much of their early diet. It also supports previous studies showing that young Lesser Scaups are chiefly carnivorous and eat mostly amphipods. Probably because Gadwalls and Widgeons previously had not been studied in detail, my results show that foliage of aquatic plants—particularly *Potamogeton pusillus* and Cladophoraceae—must be added to the list of important duckling foods. Use of grass seeds, particularly *Puccinellia* and *Beckmannia*, was also more prevalent in this study than in previous ones.

The degree of feeding overlap varies widely among the different combinations of species. Whether or not any species combinations which were not studied have greater feeding overlap is not known. Considering the many factors that tend to ecologically isolate species, it is reasonable to assume that no two species would show complete overlap during the flightless period, except perhaps during the first few days of life. Consequently, most, if not all habitats will be used most efficiently and completely when occupied by a variety of species. This, of course, is an established principle and has been demonstrated for a wide variety of species. Other comparative studies which have shown that sympatric duck species tend to eat different foods and/or use different parts of the habitat, are those of Collias and Collias (1963), Olney (1964), Dirschl (1969) and Bartonek and Hickey (1969a). By the same token, the most diversified habitat will meet the needs of the greatest variety and, hence, the largest number of ducks. Moreover, diversity is needed to meet the changing requirements of at least some species.

Summary

1. The objectives of the 5-year study were to determine the prefledgling diets of Gadwalls, Pintails, American Widgeons and Lesser Scaups in the Strathmore area of southern Alberta; investigate factors which influence food use; and determine the nutritional composition of duck foods.

2. Esophagus-proventriculus samples from 144 Pintails, 167 Gadwalls, 129 Widgeons and 135 Scaups were collected for study. Diet analyses are based on percentage of dry weight. Percentages of occurrence and gross energy are included for comparison.

3. A comparison of esophagus material with that for esophagus and proventriculus combined showed that proportions of some seeds were lower in the former though differences were small and involved minor items. There was no direct evidence that differences were caused by differential digestion.

4. The early diet of Pintails was dominated by surface invertebrates that were later replaced by aquatic invertebrates and, to a lesser extent, plants. The prefledgling diet contained 67 per cent animal food. Gastropods, insects and cladocerans made up 36, 26 and 4 per cent of the total diet, respectively. The dominant insect order was Diptera (18 per cent), chiefly chironomid larvae. Seeds of Gramineae and Cyperaceae accounted for 19 and 8 per cent, respectively.

5. Gadwalls ate chiefly surface invertebrates during their first few days. These were gradually replaced by aquatic invertebrates and plants until, by 3 weeks of age, Gadwalls were essentially herbivorous. The prefledgling diet contained 10 per cent animals—entirely invertebrates. The most important invertebrates eaten by Gadwalls were chironomid larvae and adults, aquatic beetles, cladocerans and corixids. *Potamogeton pusillus* foliage, Cladophoraceae, *Beckmannia* seeds and *Lemna minor* made up 34, 19, 10 and 7 per cent of the diet, respectively.

6. Widgeons had a diet similar to that of Gadwalls. It contained 11 per cent animal and 89 per cent plant food. At first Widgeons ate predominantly animal food, chiefly surface invertebrates. By 3 weeks they were eating less than 10 per cent animal food. Diptera adults, principally chironomids, were the most important invertebrates and made up 4 per cent of the total diet. *Potamogeton pusillus* foliage, Cladophoraceae, *Carex lanuginosa* and *Lemna minor* contributed 47, 18, 9 and 4 per cent, respectively.

7. Lesser Scaups were essentially carnivorous. Amphipods, dipterous larvae and gastropods made up 52, 16 and 16 per cent, respectively, of their diet. Chironomids were the most important Diptera. Older Scaups ate relatively more amphipods and less bottom larvae. This was attributed to brood movements to larger ponds where amphipods were more prevalent.

8. Changes in feeding methods and site use by dabbling species paralleled diet changes. As they grew, Pintails did more bottom feeding and necessarily, most of their feeding occurred in water less than 12 inches (31 cm) deep. In contrast, young Gadwalls and Widgeons replaced surface feeding principally by subsurface feeding. They tended to feed in areas deeper than those used by Pintails and much of their feeding occurred over submersed plants. Although newly-hatched Scaups did considerable surface feeding, it was not reflected in their diet, indicating that surface feeding was inefficient compared with diving for food. After the first week, virtually all feeding was done by diving. Scaups tended to use deeper parts of ponds than the dabbling ducks.

9. A comparison of food available with food eaten showed that the ducks selected the most available invertebrates considering their characteristic feeding adaptations. An exception was the low selection of gastropods which were apparently not preferred. Use of plants was influenced more by preference. There was some evidence that ducks sought a mixed diet and this may be related to selection of foods providing a nutritionally balanced diet.

10. Overlap indexes for combinations of the four species were calculated for diet, feeding method, depth at feeding site and feeding site (open water, emergent plants, submerged plants and mud flat). Only two combinations—Pintail-Scaup and Gadwall-Widgeon—had a significant diet overlap. These were .34 and .90, respectively. Total overlap between Pintails and Scaups would be insignificant because of differences in habitat and seasonal use. Total overlap between Gadwalls and Widgeons was high because of similarities in habitat and seasonal use. There appeared to be an abundance of the two species' major foods and they did not compete.

11. Newly-hatched ducklings of the three dabbling species were unspecialized in their feeding adaptations and behaviour and ate the same kinds of food. This overlap in diet occurred when food intake was minimum and when, for various reasons, the available food was restricted. Since surface invertebrates were generally insufficient to maintain them beyond their first few days, ducklings either sought more of their food in other zones, or switched to more abundant plant foods, or both.

12. Proximate analysis and calorific content of 21 duck foods and amino acid composition of 13 foods are given. Few foods by themselves would supply the nutritional requirements in adequate proportions, and a mixed diet may be needed to meet the needs of ducklings. Chironomid larvae, *Gammarus*, and corixids contained the highest quality protein in terms of amino acid requirements of chicks. Of eight plant foods analysed, *Zannichellia* and *Potamogeton pusillus* had the highest quality protein, though they did appear deficient in cystine and methionine.

13. This and previous studies have shown that a diverse habitat will meet the needs of the greatest variety of species and, hence, the largest number of ducks. Each species requires diversity of food to meet its changing requirements throughout the prefledgling period.

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