FEEDING ECOLOGY OF PINTAIL HENS DURING REPRODUCTION

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Food supply has been acknowledged as one of eight major external factors regulating the sexual cycles of birds (Marshall 1961). Several hypotheses have been advanced to explain the role of food supply as an ultimate factor regulating breeding (Marshall 1951; Lack 1954, 1968; Wynne-Edwards 1962; and others). Another potential influence of food is its being a proximate stimulus to breeding. When certain foods become available they may act as a stimulus as the female requires them to meet her dietary needs during egg formation. Lack (1966a: 24) suggested that the average date of laying by the Great Tit (*Parus major*) probably resulted from a correlation between spring temperatures and the time of appearance of the insect foods the adult females need to form eggs. He also cited other passerines whose breeding was affected by food supply available to the female. In waterfowl it has been suggested that laying females require invertebrate foods (Moyle 1961, Leitch 1964). If true, this implies that the timing of laying is influenced by those environmental changes that affect food supply.

The Pintail (*Anas acuta*) lives primarily on plant foods during much of the year (Martin et al. 1951); thus a study of feeding ecology during the nesting season provided an opportunity to evaluate the significance of an invertebrate food source to females during the period of egg formation. Marshall (1951) stated that essentially vegetarian species appear compelled to switch at least partially to a heavier protein diet when feeding their developing young. Production of a clutch of eggs, like tissue growth in the young, requires a special dietary need that presumably should be reflected in the diet of vegetarian species during the period that eggs are being formed. This paper describes the diet of the female Pintail prior to, during, and after laying and discusses the impact of certain environmental and physiological changes on Pintail breeding.

Methods

To study food habits, lone and paired females feeding in representative foraging habitats on the Drift Prairie and Missouri Coteau of east central North Dakota were collected by shooting from April through June of 1969–71.

Only birds that had been watched feeding for at least 10 minutes were taken. The digestive tract was removed immediately after collecting to minimize post-mortem digestion, and food items in the esophagus were flushed into bottles of 80% ethanol. Following removal of esophageal contents, hens were brought to the laboratory for dissection to determine reproductive condition. Each ovary was removed, weighed to the nearest 0.1 g, and examined for ruptured follicles. Ovarian

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condition served as the principal criterion for distinguishing reproductive status. A hen was considered to exhibit follicle development when the ovary showed enlargement but no laying had yet occurred. Only birds with ovaries weighing a minimum of 3 g were included in this category. Hens were considered in the laying stage when one or more ruptured follicles of an enlarged ovary indicated that laying had begun while at least one enlarged follicle remained to be ovulated or an egg remained in the oviduct. Hens placed in the postlaying category had laid at least one clutch and showed no development of the ovary preliminary to renesting. A series of regressing ruptured follicles and/or a well-developed brood patch identified this group. Ovulated follicles regress and their lips fuse quickly, making them indistinguishable from small atretic follicles. In these cases the brood patch was examined to determine breeding status.

Weights of the carcass and visceral fat were measured to the nearest g and 0.1 g, respectively, to provide information on condition of hens at certain stages of the reproductive cycle. Carcass weight in this study is defined as the weight of a feathered hen with internal organs removed. Use of the carcass reduced weight differences not attributable to changes in metabolic reserves, particularly variation attributable to ovary or oviduct size and the fullness of the digestive tract.

On the basis of previous studies, it was concluded that carcass weight would provide an accurate estimate of metabolic reserves. Connell et al. (1960) reported that fat-free weight is remarkably constant for a given species and sex. Odum et al. (1964), in discussing weight loss in migratory birds, stated that "components of the nonfat body remain essentially homeostatic despite very large and rapid changes in total body weight." Harris (1970) noted that, except for weight changes caused by involution of the ovary and oviduct, Blue-winged Teal (*Anas discors*) weight loss from laying of the 7th egg until day 5 of incubation can be considered depletion of metabolic reserves, the major loss probably being utilization of fat.

Esophageal food items were identified, segregated, and measured volumetrically while wet by displacement of water. All food habits data are expressed volumetrically unless stated otherwise, and confidence intervals are expressed at the 95% level.

Plant foods were identified to genus and frequently to species with the aid of the Martin and Barkley (1961) manual. All invertebrates were identified to order and some to family following Pennak (1953).

Foods of Breeding Hens

Follicle development period.—Esophageal contents of feeding hens in the follicle development stage that were collected from 16 April to 19 June averaged 56.0 ± 27.1% animal matter. Snails and dipteran larvae accounted for two-thirds of the invertebrates consumed (Table 1) and midge larvae (Chironomidae) formed 21% of the animal matter in the diet. Odonates ranked third among animal foods but, unlike snails and dipterans, they were an important item in the diet on only one occasion when a hen was feeding almost exclusively on damselfly naiads that were rising to the water surface.

Seeds of barnyard grass (*Echinochloa crusgalli*) and foxtail (*Setaria glauca*) formed 48% of the plant portion of the diet. Barnyard grass is

TABLE 1
ESOPHAGEAL CONTENTS OF BREEDING PINTAIL HENS IN NORTH DAKOTA

Food item		Percent occurrence			Percent volume		
Scientific name	Common name	Follicle development	Laying	Post-laying	Follicle development	Laying	Post-laying
PLANT		(14)[1]	(31)	(16)	(14)	(31)	(16)
Riccia sp.	Liverwort (vegetative)	7			tr[2]		
Potamogeton spp.	Pondweeds (nutlets)		3			tr	
Alisma spp.	Water plantains (seeds)	7	7		0.2	tr	
Sagittaria sp.	Arrowhead (seeds)			6			tr
Glyceria spp.	Mannagrasses (caryopses)	7	7	13	tr	0.3	3.0
Scolochloa festucea	Whitetop (caryopses)	7	7	6	1.1	1.7	0.1
Hordeum jubatum	Wild barley (caryopses)	7	3		tr	2.0	
Hordeum vulgare	Barley (caryopses)		7	13		0.3	6.3
Triticum aestivum	Wheat (caryopses)	7	13	63	1.1	5.6	36.6
Avena sativa	Oats (caryopses)		3	6		0.2	3.3
Beckmannia syzigachne	Sloughgrass (caryopses)	7	13	25	tr	0.1	4.2
Echinochloa crusgalli	Barnyard grass (caryopses)	21	29	31	13.6	8.1	16.2
Setaria glauca	Foxtail (caryopses)	21	3	30	7.7	tr	1.2
Setaria viridis	Green foxtail (caryopses)	14		tr	0.1		tr
Zea mays	Corn (caryopses)		3			3.0	
Eleocharis spp.	Spikerushes (achenes)	14	10	6	2.3	tr	0.1
Scirpus spp.	Bulrushes (achenes)	21	3	6	tr	0.4	tr
Carex spp.	Sedges (achenes)	14	10	6	tr	tr	tr
Lemna minor	Duckweed (vegetative)	7			5.0		
Polygonum spp.	Smartweeds (achenes)	21	16	30	5.1	tr	tr
Rumex spp.	Docks (achenes)	7	10	25	0.7	0.1	0.1
Chenopodium album	Lambsquarters (utricles)		3			tr	
Amaranthus sp.	Pigweed (seeds)		10	6		0.1	tr

TABLE 1—*Continued*

Food item		Percent occurrence			Percent volume		
Scientific name	Common name	Follicle development	Laying	Post-laying	Follicle development	Laying	Post-laying
Linum sp.	Flax (caryopses)	7	3	6	tr	0.1	tr
Ambrosia spp.	Ragweeds (achenes)		13	6		0.9	tr
TOTAL PLANT MATTER		64	65	74	44.0	22.9	71.1
ANIMAL							
Nematoda	Roundworms		3			tr	
Oligochaeta	Aquatic earthworms		3			0.5	
	Terrestrial earthworms		16	6		11.0	0.4
Hirundinea	Leeches	14		6	0.1		1.2
Anostraca	Fairy shrimp	14	29		2.7	13.9	
Conchostraca	Clam shrimp	7	3	19	0.3	tr	2.6
Cladocera	Water fleas	14	3		3.6	tr	
Amphipoda	Scuds	7	3		0.1	tr	
Hydracarina	Water mites	7			tr		
Odonata	Damselflies (naiads)	14		6	6.6		0.5
Hemiptera	Water boatman	29		6	0.5		tr
Trichoptera	Caddisflies (larvae)	7	19	6	1.8	0.7	1.3
Coleoptera	Water beetles (ad., larvae)	38	52	44	2.3	2.7	5.8
Diptera	Flies (larvae and pupae)	33	52	50	25.8	33.5	6.9
Gastropoda	Snails	29	65	38	12.2	14.8	10.2
TOTAL ANIMAL MATTER		79	97	69	56.0	77.1	28.9

[1] Sample size in parentheses.
[2] tr = trace; less than 0.1%.

a dominant annual in the cropland drawdown phase of the Class II fresh temporary ponds (Stewart and Kantrud 1971), and foxtail is an annual grass of cropland. Both foods were taken in wetland basins that had been under cultivation prior to flooding. Duckweed (*Lemna minor*) was the dominant food item in the diet of a single specimen. This was the only instance in which vegetative matter occurred in significant quantity in the diet.

Laying period.—Invertebrate content in the diet of hens was highest during the period when eggs were being laid. Dipterans, fairy shrimp, earthworms, and snails accounted for 95% of the 77.1 ± 11.6% animal portion of the diet of laying hens collected from 18 April through 22 June. Dipteran larvae and gastropods were major food items throughout the nesting season while fairy shrimp and earthworms occurred in the diet only during April and early May.

Midge larvae comprised two-thirds of the dipterans present in esophageal contents. Other dipteran families identified from esophageal samples were Culicidae, Syrphidae, Stratiomyidae, Ephydridae, Tipulidae, Tabanidae, and Ceratopogonidae. Dipterans were taken in a diverse array of habitats ranging from temporary pools remaining after spring rains (Culicidae) to receding semipermanent marshes (Stratiomyidae). Invertebrate composition of the diet varied widely from early to late spring as habitat conditions changed, but the proportion of animal matter in the diet of laying hens remained high throughout the breeding season. Late-nesting Pintails frequently gather to feed in wetlands where midge larvae are plentiful in organic detritus flooded during the current or previous spring. Esophageal contents of five hens collected in May from feeding groups of from 3–7 pairs averaged 96% midge larvae. Two of these hens were about to initiate laying and three were in the laying stage. Midge larvae formed 24% of the entire diet of 29 Pintail hens collected during May of 1969 and 1970. Consumption of midge larvae by Pintails during breeding is not restricted to North America. Dement'ev and Gladkov (1967) reported that midge larvae formed 30% of the total diet of Pintails during May and June at Rybinsk storage reservoir in the USSR.

Table 1 shows the limited importance of plant foods in the diet of hens during the laying stage. Seeds of barnyard grass and wheat formed 60% of the plant foods consumed during this period.

Postlaying period.—Invertebrate consumption among Pintail hens declined sharply from laying to postlaying. Animal foods accounted for only 28.9 $\pm$ 21.1% of the diet of postlaying hens collected from 19 May to 30 June. Snails, dipterans (principally midge larvae), and water beetle larvae were the principal animal foods in the diet. Snail content in the diet declined only slightly after the follicle development and laying periods while dipteran consumption fell markedly. *Lymnaea palustris* was the principal gastropod consumed throughout the breeding season. Preble (1908) previously reported Pintails feeding on this snail species in northern Canada. In North Dakota Pintail hens often consume empty snail shells during the breeding period.

Postlaying hens frequently fed on cropland and flooded, tilled wetlands. Cereal grain, principally wheat, regularly occurred in the diet of postlayers during late spring and early summer. Wheat was obtained generally from cropland while barnyard grass was the dominant food from bottom sediments of flooded tilled wetlands. Hens feeding on

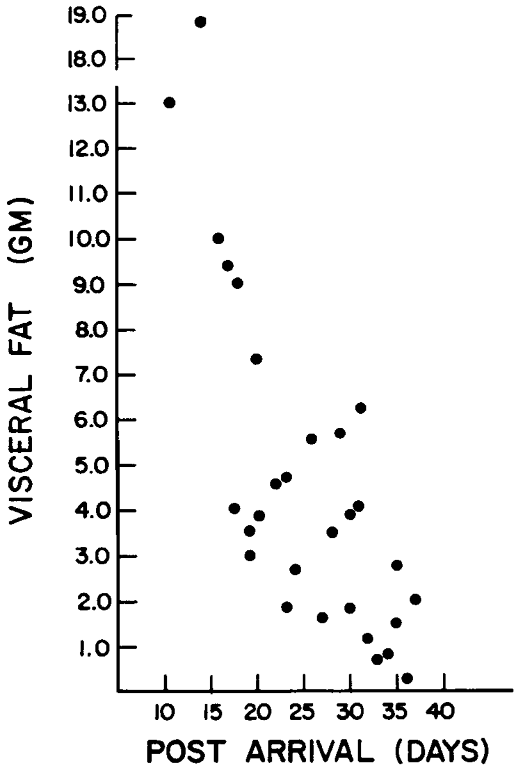

Figure 1. Visceral fat contained in Pintail hens collected during April and early May. Postarrival refers to the number of days after Pintails were initially sighted on the study area.

cropland were frequently alone, and the brood patch condition often suggested recent incubation. Wheat and barnyard grass comprised 74% of the plant portion of the diet, and seeds of at least one of these plants occurred in 69% of the esophageal samples.

Feeding Behavior

Pintails are prone to feed on or near the bottom of ponds. Their long necks and tipping feeding style permit exploitation of the benthos and seeds present at shallow depths. Temporary and seasonal wetland habitat lacks submergent aquatic plants, but the bottom often is covered with detritus formed from plants that grow at the site during drier periods. Although hens feed primarily on sluggish benthic organisms occurring in the detritus and bottom sediments, surface feeding occurs in late spring and summer when midge pupae move to the surface in large numbers.

TABLE 2

CARCASS WEIGHTS OF PINTAIL HENS AT CERTAIN STAGES IN THE BREEDING CYCLE

Period	Reproductive stage	Mean ± SD[1]	N
April	Prenesting[2]	722.7 ± 67.3	7
	Laying	660.4 ± 62.3	12
May 15–June 30	Follicle development[3]	541.9 ± 46.6	7
	Laying	541.0 ± 35.4	9
	Postlaying	540.0 ± 43.1	14

[1] Carcass weight in g.
[2] Hens that had not laid a clutch prior to collection (ovary weight < 3.0 g).
[3] Renesting birds with a well-developed brood patch.

Pintails are adept at separating small seeds from bottom sediments in aquatic habitats, but when field feeding, their alimentary tracts often contain a considerable quantity of soil with the seeds. Terrestrial invertebrates seldom occur in the diet of field-feeding hens. Although Pintails regularly consume small seeds in aquatic habitats, they seldom take small invertebrates. Copepods were not recorded and cladocerans occurred only in one instance when a hen was eating *Daphnia* in a roadside ditch. In this instance, cladocerans were sufficiently abundant to give the water a souplike appearance. Fairy shrimp did not become a major item in the diet until nearing full growth.

METABOLIC RESERVES

Pintail hens arrived on the study area each spring with large subcutaneous and visceral fat reserves, but these stores were depleted rapidly as the nesting season progressed. Mean carcass weight ± SD of hens declined from 675.5 ± 68.3 g in April to 569.9 ± 57.8 g in May, and 537.7 ± 46.9 g in June. This is a 24% average loss in carcass weight from April to June. Visceral fat was largely depleted by the end of the first week in May, about 40 days after the average arrival date of the birds on the breeding grounds (Figure 1).

Carcasses of prenesting hens taken in mid-April average 181 g or 25%, heavier than carcasses of hens initiating renesting attempts after mid-May. When collected after 15 May, hens in the follicle development, laying, and postlaying stages showed only minor variation in carcass weight (Table 2).

Loss of visible fat reserves and the stabilizing of carcass weight among hens in the three reproductive stages after mid-May suggest that most fat reserves had been utilized and that remaining weight differences were primarily from structural variation. Fat reserves may have been depleted principally during previous incubation. Harris (1970) noted that the free fatty acid (FFA) level in Blue-winged Teal declined during the late weeks of incubation and suggested this was due to utilization of fat reserves during incubation. Nearly all Pintail hens collected after mid-May had brood patches indicating current or prior incubation. The low carcass weights of these hens, in comparison to hens collected in April that had not incubated, suggest that a substantial part of the fat loss may have occurred during incubation. Carcass weight similarity between postlayers and those hens that had laid a previous clutch suggests that hens do not (and presumably cannot) accumulate major fat reserves in preparation for renesting attempts in late spring and early summer. Declines in body weight during the nesting period were reported by Weller (1957) for the female Redhead (*Aythya americana*) and by Folk et al. (1966) for female Mallards (*Anas platyrhynchos*).

Flooding and Food Supply

Pintail hens consume aquatic invertebrates principally in wetland habitat subject to frequent drying. Aquatic invertebrate populations in such temporary and seasonal wetlands develop either from adults coming to ponds to lay eggs after flooding or from dormant forms able to withstand prolonged dry periods. Fairy shrimp readily survive prolonged drying of wetlands in a resting egg stage (Pennak 1953), hatch after the wetland bottoms flood in early spring, and become a major food source in 2–3 weeks. During years when water is maintained in shallow wetland habitats most of the breeding season or more than one season, midge larvae become the principal food. Mosquito larvae (Culicidae) often are abundant in temporary wetlands filled by spring and early summer rains and, in some instances, are an important food source.

Earthworms were the first invertebrate available to Pintails after extensive flooding of dried wetlands in the early spring of 1970. Flooding from approximately 2 inches of precipitation during the week of 14–20 April replenished class I, II, and III wetlands on the Drift Prairie of eastern North Dakota. Saturation of the soil of dried wetlands made earthworms move to the surface in considerable numbers. Six laying hens collected during a 2-week period beginning 16 April were feeding largely on earthworms. Five of the hens were feeding on earthworms in the water, while one laying hen was probing the moist soil of a class I wetland for them. Fairy shrimp hatched with flooding of the shallow wetlands in mid-April and were first noted in the diet on 24 April in 1970. Of the 15 Pintail hens collected from 24 April to 5 May, 8 had fairy shrimp among their esophageal contents. None were seen in the diet after 5 May. Stranded earthworms formed an immediate but temporary food supply following drouth in 1970, whereas populations of aquatic organisms required time for growth.

Water conditions in the Drift Prairie region were generally poor throughout April 1971, and Pintail numbers decreased sharply from the two previous years. Scattered pairs that did remain to nest fed predominantly on fairy shrimp where shallow ponds existed and on midge larvae that had overwintered in receding semipermanent ponds. No earthworms were found in the diet in 1971.

DISCUSSION

The findings of this study lend support to the suggestion that availability of aquatic invertebrates is a major proximate factor influencing the onset of laying. Invertebrate supply, in turn, is controlled by existing water conditions. Smith (1963: 67) noted that the Pintail takes advantage of suitable breeding conditions when and where it finds them and females respond to breeding conditions quickly. The ability of Pintails to start breeding shortly after extensive flooding may be influenced by their ability to utilize earthworms and possibly other terrestrial invertebrates. A need for invertebrates during egg production probably is a major factor contributing to the response of this species to both flooding and drouth. Following flooding of a dried, shallow wetland basin, certain aquatic invertebrates hatch, grow, and become available to Pintail hens during the critical period of egg production. Direct relationships among water level fluctuation, food supply, and waterfowl breeding have been cited previously by Frith (1967) and Braithwaite and Frith (1969). After studying breeding cycles of nine species of waterfowl in an Australian wetland, Braithwaite and Frith (1969: 65) concluded that the most important effects of water level changes are on food supply of adult birds, which in turn determines time of breeding. Food supply included either plant or animal components, and no special significance was attributed to either. Their work also indicated that fixed annual factors were more influential in initiating the sexual cycle among those waterfowl species that occupied the deep water habitats of the wetland than among species associated with the less stable shallow habitats.

If the breeding response of Pintails to flooding of shallow wetlands is governed, in part, by the emergence of an invertebrate food supply, reduced breeding activity during drouth is understandable as the major foods of egg-producing hens are not available. Leitch (1964) reported that during the drouth of 1959 "loose flocks" of nonbreeding Pintails and Mallards were seen throughout spring and summer. Smith (1969) noted that large numbers of waterfowl (including Pintails) failed to breed on the Canadian prairies even where permanent water and excellent nesting cover were present. When extensive drouth occurs in the prairie pothole region, many Pintails apparently move to northern breeding grounds where they are less successful (Smith 1970).

Loss of subcutaneous and visceral fat reserves by mid-May suggests that renesting hens must obtain fat required for egg formation and energy for incubation from daily food intake. Hens apparently need an abundant high quality protein source during each nesting attempt. Maynard and Loosli (1962: 118) state "that protein [consumed] in excess of what the body can use tends to be wasted insofar as its specific functions as protein is [sic] concerned since it cannot be stored in any but very limited amounts but must be catabolized."

Smaller clutch size among renesting waterfowl has been documented by Sowls (1955: 132) for Pintails and reported widely among waterfowl by Dane (1966). Loss of fat reserves coupled with a continued need for fat to form yolk in clutches laid in late spring and early summer suggests that reduced clutch size may be in response to the loss of fat reserves during early nesting attempts. Presumably reduction of clutch size is more advantageous to the species than reduction of stored energy reserves in each egg because of greater survival of the young when provided the additional energy. Lack (1966b) speculated that large fat stores available to newly hatched ducklings may permit hens to nest at safer sites away from water. Large fat reserves would seem of particular value to Pintail young because nests are often at a considerable distance from wetlands suitable for rearing broods. That Pintail young are equipped for long movements to water without food was suggested by an experiment I conducted at the Northern Prairie Wildlife Research Center during the summer of 1970; 40 pintail ducklings given no food after hatching survived an average of 5 days.

Food supply and accumulated metabolic reserves undoubtedly have been major selective forces shaping the evolutionary development of the Pintail reproductive cycle. Lack (1966b, 1968) has hypothesized that average clutch size in waterfowl evolved in relation to average availability of food to the hen at the time of laying, modified by the relative size of the egg. If we assume that Pintails have evolved under a limited food supply, mechanisms to reduce competition presumably would have evolved. The pursuit flight is one possible mechanism for dispersing pairs (McKinney 1964) and thereby may reduce competition for food during early spring when the supply of invertebrates is low. It is noteworthy that Smith (1968) reported that the highest frequency of pursuit flights occurs during egg laying.

Successful crowding of breeding Pintail pairs into certain preferred ponds was noted during the present study. Limited food habits information gathered on paired hens that were feeding in close proximity to other pairs during the follicle-development and laying periods suggested that crowding occurred most frequently in wetland habitat where midge larvae were abundant and available in shallow water. Also similar crowding of pairs probably occurs when other aquatic invertebrates become abundant and readily available.

The high invertebrate/seed ratio in the diet during egg formation presumably is attributable, at least in part, to invertebrates being a superior source of high quality protein, calcium, and possibly other nutrients required for egg production (Krapu 1972). Pintail hens making initial nesting attempts have large fat reserves, but these do not appear to make the species independent of food supply during laying as Ryder (1970) suggested for the Ross' Goose (*Chen rossii*) in the arctic. Fat deposits reduce food intake necessary to meet energy needs and provide fat reserves for developing follicles, but perhaps just as importantly, these reserves enable hens to feed more on foods rich in nutrients that are not stored or synthesized by the body. Greater consumption of seeds following laying probably reflects changes in nutrient demands. While egg-producing hens are in need of a high protein diet, postlaying hens are primarily in need of high energy foods to maintain body functions. Scott et al. (1969: 40) note that cereal grains contain relatively high levels of the digestible carbohydrate, starch, and so are good sources of energy.

The Pintail is among the most widely distributed of waterfowl species in the Northern Hemisphere (Delacour 1956: 132). Various morphological, behavioral, and physiological adaptations enable the species to occupy shallow wetlands where an invertebrate food supply soon becomes available after flooding. Presumably, association with this habitat has been a major factor contributing to the Pintail's widespread dispersal.

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SUMMARY

Feeding ecology of breeding Pintail hens was studied during a 3-year period in east central North Dakota. Invertebrates formed 56% and 77% of the diet of hens collected during follicle development and laying, respectively, but only 29% during postlaying. Fairy shrimp, dipteran larvae, snails, and earthworms accounted for 95% of the animal portion of the diet of 31 laying hens. Wheat and barnyard grass were the

dominant food items in the diet of postlaying hens. Throughout the breeding season Pintails forage primarily in detritus and sediments of shallow wetlands but occasionally feed at the water surface. Foraging occurs primarily on wetland habitats that characteristically undergo drying during summer and fall. Availability of the invertebrate foods consumed by Pintail hens therefore varies widely from year to year depending on the extent of early spring flooding of shallow wetlands. Terrestrial earthworms forced out of the soil of dried-out shallow wetlands following flooding became a dominant food item in the early spring of 1970; aquatic invertebrates formed the bulk of the animal portion of the diet during the remainder of the study.

Breeding hens arrived with large subcutaneous and visceral fat reserves, which were mostly depleted during the early nesting attempts. Visceral fat was gone by mid-May. Renesting hens about to start laying after mid-May had carcass weights averaging 181 g (25%) less than prenesting hens collected in April. Loss of fat reserves increases the dependency of renesting hens on an available food source during the egg-laying period.

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